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The fish is bad: Negative food odors elicit faster and more accurate reactions than other odors

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ABSTRACT

Dissociating between ‘good’ or ‘bad’ odors is arguable of crucial value for human survival, since unpleasant odors often signal danger. Therefore, negative odors demand a faster response in order to quickly avoid or move away from negative situations. We know from other sensory systems that this effect is most evident for stimuli from ecologically-relevant categories. In the olfactory system the classification of odors into the food or non-food category is of eminent importance. We therefore aimed to explore the link between odor processing speed and accuracy and odor edibility and valence by assessing response time and detection accuracy. We observed that reaction time and detection accuracy are influenced by both pleasantness and edibility. Specifically, we showed that an unpleasant food odor is detected faster and more accurately than odors of other categories. These results suggest that the olfactory system reacts faster and more accurately to ecologically-relevant stimuli that signal a potential danger.

1. Introduction

Discrimination between ‘good’ and ‘bad’ odors is arguably of crucial value for human survival. As is well known, unpleasant odors often signal danger, such as spoiled food or a toxin, and, in some non-human species, they even serve as a warning signal of nearby predators (Dielenberg and McGregor, 2001). Negative odors demand a faster response than neutral or pleasant odors because survival depends more often on an organism’s quick response to signals of negative rather than positive situations. Two behavioral studies support this basic assumption by demonstrating that response times of human subjects to unpleasant odors were significantly shorter than for pleasant odors (Bensafi et al., 2002c; Jacob and Wang, 2006).

The same principle has been demonstrated in the visual system. Hansen and Hansen showed that an angry face in a crowd of benign or happy faces was detected faster than a happy or benign face in a crowd of angry faces, suggesting that humans are more attentive to threatening signals (Hansen and Hansen, 1988). These findings were later confirmed and extended (Ohman et al., 2001b). The coupling of emotional activation and efficient capture of attention goes beyond faces, as demonstrated by findings that fear-relevant pictures of snakes and spiders were detected faster than fear-irrelevant pictures, such as flowers and mushrooms (Ohman et al., 2001a). These and similar data have been taken as evidence that natural selection has honed the human ability to identify and react to stimuli important for survival (Mineka and Ohman, 2002; Tooby and Cosmides, 1990). Threatening stimuli, such as indicators of spoiled food or the presence of a snake, are prioritized by the cerebral system to effect faster preparation for “fight or flight” action. In the rodent brain, there appears to be a specific neural circuitry – direct linkage of the perceptual and defense systems via the thalamus and amygdala – to achieve this fast mobilization (for a review, please see LeDoux, 2000). There is evidence of a similar system in the human brain (Ohman et al., 2007), also for olfactory stimuli, since the amygdala is located only one synapse away from the olfactory receptors. Moreover, although it is widely assumed that the human olfactory system, unlike the other senses, is independent of thalamic relay, it was recently demonstrated that the thalamus indeed has a functional role in odor processing (Plailly et al., 2008). The transthalamic network is suggested to be a modulatory target of olfactory attentional processing and may serve as an attentional filter, helping to select only those inputs with behavioral relevance for processing downstream of the orbitofrontal cortex (Plailly et al., 2008). Further evidence from research on human subjects demonstrates that biologically relevant stimuli enjoy faster (Lundstrom et al., 2006a) or more direct neuronal pathways (Lundstrom et al., 2008; Morris et al., 1999), resulting in both decreased processing times and lower reaction thresholds than perceptually similar stimuli with no obvious evolutionary importance.

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Whether the human brain performs categorical olfactory processing akin to that which has been demonstrated in the visual system is not known. Collectively, food odors seem to comprise a category of particular importance to humans: our ability to identify food odors is superior to our performance with odors of non-food objects (Boesveldt et al., 2009; Fusari and Ballesteros, 2008). Further evidence that the human olfactory system is capable of categorical discrimination comes from the previously-mentioned studies showing that reactions to negative odors are faster than to positive odors (Bensafi et al., 2002c; Jacob and Wang, 2006). Unfortunately, in both of those studies, the pleasant stimulus was a food-related odor (vanillin or amyl acetate) and the unpleasant stimulus was a non-food-related odor (indole or valeric acid), thereby making a direct comparison between odor categories – either pleasant versus unpleasant or food versus non-food – impossible.

