

Fear-Related Chemosignal

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Research Article

Fear-Related Chemosignal Modulates Recognition of Fear in Ambiguous Facial Expressions

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ABSTRACT—Integrating emotional cues from different senses is critical for adaptive behavior. Much of the evidence on cross-modal perception of emotions has come from studies of vision and audition. This research has shown that an emotion signaled by one sense modulates how the same emotion is perceived in another sense, especially when the input to the latter sense is ambiguous. We tested whether olfaction causes similar sensory modulation of emotion perception. In two experiments, the chemosignal of fearful sweat biased women toward interpreting ambiguous expressions as more fearful, but had no effect when the facial emotion was more discernible. Our findings provide direct behavioral evidence that social chemosignals can communicate emotions and demonstrate that fear-related chemosignals modulate humans' visual emotion perception in an emotion-specific way—an effect that has been hitherto unsuspected.

Whereas knowledge of chemosensory communication of emotion in humans is still limited, it is known that humans do communicate social information through chemical signals. The most well-known case is the olfactory modulation of the female reproductive cycle (Stern & McClintock, 1998). There has been some indirect evidence that social chemosignals communicate emotions. Chemosignals generated by people experiencing anxiety and fear have a significant, albeit subtle, effect on implicit perception and cognitive performance. For instance, one study showed that although a subliminally presented happy face increased the likelihood that people would see a subsequent neutral face as happy when no olfactory stimuli were present, this effect was weakened in women when they were exposed to the anxiety-related chemosignal (Pause, Ohrt, Prehn, & Ferstl, 2004). In another study, the anxiety-related chemosignal augmented the startle reflex (Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006), an indirect measure of emotion. A third study showed that the fear-related chemosignal increased cautiousness; it made women perform more accurately on a word-association task and react more slowly to ambiguous word pairs (Chen, Katdare, & Lucas, 2006).

It is commonly believed that the role of chemosensory communication is limited in species, such as humans, in which vision and hearing play dominant roles. Although the affective content of subliminal common household smells has been found to prime likeability for neutral faces (Li, Moallem, Paller, & Gottfried, 2007), the effect of social chemosensory input on vision—in particular, the extent to which emotional chemosignals modulate visual emotion perception—is largely an open question. Integrating information from different sensory modalities is critical for adaptive behavior, but existing work has mostly focused on cross-modal influence between facial and vocal cues (McGurk & MacDonald, 1976). In the case of emotion perception, studies have found that emotional cues from both the face and the voice are evaluated

and integrated. Given that the influence of one emotional modality has the greatest effect on the other when the latter is ambiguous (de Gelder & Vroomen, 2000; Massaro & Egan, 1996), it is natural to predict that if chemosensory modulation of visual emotion perception occurs, it will be strongest when the visual emotional cues are most ambiguous.

To test for chemosensory modulation of visual emotion perception, we conducted two experiments focused on the effect of a fear-related chemosignal (sweat collected from donors viewing horror videos) in an emotion-identification task. We used the same type of olfactory stimuli (emotional sweat collected on gauze pads and gauze pads with no sweat) throughout, but varied the effectiveness of the visual input by varying the ambiguity of the facial emotions (from somewhat happy to ambiguous to somewhat fearful). Our manipulation of ambiguity was achieved through morphing between happy and fearful faces. The gauze pads free of chemosensory social information provided a baseline for comparison.

METHOD

Participants

Informed consent was obtained from all subjects. We recruited only men as sweat donors because the apocrine glands in the underarm are larger in men than in women (Doty, 1981). We recruited only women as odor recipients because of women's superior sense of smell (Brand & Millot, 2001) and sensitivity to emotional signals (Brody & Hall, 2000).

Eight healthy male nonsmokers (mean age = 26.1 years, SEM = 0.83) from a larger study were chosen as sweat donors (see Selection and Preparation of Olfactory Stimuli). Six of these men served as sweat donors for the first experiment, and two served as sweat donors for the second experiment.

Twenty right-handed women (mean age = 19.7 years, SEM = 0.26) participated in a pilot test in which they performed the emotion-identification task in the absence of olfactory stimuli (see Selection of Visual Stimuli). None of them participated in the actual experiments.

