Mirror Sniffing: Humans Mimic Olfactory Sampling Behavior

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Abstract

Ample evidence suggests that social chemosignaling plays a significant role in human behavior. Processing of odors and chemosignals depends on sniffing. Given this, we hypothesized that humans may have evolved an automatic mechanism driving sniffs in response to conspecific sniffing. To test this, we measured sniffing behavior of human subjects watching the movie Perfume, which contains many olfactory sniffing events. Despite the total absence of odor, observers sniffed when characters in the movie sniffed. Moreover, this effect was most pronounced in scenes where subjects heard the sniff but did not see the sniffed-at object. We liken this response to the orienting towards conspecific gaze in vision and argue that its robustness further highlights the significance of olfactory information processing in human behavior.

Key words: contagious behavior, mimicry, mirror behavior, mirror neurons, sniffing

Introduction

Humans have a superb sense of smell (Shepherd 2004; Yeshurun and Sobel 2010), which they use for food preferences, hazard avoidance, and mate selection (reviewed in Stevenson 2010). Indeed, there is increasing evidence that olfactory information, especially social chemosignaling, plays a greater role in human behavior than previously appreciated (Savic et al. 2001; Jacob et al. 2002; Lundström et al. 2006; Zhou and Chen 2008; Miller and Maner 2010; Gelstein et al. 2011; de Groot et al. 2012). Given the importance of general olfaction and social chemosignaling, it is likely that humans evolved behavioral mechanisms to optimize signal acquisition. Olfactory processing depends on stimulus acquisition in the form of sniffing (Mainland and Sobel 2006; Kepecs et al. 2007). Therefore, we hypothesized that humans may be tuned to the olfactory sampling behavior of others and then mimic such behavior in order to obtain timely olfactory information. More specifically, macrosmatic mammals are mostly nose breathers, and their olfactory sniffing differs from their ongoing nasal respiration primarily in frequency (Youngentob et al. 1987; Kepecs et al. 2007; Wesson et al. 2008; Deschênes et al. 2012). In humans, rather than changes in frequency, olfactory sniffing differs from ongoing nasal respiration primarily in nasal airflow dynamics such as sniff duration and volume (Laing 1983). With this in mind, we hypothesized that human sniff dynamics would shift in response to conspecific sniffing, even in the absence of odor.

Materials and methods

Participants

Twenty-seven healthy subjects participated in the study after providing written informed consent to procedures approved by the Wolfson Hospital Ethics committee. Subjects were screened for history of nasal trauma and use of medications. Exclusion criteria were irregular breathing patterns or excessive movement during the experiment. Three subjects failed to meet these study criteria and were therefore excluded from analysis, retaining 24 participants (12 women, mean age $= 25.4 \pm 2.7$ years).

Stimuli and procedures

Subjects watched the movie "Perfume" (http://en.wikipedia.org/wiki/Perfume:_The_Story_of_a_Murderer_(film)) in an "odor clean room." This room is subserved by high-throughput high-efficiency particulate absorption and carbon filtration and is entirely coated in stainless steel so as to prevent odor adherence. The movie Perfume was selected because in its first 60 min, it contains 28 movie sniff events (MSEs) where a character takes a sniff. We identified 3 types of MSEs: auditory–visual MSEs (AV-MSE, $n = 15$) where the observer both hears and sees the on-screen character take a sniff, auditory-only MSEs (A-MSE, $n = 8$) where the observer hears but does not see the on-screen character

take a sniff, and visual-only MSEs (V-MSE, $n = 5$) where the observer sees but does not hear the on-screen character take a sniff. In order to prevent awareness to the aims of the study, subjects were told that they are being studied for calibration of physiological recording devices, and the movie is to alleviate their boredom. To increase reliability of the cover story, in addition to recording our parameter of interest, namely nasal airflow, we also secured the subjects with sensors for galvanic skin response (GSR), electromyogram (EMG), and oximetry. Onset of MSEs was automatically marked on the physiological trace.

