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Mechanisms of scent-tracking in humans

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Whether mammalian scent-tracking is aided by inter-nostril comparisons is unknown. We assessed this in humans and found that (i) humans can scent-track, (ii) they improve with practice, (iii) the human nostrils sample spatially distinct regions separated by ~3.5 cm and, critically, (iv) scent-tracking is aided by inter-nostril comparisons. These findings reveal fundamental mechanisms of scent-tracking and suggest that the poor reputation of human olfaction may reflect, in part, behavioral demands rather than ultimate abilities.

Two major roles of olfaction are identifying odorants and spatially localizing their sources. Whereas odor plume navigation in air (for example, in moths[1]) and water (for example, in lobsters[2]) has received some attention, the mechanisms of scent-trail tracking, a critical ability for macrosmatic mammals ranging from rats to dogs[3] (see **Fig. 1a**), remain unknown, and key questions, such as whether mammals use inter-nostril comparisons to aid scent-tracking, remain unanswered.

Humans are an appealing animal model for addressing such questions because they can follow task instructions and accurately report behavioral strategies. Humans also tolerate manipulations, such as nostril occlusion, that may aggravate even well-trained dogs. However, whether humans are a valid model for this task is unknown. Therefore, we first set out to ask whether humans can scent-track.

In Experiment 1 we asked whether 32 naive human subjects were capable of using only their noses (all other sensory input being blocked) to follow a ~10-m-long scent trail in an open grass field (**Supplementary Methods** online). All subjects gave informed consent to procedures approved by the University of California Berkeley Committee for the Protection of Human Subjects. Two-thirds of the subjects were capable of following the scent trail (21 of 32 subjects, 9 women, 12 men). **Figure 1b** shows a time-lapsed image of one trial, and **Supplementary Video 1** online contains a movie of one trial. To ask whether subjects were aided by any unintended non-olfactory cues, we repeated the task with nostril occlusion. None of the subjects were able to follow the scent trail under these conditions, assuring the olfactory nature of the task.

We next asked whether subjects could improve with practice. In Experiment 2, four subjects (two men, two women) trained on this same task, three times a day, for 3 d within a 2-week period. With training, subjects decreased their deviation from the scent track (decaying exponential fit: $R^2 = 0.2862$, $F_{1,28} = 10.82$, asymptote 0.1 m, $P = 0.0028$, **Fig. 2a**) and increased their velocity (0.026 $ms^{-1} \pm 0.003$ on day 1, 0.057 $ms^{-1} \pm 0.01$ on the last day; local linear fit, $R^2 = 0.94$, $P = 0.0006$, **Fig. 2b**). Considering that tracking velocity more than doubled within a few days, we suggest that longer-term training would lead to further increases in tracking velocity. The plateau we observed in lateral deviation reflects the zigzagging nature of the tracking path (**Fig. 1b** and **Supplementary Fig. 1** online), a characteristic also observed in macrosmatic animals during scent-tracking[3].

An important factor in mammalian olfactory behavior is active sniffing[4,5]. We therefore next asked whether sniffing behavior was related to humans' ability to follow a scent trail. We calculated mean sniffing frequencies for each trial (**Supplementary Methods**). Whereas performance on the initial day of testing (mean velocity or deviation) did not correlate with sniffing frequency ($R^2 = 0.0135$, $t_{1,9} = 0.1094$, $P = 0.75$), sniffing frequency increased with tracking velocity over the three subsequent days of training (frequency versus day: $R^2 = 0.2932$, $t_{1,28} = 11.20$, $P = 0.0024$; velocity versus day: $R^2 = 0.3608$, $F_{1,28} = 15.23$, $P = 0.0006$; **Fig. 2c**). We interpret these results to suggest that, as subjects increased their speed, it was necessary for them to sniff more quickly to get the same quality of information. One notable difference between these results and those from dogs is that dogs

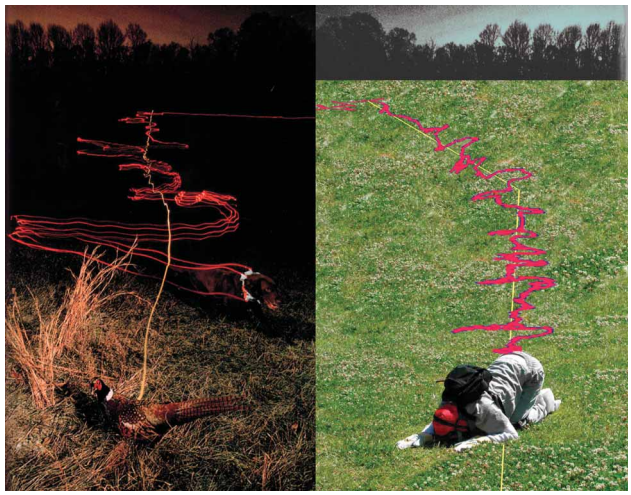

Figure 1 Human subject's path following a scent trail, as compared to a dog's path. (**a**) Path of a dog following the scent trail of a pheasant dragged through a field (scent trail in yellow, dog's path in red; from ref. 15). (**b**) Path of a human following a scent trail of chocolate essential oil through a field (scent trail in yellow, human's path in red).