In the first experiment, we tested 48 right-handed female nonsmokers (mean age = 19.6 years, SEM = 0.25) with a normal sense of smell (phenyl ethyl alcohol threshold: M = 10.78 binary dilution steps, SEM = 0.61; this mean corresponds to 0.0047% in propylene glycol) and regular menstrual cycles (M = 28.7 days, SEM = 0.24). Smell threshold was assessed using Sniffin' Sticks (Burghart Instruments, Wedel, Germany). Eighteen subjects were on hormone contraceptives. The remainder were tested, on average, 12.8 days (SEM = 1.37 days) from the 1st day of their menstrual period.

In the second experiment, we tested 16 right-handed female nonsmokers (mean age = 19.6 years, SEM = 0.32) with a normal sense of smell (phenyl ethyl alcohol threshold ≥ 7 binary dilution steps, which corresponds to 0.0625% in propylene glycol) and regular menstrual cycles (M = 30.6 days, SEM = 2.06). Two subjects were on hormone contraceptives. The remainder were tested, on average, 14.6 days (SEM = 2.34 days) from the 1st day of their menstrual period.

Materials

Selection and Preparation of Olfactory Stimuli

As noted, donors were selected from a larger study. The donors in that study were informed that the study was about physiological and psychological responses to sensory stimuli. They refrained from using deodorant, antiperspirant, and scented products, and used scent-free shampoo, conditioner, soap, and lotion (provided by the experimenter), from 2 days prior to the sweat-collection experiment until after the experiment was over. They washed their sheets with

scent-free detergent provided by the experimenter, kept a diet diary, and avoided odorous food such as garlic, onion, asparagus, and spices.

Each donor went through sweat-collection sessions held at the same time of day on 3 consecutive days (one session per day). On the day of each session, they wore next to their skin a new T-shirt (provided by the experimenter), to prevent odor contamination by their regular clothes. During each session, they kept a 4- × 4-in. pad (rayon-polyester blend for maximum absorbance) under each armpit while they watched each of three 20-min video segments intended to produce the emotions of fear (horror movies), happiness (slapstick comedies), and neutrality, respectively. Different videos were shown in each session. During the videos, participants' heart rate was recorded using disposable snap electrodes attached to the right collarbone and the left and right (ground) rib cage (BIOPAC Systems, Inc., Goleta, CA). The order in which the videos were presented was counterbalanced. Each video was preceded by a 5-min segment of the same emotional content, which served as an emotional transition. New pads were used for each video.

After watching each video, the donors rated how angry, fearful, happy, neutral, and sad they felt during the video, using a 100-mm visual analog scale. From each donor, we selected the pads worn during the 20-min videos that elicited the highest level of self-reported happy feelings and the highest level of self-reported fearful feelings. Compared with heart rate during the corresponding (i.e., viewed on the same day) neutral video, heart rate increased during the horror movies, $t(19) = 2.26$, $p = .036$, Cohen's $d = 0.61$, but not during the slapstick comedies, $t(18) = 0.69$, $p = .50$, Cohen's $d = 0.21$ (one donor's heart rate data during the selected happy video segment were excluded because of electrode detachment). From the group of donors, we identified eight whose self-reported happiness and fear were the highest and used their sweat

pads in the experiments reported here (Fig. S1 of the supplementary materials available on-line shows the donors' mean mood ratings for the videos during which they wore these pads—see p. XXX).

The selected sweat pads were each cut into eight pieces (1 in. × 2 in.), separated by video type, and stored at −80 °C. The control gauze pad (with no sweat) was cut and stored in the same fashion. The pads were defrosted to room temperature 30 min prior to the emotion-identification task. During the computer-administered emotion-identification task, a pad was taped underneath the subject's nostrils without directly touching the skin (i.e., it rested on a plastic wrap).