Nasal airflow measurement

Physiological measurements were recorded using a Power-Lab 16SP Monitoring System (ADInstruments) running off a Macintosh computer using a sampling rate of 1000 Hz and a 50-Hz notch filter to remove electrical artifacts. We recorded nasal airflow using a nasal cannula (1103, Teleflex medical) attached to a spirometer (ML141, ADInstruments) that delivered a voltage to the instrumentation amplifier (Johnson et al. 2006). As decoys (see above), we also attached 2 bipolar finger Ag/AgCl GSR electrodes (1 cm^2 squared, placed on the second phalanx of the index and the third digit of the nondominant hand), 2 circular Ag/AgCl conductive adhesive EMG electrodes (0.9 cm diameter, located bilaterally adjacent to the submentalis muscles), and an oxymeter (MLT321 SpO$_2$ Finger Clip Sensor, ADInstruments) embedded within a finger clip placed on the left index finger.

Analysis

Nasal inhalations were aligned in time by setting the point at which airflow shifted from the expiratory phase to the inspiratory phase as time 0. Given that "sniff duration" is the primary sniff parameter humans modulate to account for minute changes in odor (Sobel et al. 2000), we concentrated on this measure. Sniff duration was defined as the duration between the 2 points of crossing the inhalation–exhalation baseline (Figure 1A). MSE onsets could occur at any point during the respiratory cycle. If a nasal inspiration started directly before MSE onset, it is unlikely that this specific nasal inhalation was influenced by the MSE even if they overlap. In order to include in the analysis only sniffs that could be influenced by the MSE, we analyzed all the sniffs with onset within a 7-s interval succeeding the MSE onset. In addition, any sniffs that reached 75% of their peak prior to MSE onset were excluded, and the following sniff was included. Sniff exclusion criteria were: 1) severe movement artifacts during the sniff and 2) sniff onset of more than 7 s after on-screen sniff event onset (i.e., breath-holding or mouth-breathing only). This led to exclusion of only 31 events out of the 672 events analyzed (less than 5%). A potentially critical analysis decision is the selection of a subject-specific nasal airflow baseline for comparison.

To allow full consideration of this issue, we identified 3 potential baselines. Baseine 1: a nasal inhalation from 1 min before the sniff event in the movie (a total of 28 inhalations). Baseline 2: a nasal inhalation from 1 min after the sniff event in the movie (a total of 28 inhalations). Baseline 3: an average of 180 nasal inhalations across the movie (6 epochs of 30 consecutive inhalations every ~10 min, generating a total of 180 inhalations). To compare across subjects, sniff duration was normalized through dividing each sniff by the baseline. Change-from-baseline duration values were then analyzed using an analysis of variance (ANOVA).

Results

To ask whether subjects sniff following an MSE, we conducted a repeated-measures ANOVA on sniff duration for "event type" (MSE/baseline 1/baseline 2/basline 3). We found a significant main effect of "event type" ($F_{(3,23)} = 6.95$, $P < 0.0005$), reflecting longer sniff duration following an MSE in comparison to each of the 3 baselines (average increase = 3.7% ± 5.2%, baselines 1, 2, and 3: all $t_{(23)} > 2.3$, all $P < 0.05$) (Figure 1B). This implies that humans sniff when someone else sniffs on screen, or in other words, humans engage in mirror sniffing (see Supplementary Video).

