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Olfactory-visual integration facilitates perception of subthreshold negative emotion

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ABSTRACT

A fast growing literature of multisensory emotion integration notwithstanding, the chemical senses, intimately associated with emotion, have been largely overlooked. Moreover, an ecologically highly relevant principle of "inverse effectiveness", rendering maximal integration efficacy with impoverished sensory input, remains to be assessed in emotion integration. Presenting minute, subthreshold negative (vs. neutral) cues in faces and odors, we demonstrated olfactory-visual emotion integration in improved emotion detection (especially among individuals with weaker perception of unimodal negative cues) and response enhancement in the amygdala. Moreover, while perceptual gain for visual negative emotion involved the posterior superior temporal sulcus/pSTS, perceptual gain for olfactory negative emotion engaged both the associative olfactory (orbitofrontal) cortex and amygdala. Dynamic causal modeling (DCM) analysis of fMRI timeseries further revealed connectivity strengthening among these areas during crossmodal emotion integration. That multisensory (but not low-level unisensory) areas exhibited both enhanced response and region-to-region coupling favors a top-down (vs. bottom-up) account for olfactory-visual emotion integration. Current findings thus confirm the involvement of multisensory convergence areas, while highlighting unique characteristics of olfaction-related integration. Furthermore, successful crossmodal binding of subthreshold aversive cues not only supports the principle of "inverse effectiveness" in emotion integration but also accentuates the automatic, unconscious quality of crossmodal emotion synthesis.

Organisms as primitive as a progenitor cell integrate information from multiple senses to optimize perception (Calvert et al., 2004; Driver and Noesselt, 2008; based on human and nonhuman primate data). This synergy is especially prominent with minimal sensory input, facilitating signal processing in impoverished or ambiguous situations (known as the principle of "inverse effectiveness"; Stein and Meredith, 1993). Fusing minute, discrete traces of biological/emotional significance (e.g., a fleeting malodor, a faint discoloration) into a discernible percept of a harmful object (e.g., contaminated food), multisensory emotion integration would afford particular survival advantage by promoting defense behavior. Research in multisensory emotion integration has grown rapidly (cf. Maurage and Campanella, 2013), but the prevalent application of explicit (vs. subtle, implicit) emotion cues has limited the assessment of this ecologically highly relevant principle in integrating emotion across modalities.

Furthermore, the "physical senses" (vision, audition and somatosensation) have dominated this research, with the "chemical senses" (olfaction and gustation) largely overlooked (Maurage and Campanella, 2013). Nevertheless, among all senses, olfaction holds a unique intimacy with the emotion system, and olfactory processing closely interacts with emotion processing (Yeshurun and Sobel, 2010; Krusemark et al., 2013). This intimate association stands on a strong anatomical basis: the olfactory system is intertwined via dense reciprocal fibers with primary emotion areas, including the amygdala and orbitofrontal cortex (OFC; Carmichael et al., 1994; based on the macaque monkey), and these emotion-proficient regions reliably participate in basic olfactory processing to the extent that the OFC (the posterior OFC in rodents and the middle OFC in humans) is considered as a key associative olfactory cortex (Zelano and Sobel, 2005; Gottfried, 2010; based on human and rodent data). Importantly, olfaction interacts with emotion processing across sensory modalities. Olfactory cues can modulate visual perception of facial emotion and social likability, even at minute/subthreshold concentrations (Leppanen and Hietanen 2003; Li et al., 2007; Zhou and Chen, 2009; Forscher and Li, 2012; Seubert et al., 2014). Preliminary neural evidence further indicates that emotionally charged odors modulate visual cortical response to ensuing emotional faces (Seubert et al., 2010; Forscher and Li, 2012). However, mechanisms underlying olfactory-visual emotion

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integration remain elusive. It is especially unclear how visual cues influence olfactory emotion processing, although the effect of visual cues (e.g., color, image) on standard olfactory perception is well known (Sakai et al., 2005; Demattè et al., 2006; Mizutani et al., 2010), with the OFC potentially mediating this crossmodal modulation (Gottfried and Dolan, 2003; Osterbauer et al., 2005).

Prior research has provided compelling evidnece of key multisensory convergence zones linking the physical sensory systems (e.g., the posterior superior temporal sulcus/pSTS and superior colliculus) being primary sites of multisensory integration of both emotion and object information (cf. Calvert et al., 2004; Driver and Noesselt, 2008). However, those studies concerned only the physical senses, and absent such direct, dense connections between the olfactory and visual systems, olfactory-visual integration is likely to engage additional brain circuits. Of particular relevance here, the amygdala has been repeatedly implicated in multisensory emotion integration (Maurage and Campanella, 2013) and, as mentioned above, the OFC in olfactory-visual synthesis in standard odor quality encoding (Gottfried and Dolan, 2003; Osterbauer et al., 2005). Indeed, as these areas are not only multimodal and emotion-proficient but also integral to olfactory processing (Amaral et al., 1992; Carmichael et al., 1994; Rolls 2004; based on human and nonhuman primate data), they could be instrumental in integrating emotion information between olfaction and vision. Therefore, examining possible common and distinct mechanisms underlying crossmodal facilitation in visual and olfactory processing would provide unique insights into the literature.