Selection of Visual Stimuli

To create ambiguity in facial emotions, we morphed prototypical examples of happy and fearful faces from nine actors (five females and four males; Ekman & Friesen, 1976). Using 2.5% increments, we generated a continuum of 40 images (morphs) between each actor's happy photo and fearful photo (Morpher 3.1, shareware by M. Fujimiya, <http://www.asahi-net.or.jp/~FX6M-FJMY/mop00e.html>). The resulting 360 morphs represented gradual transitions from the prototypical happy expressions (0% fear) to the prototypical fearful expressions (100% fear). All morphs were included in our pilot testing, which employed the same task and procedure as the actual experiments, but without any olfactory stimuli. Subjects judged whether each morph was happy or fearful.

To locate the ambiguous morphs to be used in the experiments, we plotted the proportion of "fearful" responses for each morph in the pilot test, separately for each actor, and then performed a sigmoidal-curve fit using the function $y = a_0 + a_1 / (1 + \exp(-(x - a_2) / a_3))$ (Moradi, Koch, & Shimojo, 2005). In this function, a_0 , a_1 , a_2 , and a_3 are coefficients for the y -offset, height, center, and width of the curve, respectively; x is the morphing step, and y is the

proportion of fear responses. (For examples of the data and sigmoidal fits, see Fig. S2 in the supplementary material available on-line). From the fitted curve for each actor, we were able to identify a morph that was judged as fearful around 50% (45%–55%) of the time. This morph and the morphs that were one, two, and three steps before and after it (a total of seven intermediate images per actor) were used in the first experiment, assigned to Morphing Levels 1 (somewhat happy), 2, 3, 4 (ambiguous), 5, 6, and 7 (somewhat fearful), respectively (see Fig. 1a). For the second experiment, we selected the morphs at Levels 2 through 6 from the two actors whose images produced the greatest chemosensory modulation in the first experiment. We included Levels 2 through 6 (not just the most ambiguous level, Level 4) in order to familiarize the subjects with a range of fearful and happy expressions.

Experimental Procedure

In our emotion-identification task, female subjects viewed a series of the morphed faces and were asked to indicate whether each face was happy or fearful, responding as accurately and as quickly as possible. The visual angle of the faces was $17^\circ \times 24^\circ$; subjects' head position was fixed using a chin rest. The faces were presented on a computer monitor in a randomized sequence; each face was presented for 250 ms, preceded by a 1,000-ms fixation cross and followed by a gray background (see Fig. 1b). A response received within 2,250 ms of the onset of a face started the next trial. The next trial began 2,250 ms after the onset of the previous face if no response was made within this time. Half the subjects used their left index finger to press the "z" key of the computer keyboard to indicate a happy face and used their right index finger to press the "/" key to indicate a fearful face. For the other half of the subjects, the assignment of responses to the keys was reversed. In each condition, subjects were exposed to a different type of olfactory stimulus applied underneath their nostrils; the conditions were separated by at least 5

min. The order of the olfactory applications was counterbalanced across subjects. Care was taken so that the olfactory stimuli did not come into direct contact with the subjects' skin. Both the subjects and the experimenters were blind to the nature of the olfactory stimuli.

In the first experiment, two types of chemosignals (sweat obtained from male donors while they watched horror movies and sweat obtained from the same donors while they watched comedies, each carried on a gauze pad) and one nonsocial control stimulus (a gauze pad with no sweat) were tested. Each condition consisted of 63 trials (seven morphs from each of nine actors, shown once each). Subjects completed the State Anxiety Inventory (Spielberger, Gorsuch, & Lushene, 1970) at the end of each condition, before the olfactory stimulus was removed. They smelled the three olfactory stimuli again at the end of the experiment, and described what each smelled like in an open-ended manner. Thirty-six of the subjects also rated the olfactory stimuli by their intensity and pleasantness on a 7-point Likert scale.

Based on the results of the first experiment, the second experiment focused on comparing women's perceptions of fear in the most ambiguous faces during exposure to fearful sweat versus the control pad. Each condition consisted of 50 trials. (Each morphed image was presented independently five times.) The procedure was otherwise the same as in the first experiment except that the anxiety questionnaire was not used, given that olfactory condition did not have a significant effect on subjects' anxiety scores in the first experiment, $F(2, 94) = 0.46$, $p = .63$.