Next, to ask whether mirror sniffing is selectively driven by modality, we divided the 28 MSEs into auditory-only MSEs (A: the sound of a sniff with no image of a person sniffing, $n = 8$), visual-only MSEs (V: scene of a person sniffing with no sniff sound, $n = 5$), and full auditory–visual MSEs (AV, $n = 15$). An ANOVA with conditions of "modality" (AV/A/V) and "event type" (MSE/baseline 1/baseline 2/basline 3) revealed a main effect of "modality" ($F_{(2,46)} = 11.51$, $P < 0.0001$), a main effect of "event type" ($F_{(3,69)} = 5.34$, $P < 0.005$), and a significant interaction ($F_{(6,138)} = 3.63$, $P < 0.005$). Planned comparisons revealed that subjects took the largest sniffs following A-MSEs (average increase = 8.4% ± 13.3%, difference from baselines 1, 2, and 3: all $t_{(23)} > 2.2$, all $P < 0.05$; difference from AV-MSE $t_{(23)} = 2.1$, $P < 0.05$; difference from V-MSE: ($t_{(23)} = 2.9$, $P < 0.01$), the next largest sniffs following AV-MSEs (average increase = 3.0% ± 4.8%, difference from baselines 1, 2, and 3: all $t_{(23)} > 2$, all $P < 0.05$; trend to difference from V-MSE: $t_{(23)} = 2.02$, $P = 0.055$), yet subjects did not sniff following V-MSEs (average increase = 0.05% ± 5.9%, difference from baselines 1, 2, and 3: all $t_{(23)} < 0.43$, all $P > 0.67$) (Figure 1C). In other words, mirror sniffing is most prominent when humans hear someone taking a sniff, yet do not see the sniffed-at object. Finally, we replicated the entire above analysis for both sniff volume and sniff amplitude. The effects mostly replicated in sniff volume, albeit with reduced power, yet did not materialize in sniff amplitude. This is consistent with previous findings implicating sniff duration as the primary sniff parameter under modulation following minute alterations in olfactory content (Sobel et al. 2000).
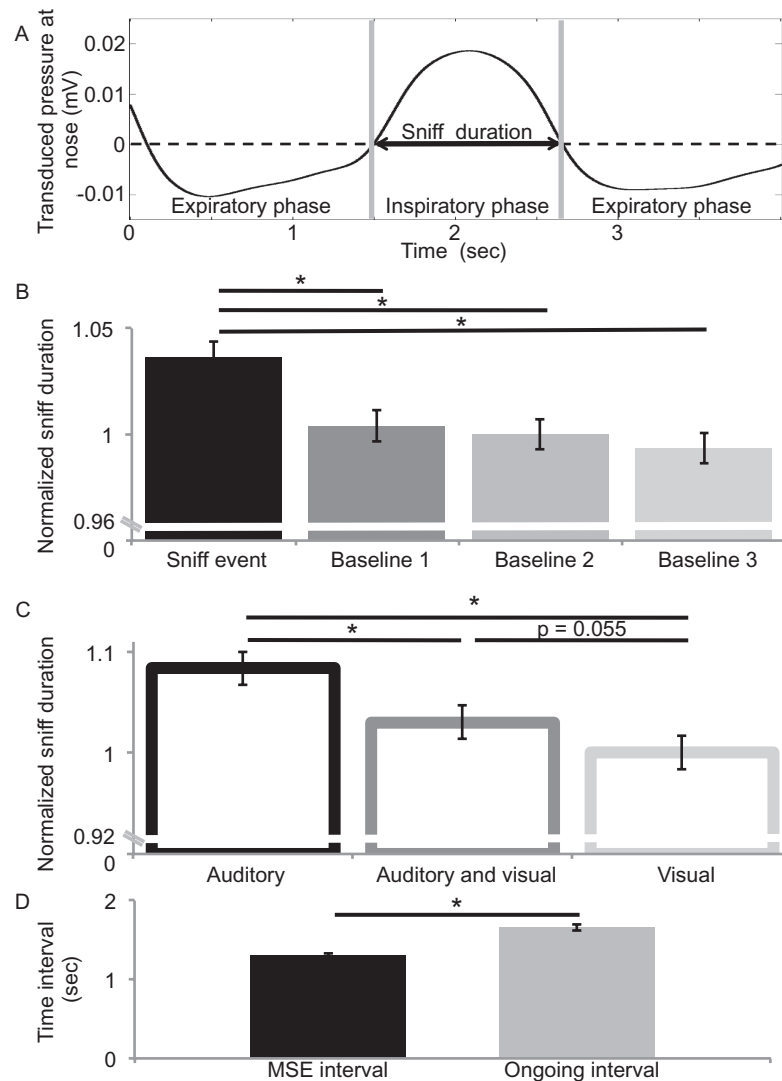
Figure 1 Humans engage in mirror sniffing. (**A**) A typical sniff trace with a black arrow indicating sniff duration. (**B**) Normalized duration for the nasal inhalation immediately following a MSE compared with 3 different nasal inhalation baselines. (**C**) Normalized duration for the nasal inhalation immediately following a MSE that was either only heard but not seen, heard and seen, or only seen but not heard. (**D**) Averaged time interval between MSE and succeeding sniff onset (MSE interval in blank) and the inter-inhalation interval divided by 2 (ISI/2) (ongoing interval in gray) (*$P < 0.05$). Error bars are standard error of the mean.