The present study sought to explore the link between odor processing speed, edibility and valence. To this end, we measured subjects' reaction time and detection accuracy with two food odors and two non-food odors. In contrast to previous studies, each edibility category was comprised of one pleasant and one unpleasant odor. Based on what is known for the visual system, we hypothesized that, due to its ecological relevance, negative food odors would be processed faster and with higher accuracy than odors from other categories (i.e. pleasant versus unpleasant, food versus non-food).

2. Materials and methods

2.1. Participants

A total of 40 young healthy participants (mean age 25 years, range 18–31 years; 20 women) were recruited via posters on the university campus. Subjects were screened prior to inclusion by means of a self-report survey for numerous nasal and neurological disorders known to affect olfactory function. None of the participating women were pregnant, and all had regular menstrual cycles of normal length. Detailed information regarding the experiment was given and written informed consent was obtained from all subjects prior to testing. All aspects of the study were performed in accordance with the University of Pennsylvania IRB and internal regulation at the Monell Chemical Senses Center.

2.2. Stimulus presentation

The odors were presented with a computer-controlled 8-channel olfactometer to assure accurate odor onset and a steep odor rise-time. The premise of the olfactometer is that a valve control unit regulates the state of the olfactometer's eight solenoid valves, each of which directs a continuous airstream of 4 liters per minute (lpm) either into the olfactometer (un-triggered state) or into an odor reservoir (triggered state). When triggered by the valve control unit, a valve directs the airstream into an odor reservoir, and the odorized headspace is transported to the birhinal nosepiece. One of the eight channels serves as a conduit for the control odor and operates in a manner identical to the other channels. Closure of an odor valve triggers the control valve such that whenever an odor is not being delivered, the control air flow is directed to the nosepiece. In the nosepiece, air carrying an odor or the control air mixes with a continuous, low-flow airstream (0.5 lpm). This continuous flow airstream masks the tactile cues that might otherwise alert the subject to channel-switching (Lundstrom et al., submitted for publication). The temporal characteristics of the odor stimulus delivered with the olfactometer settings used in this study (length of tubing, selected airflow rate, etc.) were measured with a photoionization detector (miniPID 200A, Aurora Scientific Inc., Aurora, ON, Canada). The delay to odor delivery, the lapse between the time at which a computer triggers the solenoid valve to the time at which the delivered odor reaches 90% strength, was approximately 450 ms. This calculation is based on the combined lengths of stimulus onset (400 ms, measured from computer trigger) and 10/90% odor rise-time (53 ms, from 10% to 90% odor strength).

The stimulus presentation program E-Prime 2.0 Professional (Psychology Software Tools Inc., Pittsburgh, PA) was used to trigger the olfactometer, present the visual cues, and record subjects' reaction time.

2.3. Odor stimuli

Four odors were chosen on the basis of their edibility (food, non-food) and valence. The two food odorants were natural mixtures chosen to mimic the odor of the food object, and the two non-food odorants were single compounds. The food odors were orange (cold-pressed Californian orange oil, Sigma Aldrich, St. Louis, MO, USA) and fish (Fish flavor oil, Givaudan Inc., Geneva, Switzerland), which were diluted with mineral oil (70%, v/v) and 1,2-propanediol (27%, v/v), respectively. The non-food odors were rose (Phenylethyl alcohol, Sigma Aldrich, St. Louis, MO, USA) and dirty socks (Isovaleric acid, Sigma Aldrich, St. Louis, MO, USA), both of which were diluted with 1,2-propanediol to concentrations of 90% (v/v) and 40% (v/v), respectively. Pilot data indicated that these concentrations were iso-intense. Furthermore, each edibility category contained one pleasant odor (orange, rose) and one unpleasant odor (fish, dirty socks).