Analyses

Trials on which the subject did not respond or on which the response time (RT) was less than 200 ms after the onset of the face were excluded from further analysis. When analyzing the

RT data, we also excluded trials on which the subject responded more than 1 s after the disappearance of the face ($RT > 1,250$ ms). Fewer than 5% of the trials were excluded.

The key dependent variable was the proportion of faces identified as fearful. Given our hypothesis that the strongest chemosensory modulation of visual emotion perception occurs when the visual emotional cues are most ambiguous, we first examined the effect of chemosensory input on categorization of the most ambiguous faces. In the first experiment, we tested the effect of chemosignal by using repeated measures analysis variance (ANOVA), with olfactory condition (fearful sweat vs. happy sweat vs. control pad) as the within-subjects factor, and in the second experiment, we used a paired-sample t test (fearful sweat vs. control pad). The same tests were then performed for the less ambiguous levels of morphing.

We conducted similar tests to assess whether RT (at each level of morphing), rated intensity, rated pleasantness, and (in the first experiment) state anxiety (as measured with the State Anxiety Inventory; Spielberger et al., 1970) differed across olfactory conditions.

In the first experiment, to confirm the effect of visual input on the proportion of faces categorized as fearful, we conducted a repeated measures ANOVA with morphing level (1–7) and olfactory condition (fearful sweat vs. happy sweat vs. control pad) as within-subjects factors.

RESULTS AND DISCUSSION

Figure 2a plots the proportion of fear identifications for faces at each level of morphing in each of the three olfactory conditions of the first experiment. Visual input clearly had a strong impact on subjects' judgments, $F(4.24, 199.05) = 158.70$, $p < .001$: Morphs that were closer to the original fearful pictures were more likely to be judged as fearful. In the control condition, the proportion of fear identifications grew monotonically with the level of morphing. Nevertheless, olfactory input affected identifications when the visual cues became most ambiguous; olfactory

condition had a significant effect at Level 4, $F(2, 94) = 3.17$, $p = .047$, $\eta_p^2 = .063$, but not at the other levels ($ps > .50$). Post hoc analysis showed that at Level 4 (see Fig. 2b), subjects were more likely to judge a face to be fearful when they were exposed to the fearful sweat, as compared with the control pad (Tukey's $p = .046$, Cohen's $d = 0.37$). No difference was found between the happy-sweat and the control conditions (Tukey's $p = .82$, Cohen's $d = 0.09$), perhaps because social chemosensory modulation of visual cues is controlled mainly by negative affect. Such a negativity bias—greater weight given to negative than to nonnegative events—is widely observed in the domains of emotion and cognition (Cacioppo & Gardner, 1999). It may be argued that happy sweat, which is generated in response to stimuli with socially acquired value, does not carry as much evolutionary salience as fearful sweat, which is generated in response to stimuli that threaten survival.

To further explore the observed effect, we conducted the second experiment, removing the least ambiguous faces (Levels 1 and 7) from the materials and focusing on perceptions of fear during exposure to fearful sweat from two new donors versus the control pad. Subjects were more likely to judge a face at the most ambiguous level (4) to be fearful when they were exposed to the chemosignal of fearful sweat, as compared with the control pad, $t(15) = 3.27$, $p = .005$, Cohen's $d = 0.74$ (see Fig. 3). For each of the other levels, the difference between conditions was not significant ($ps > .18$). Both the significant finding for Level 4 and the null findings for the other morphing levels are compatible with the results of the first experiment.

The effect of chemosignal of fearful sweat could not have originated from the speed of processing. Olfactory input did not significantly affect how quickly the subjects responded to the faces at any morphing level ($ps > .46$ in the first experiment, $ps > .51$ in the second experiment). In addition, the effect cannot have been due to the intensity or pleasantness of the odor stimuli.