In order to assess whether sniff timing was affected by MSE, we calculated the interval between MSE onset and the succeeding sniff onset for each MSE ($n = 28$). As a measure for averaged nasal inhalation onset from a random event we calculated the averaged inter-inhalation interval divided by 2 (ISI/2) along the 1-h experiment for each subject. We found that the interval between MSE and the succeeding sniff onset was significantly shorter than the mean ISI/2 (interval between MSE and succeeding sniff onset = 1308.5 ms, mean ISI/2 = 1654.7 ms, $t(23) = 7.0$, $P < 0.00001$; Figure 1D). To test whether sniff timing was affected by MSE at a single-subject level, we generated 28 random event onsets and calculated the interval between each of the random events and the succeeding nasal inhalation for each subject. We performed a t-test to compare between the intervals initiated by MSE onset and the intervals initiated by the 28 random event onsets. This procedure was repeated 1000 times per subject. We found that in all subjects, more than 97.5% of the t-test comparisons were statistically significant ($P < 0.05$). In other words, all 24 participants shortened their sniff onset relative to MSE onset.

Discussion

We found that humans sniff in response to olfactory sniffing of characters on screen in a movie (see Supplementary Video). Moreover, the auditory component of on-screen sniffing behavior was the dominant aspect driving sniffing in

observers. Although these sniff modulations were not over-whelming in their size (~8% modulation in duration), they were similar in extent to modulations in response to changes of one order of magnitude in odor concentration (Johnson et al. 2003). This phenomenon, we will call mirror sniffing, may stem from several different mechanisms: One can consider mirror sniffing in the context of mimicry, namely the unaware tendency of individuals to take on posture and mannerisms of those around them. For example, when one sees another person rubbing their face or shaking their foot, one will have an increased tendency to perform the same action (Chartrand and Bargh 1999; Lakin and Chartrand 2003). Mimicry also exists for emotional facial expressions, which like the current example, are stronger when driven by one modality (vision) over another (audition) (Sestito et al. 2013). The current result, however, differs from such mimicry in a critical aspect, and that is that it consists of a behavior directed at sensory acquisition, whereas mirror face-rubbing, foot-shacking, or emotional expression will not provide the mirroring individual with new information, mirror sniffing will.

An additional related and relevant context is that of contagious behavior, namely the unconscious automated transmission of actions or emotions from one individual to another. Contagious behaviors, such as yawning, laughing, or crying, can be triggered by seeing, hearing, or even thinking of another person's behavior (Platek et al. 2005; Provine 2005).

Finally, a particularly appealing context for consideration of mirror sniffing is as a form of orienting response rather than imitation per se, much like the shifting of visual gaze towards the direction of gaze in conspecifics (Emery 2000; Zentall 2006). The potential value of such a response is clear, as it would direct awareness towards valuable olfactory information such as danger, food, or a potential mate. This is consistent with the increased effect for auditory-only sniffs: When a visual component is present, then the identity of the stimulus is known without mirror sniffing. For example, if we see someone sniffing an apple, then the smell is likely "apple." However, if we hear someone sniffing without a visual target, this implies that there is "something important in the air," and we better find out what it is. Moreover, the persistence of the mirror-sniffing response within a setting where a real olfactory signal was highly unlikely (a movie) implies an extremely robust and automatic mechanism and may suggest social sniffing irrespective of odor presence (Wesson 2013). This mechanism is possibly reliant on a neural mirror system (di Pellegrino et al. 1992; Rizzolatti 2005), as is the case with other instances of mirroring behavior (Iacoboni 2009; Cooper et al. 2012).

In conclusion, olfaction plays a key role in human interactions with the environment and human interactions with conspecifics. The phenomenon of mirror sniffing is yet one more indication that olfactory information plays a larger part than commonly assumed in human behavior.

Supplementary material

Supplementary material can be found at http://www.chemse.oxfordjournals.org/

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