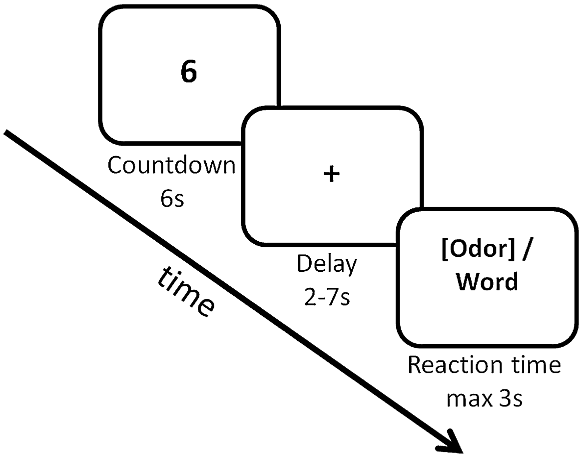

Fig. 1. Experimental design of reaction time task and timing.

2.4. Experimental paradigm

Perceptual ratings of pleasantness and intensity were obtained by presenting each odorant (10 ml) in individual 100 ml amber glass bottles devoid of visual markers. Odor pleasantness and familiarity were rated on a visual analogue scale (VAS, 10 cm) ranging from 'Extremely unpleasant/unfamiliar' to 'Extremely pleasant/familiar', and odor intensity was rated on a labeled magnitude scale (LMS, 10 cm) ranging from 'No sensation' to 'Strongest imaginable'.

Subjects were seated in a comfortable chair, fitted with the olfactometer nosepiece and in-ear headphones, oriented towards an adjustable computer monitor set at eye-level (1 m viewing distance). To exclude the possibility that auditory cues might influence subjects' performances, low volume brown noise was played through the headphones throughout the task. To limit the influence of nasal airflow on stimulus delivery, subjects were instructed to breathe through their mouth for the duration of the task.

Each trial was initiated by viewing 4 s of blank screen, followed by an on-screen 6-s countdown to the appearance of a random duration of a fixation cross (mean 4.2 s, range 2–7 s) in the center of the screen. This fixation cross remained visible during a delay of random length, making a total interstimulus interval of 12–17 s between the end of the first odor presentation and the beginning of the next odor presentation. After the fixation cross, either an odor was presented or a random word appeared in place of the fixation cross; alternatively, no odor or word appeared (blank stimulus). If an odor was presented, the fixation cross remained visible to prevent visually alerting the subject to olfactory stimulation. The odor was presented between 1 and 3 s, leading to an intertrial interval of 13–20 s. The random duration of presentation of the fixation cross was chosen in order to limit a priming effect on subjects to respond to the upcoming stimulus. Subjects were instructed to use a keyboard to indicate whether or not they detected either an odor or a word on the screen and were allowed a maximum of 3 s to respond. The visual reaction task was included to limit subjects' focus on the odor itself. Subjects' responses triggered termination of an olfactory or visual stimulus, and delivery of the control air flow was initiated (see Fig. 1). Subjects were presented with two blocks of 32 trials, each split evenly between 16 olfactory trials (4 per odor) and 16 visual distracter trials, resulting in 8 presentations of each odor per subject. A 5-min break was inserted between the two blocks to prevent fatigue and odor adaptation. No performance feedback was given to the subject at any time.

2.5. Statistical analysis

The delay to odor delivery (450 ms) was first subtracted from all individual responses. Outliers were then identified and removed by means of two data reduction steps. First, we removed responses with reaction times shorter than 100 ms, the minimum possible reaction time. Second, we removed responses with reaction times that differed from the category mean by more than three standard deviations; this second step was not performed for the analyses of detection accuracy. Statistical analysis was performed using SPSS 17.0 (SPSS Inc., Chicago, IL). We computed a repeated measure mixed general linear model (with a compound symmetric