In the first experiment, subjects' intensity and pleasantness ratings did not differ significantly across the three kinds of olfactory stimuli, $F(2, 70) = 1.84$, $p = .17$, $\eta_p^2 = .050$, and $F(2, 70) = 1.15$, $p = .32$, $\eta_p^2 = .032$, respectively (see Fig. S3a in the supplementary material available on-line). In the second experiment, subjects perceived the fearful sweat to be as intense as the control pad, $t(15) = -0.48$, $p = .64$, Cohen's $d = 0.18$, but less pleasant, $t(15) = -2.91$, $p = .011$, Cohen's $d = 0.81$ (see Fig. S3b in the supplementary material). To assess whether pleasantness differences contributed to the increased proportion of faces identified as fearful at the most ambiguous morphing level in the fearful-sweat condition, we built a linear mixed model using proportion of faces identified as fearful at the most ambiguous level as the dependent variable, olfactory condition (fearful sweat vs. control) as the factor, and pleasantness rating as the covariate. The difference in pleasantness did not affect perception of emotion in the ambiguous faces, $F(1, 25.71) = 0.43$, $p = .52$.

In addition, the subjects did not distinguish the olfactory stimuli on the basis of odor quality. We classified the verbal descriptions of the olfactory stimuli into nine categories (see Table S1 in the supplementary material available on-line) on the basis of their semantic similarity. We then performed chi-square tests to determine if the three kinds of olfactory stimuli in the first experiment and the two kinds of olfactory stimuli in the second experiment differed in how often their descriptions fell into any of the nine categories. They did not: $\chi^2(2, N = 48) < 8.4$, Bonferroni corrected $ps > .13$ in the first experiment; $\chi^2(1, N = 16) < 1$, Bonferroni corrected $ps > .9$ in the second experiment. Finally, the effect cannot have been due to fear- and anxiety-related arousal, as the conditions did not differ in subjects' self-reported anxiety in the first experiment, $F(2, 94) = 0.46$, $p = .63$, $\eta_p^2 = .01$.

Instead, we propose that the effect we observed has its origin in evolution. Through learning, certain chemosensory input became associated with fearful visual information and acquired emotional value, and the ability to form such associations may have increased fitness. Encountering fear-related chemosignals in the presence of an ambiguous face triggers previously stored association, and leads to greater perception of fear in the ambiguous face (i.e., people err on the side of caution, much as they may freeze upon seeing a twig that looks like a snake; LeDoux, 1996). This likely occurs on a subconscious level, as subjects reported the same level of fear-related anxiety across the different olfactory conditions, and their verbal reports indicated they were unaware of the nature of the conditions.

Chemosignaling of fear in the form of alarm pheromones is well documented in many animals. It serves warning purposes, produces heightened vigilance or escape behavior, and alters autonomic (stress-induced hyperthermia), and immune (analgesia) responses in the conspecific recipients (Wyatt, 2004; Zalaquett & Thiessen, 1991). Although the vomeronasal organ is usually implicated in the detections of alarm pheromones (Kiyokawa, Kikusui, Takeuchi, & Mori, 2007), the olfactory epithelium (input site of the main olfactory system; Kobayakawa et al., 2007; Liberles & Buck, 2006; Rottman & Snowdon, 1972) has also been shown to respond to these social cues. Moving down the main olfactory pathway, the amygdala, a primary olfactory region that receives direct chemosensory input from the olfactory bulb, has been widely implicated in fear recognition and in learning of associations between fearful stimuli in different sensory modalities (Dolan, Morris, & de Gelder, 2001; Otto, Cousens, & Herzog, 2000; Rosenkranz & Grace, 2002). It receives parallel subcortical and cortical visual input and processes fearful visual information (Morris, Öhman, & Dolan, 1999). It also processes fear-related chemosignals in rats (Kiyokawa, Kikusui, Takeuchi, & Mori, 2005), sending the input

from the olfactory bulb to the bed nucleus of the stria terminalis, from which it is forwarded to the hypothalamus and the brain stem. This main olfactory pathway for fear-related chemosignals likely applies to humans, who lack typical receptor cells in the vomeronasal organ (Bhatnagar & Smith, 2001). It is thus plausible that the amygdala is the site where the integration of fearful visual and chemosensory information takes place. We propose that when a facial expression is ambiguous, fear-related chemosignal can augment the recognition of fearful signals in the face, and push it above a threshold level.