Here, using paired presentation of (negative or neutral) faces and odors in an emotion detection task, we assessed general and visual- or olfactory-relevant facilitation via olfactory-visual (OV) emotion integration (Fig. 1). Importantly, to interrogate the principle of inverse effectiveness (i.e., multisensory integration is especially effective when individual sensory input is minimal) in emotion integration, we applied the negative emotion at a minute, imperceptible level and examined whether improved emotion perception via OV integration negatively correlated with the strength of unimodal emotion perception (Kayser et al., 2008; based on the macaque monkey). Lastly, we employed functional magnetic resonance imaging (fMRI) analysis with effective connectivity analysis (using dynamic causal modeling/DCM, Friston et al., 2003) to specify key regions subserving OV emotion integration and the neural network in which they operate in concert.

1. Materials and methods

1.1. Participants

Sixteen individuals (8 females; age 19.6 ± 3.0 years, range 18–30) participated in the study in exchange for course credit and/or monetary compensation. Participants were screened prior to the experiment to exclude any history of severe head injury, psychological/neurological disorders or current use of psychotropic medication, and to ensure normal olfaction and normal or corrected-to-normal vision. Individuals with acute nasal infections or allergies affecting olfaction were excluded. All participants provided informed consent to participate in the study, which was approved by the University of Wisconsin–Madison Institutional Review Board.

1.2. Stimuli

1.2.1. Face stimuli

Fearful and neutral face images of 4 individuals were selected from the Karolinska Directed Emotional Faces set, a collection of color face stimuli with consistent background, brightness, and saturation (Lundqvist et al., 1998). This resulted in a total of eight face images (four neutral and four fearful). To create minute (potentially subthreshold) negative face stimuli, fearful and neutral faces from the same actor were morphed together using Fantamorph (Abrosoft, Beijing, China), resulting in graded fearful expressions. Based on previous research in our lab (Forscher and Li, 2012), we set the subthreshold fear expression level at 10–15% of the neutral-to-fear gradient (i.e., containing 10–15% of the full fear expression; varying based on the expressiveness of the individual actors), and set neutral face stimuli at a 2% morph to generally match the fearful face images in morphing-induced image alterations (Fig. 1). Our previous data indicate that these very weak negative cues can elicit subliminal emotion processing (Forscher and Li, 2012).

1.2.2. Odor stimuli

Four prototypical aversive odorants (trimethyl amine/TMA —"rotten fish"; valeric acid/VA—"sweat/rotten cheese"; hexanoic acid/HA—"rotten meat/fat"; and butyric acid/BA—"rotten egg") were chosen as olfactory negative stimuli. Neutral odor stimuli included four neutral odorants (acetophenone/AC, 5%; guaiacol/GU, 5%; rose oxide/RO, 5%; and eugenol/EG, 5%; all diluted in mineral oil). To render the negative odor hardly detectable, we applied an olfactory "morphing" procedure by mixing very weak concentrations of these odors into the neutral odor solution, resulting in four negative odor mixtures as the olfactory negative stimuli: AC 5%/TMA .000125%; GU 5%/VA .0025%; RO 5%/HA .0002%; EG 5%/BA .0002% (Fig. 1A; Krusemark and Li, 2012). As components in a mixture can suppress the perceived intensity of other components, and a strong component can even mask the perceived presence of a weak component (Cain, 1975; Laing and Willcox 1983), these odor mixtures allowed us to present the threat odors below conscious awareness at practically meaningful concentrations. As shown in our prior study, these minute

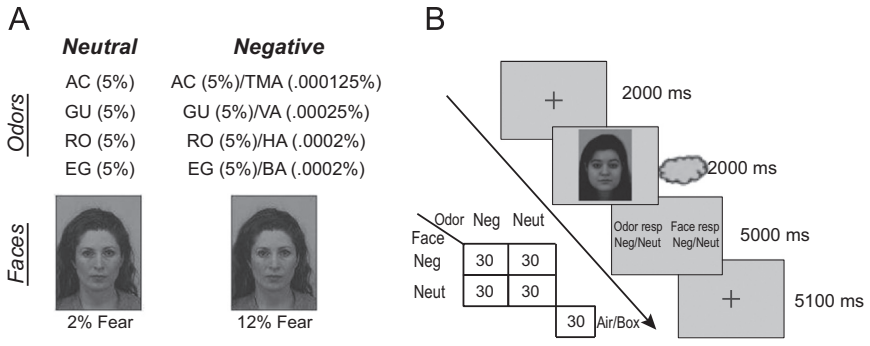

Fig. 1. Stimuli and experimental paradigm. A) Odors and face examples used in the experiment. AC = Acetophenone; TMA = Trimethyl amine; GU = Guaiacol; VA = Valeric acid; RO = Rose oxide; HA = Hexanoic acid; EG = Eugenol; BA = Butyric acid. B) Subjects responded to a face and an odor on each trial as to whether they contained negative emotion. Four odor–face combinations (each consisting of 30 trials; congruent negative stimuli, incongruent combinations with negative cues in either faces or odors, and congruent neutral) were included, forming a 2-by-2 factorial design.