Our results directly support the view that human emotional chemosignals act on behavior and cognition in a manner that is consistent with their inherent emotional content, as implicated in several previous studies (Ackerl, Atzmueller, & Grammer, 2002; Chen & Haviland-Jones, 2000; Chen et al., 2006; Pause et al., 2004; Prehn et al., 2006). Our study focused on one negative emotion, fear, and future studies are needed to examine additional negative emotions (e.g., by using happy-angry and angry-fearful morphs). Such studies will be important to fully establish the extent to which the chemosensory modulation of emotion recognition extends beyond fear.

Finally, we note that our findings on emotional chemosensory modulation of visual emotion perception add the olfactory dimension to the cross-modal integration of emotional cues, which has previously been discussed in the context of visual and auditory stimuli (de Gelder & Vroomen, 2000; Massaro & Egan, 1996). The latter literature has established that the perception of an ambiguous stimulus in one sense is modified by the perception of a less ambiguous stimulus in the other sense. Interestingly, in our study, the less ambiguous sense was emotional olfaction, given the context of the ambiguous morphed faces, yet emotional olfaction is itself still ambiguous. Its nature is not accessible through verbal descriptions, and its effects

occur at the subliminal level. These features are also characteristics of the nonsocial pleasant and unpleasant smells that were used to study the effect of olfaction on judged likeability of neutral faces (Li et al., 2007). However, we have shown that the intensity and pleasantness of the emotional olfactory stimuli we used did not contribute to their effect on perception of fear in ambiguous faces.

CONCLUSIONS

In two experiments, we examined the modulation of the perception of facial emotions by emotional chemosignals. We demonstrated that the chemosignal of fearful sweat, compared with a control pad, biased women toward interpreting ambiguous expressions as more fearful, but had no effect when the facial emotions were more discernible. Our findings provide direct behavioral evidence that social chemosignals can communicate emotions (as do visual and auditory signals), and demonstrate that fear social chemosignals modulate visual emotion perception in an emotion-specific way.

Acknowledgments—We thank Dana Brown, Jennifer Edward, Beth Leimbach, Marissa Rivera, Dominique Shelton, and Kathy Zhang for their assistance. This work was supported in part by National Institutes of Health Grant R03DC4956.

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Fig. 1. Visual stimuli and procedure in the emotion-identification task of the first experiment. The illustrations in (a) are examples of the morphed faces of two actors. For each actor, we selected seven morphs, ranging from somewhat happy to somewhat fearful. These faces were

judged to be fearful 20% to 80% of the time in our pilot experiment, in the absence of any olfactory stimuli. Specifically, the Level 4 morph for each actor was the most ambiguous, judged to be fearful in the pilot study 45% to 55% of the time. During the task (b), subjects first saw a fixation cross for 1 s. Then a picture was presented for 250 ms, followed by the gray background. The next trial began immediately after the subject made a response, or after 2 s if no response was made. Subjects' task was to indicate whether each face was happy or fearful.

Fig. 2. Results from the first experiment: (a) proportion of faces identified as fearful as a function of morphing level and olfactory condition and (b) the difference between the observed and predicted proportion of Level 4 morphs identified as fearful in each olfactory condition. The dotted line in (a) is the sigmoidal curve fit for the control condition. The differences plotted in (b) were calculated from the observed values highlighted by the dotted ellipse and the predicted value shown by the fitted curve. Error bars represent the standard errors of the means. The asterisk indicates a significant difference between conditions, $p < .05$.

Fig. 3. Results from the second experiment: (a) proportion of faces identified as fearful as a function of morphing level and olfactory condition and (b) the difference between the observed and predicted proportion of Level 4 morphs identified as fearful in each olfactory condition. The dotted line in (a) is the sigmoidal curve fit for the control condition. The differences plotted in (b) were calculated from the observed values highlighted by the dotted ellipse and the predicted value shown by the fitted curve. Error bars represent the standard errors of the means. The asterisk indicates a significant difference between conditions, $p < .05$.