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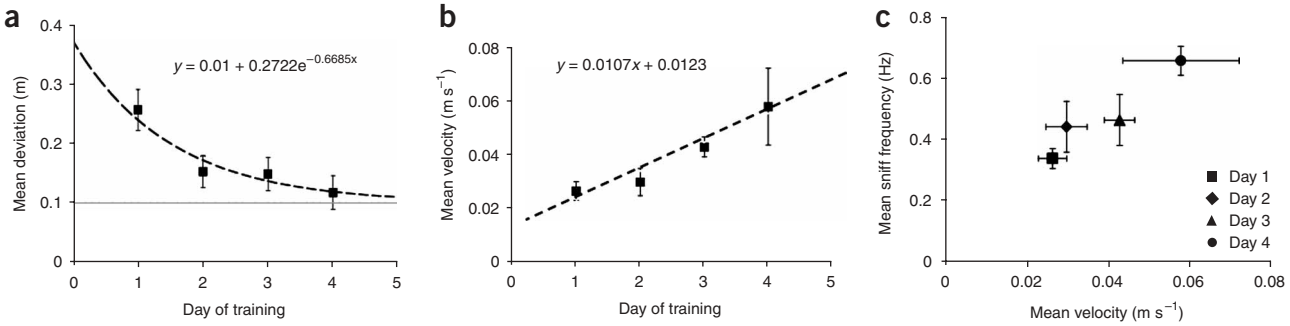

Figure 2 Training increased tracking velocity, decreased deviation from track, and increased sniffing frequency. (**a**) The mean deviation from the scent trail is plotted for all subjects for each day of training. Dashed line, decaying exponential fit; solid gray line, asymptote. (**b**) The mean tracking velocity is plotted for each day of training. Dashed line, linear fit. (**c**) The mean tracking velocity is plotted against the mean sniffing frequency for each day of training. Error bars, s.e.m.

sniff much faster (~6 Hz)[3], which may partially account for their greater scent-tracking proficiency.

Mammals localize auditory sources by comparing simultaneous inputs across two ears, converting differences in sound timing and intensity to spatial coordinates. It has been asserted that mammals cannot similarly exploit their two-nostril geometry to localize and track scent trails, because the nostrils are too closely spaced to provide spatially distinct information[6].

In Experiment 3, we tested this assertion using particle image velocimetry (PIV) to measure the velocity of neutrally buoyant particles in a coronal plane intersecting the human nose during sniffing (**Fig. 3a**; **Supplementary Methods**). **Figures 3b** and **c** shows sample PIV images of the nasal inspiratory airstreams and **Figure 3d** a contour plot of the magnitude and direction of inspired air. In contrast to the common notion, each nostril clearly inspired air from distinct, non-overlapping regions in space. In addition, the natural asymmetry in airflow across nostrils shaped this reach pattern. A maximum velocity of 0.45 ms^{-1} at the right nostril and 0.30 ms^{-1} at the left (see **Fig. 3e**) led to a right nostril reach of ~1.5–2.0 cm to the right and a left nostril reach of ~1.0–1.5 cm to the left. In other words, the two nostrils sampled information from centroids laterally separated by ~3.5 cm. Considering that the boundary of a scent plume can be ~10 mm[7], this result demonstrated that one nostril can be within a plume while the other is out of the plume. Having found that the nostrils provide spatially distinct information that could in principle[8] be exploited to scent-track, we next asked whether this information is exploited.

In Experiment 4, 14 subjects performed the scent-tracking task, once with one nostril taped closed, and once with both nostrils open (order counterbalanced). Compared to dual-nostril tracking, single-nostril tracking was less accurate (36% versus 66% accuracy, binomial $P < 0.003$) and slower (26% reduction in speed, binomial $P < 0.02$).

To control for some limitations in the interpretation of the critical Experiment 4 (see **Supplementary Methods**), in Experiment 5 we re-tested the four trained subjects from Experiment 2 using a nasal 'prism' device that maintained input into two nostrils, while within the prism both flow paths were conjoined to form a single virtual nostril located in the middle of the nose (**Fig. 3f**). Now, the external environment was sampled by two nostrils, but without spatial separation. To control for the effect of the prism device, we used a control prism with two straight flow paths that maintained natural spatial separation (schematic in **Fig. 3f**). After getting used to the prisms, each subject performed three tracking runs with the control prisms and three runs with the non-spatial prisms on two more days in counterbalanced order.

Subjects were significantly less accurate (9/12 successful with control, 5/12 with non-spatial prism; binomial, $P < 0.015$) (**Fig. 3g**) and

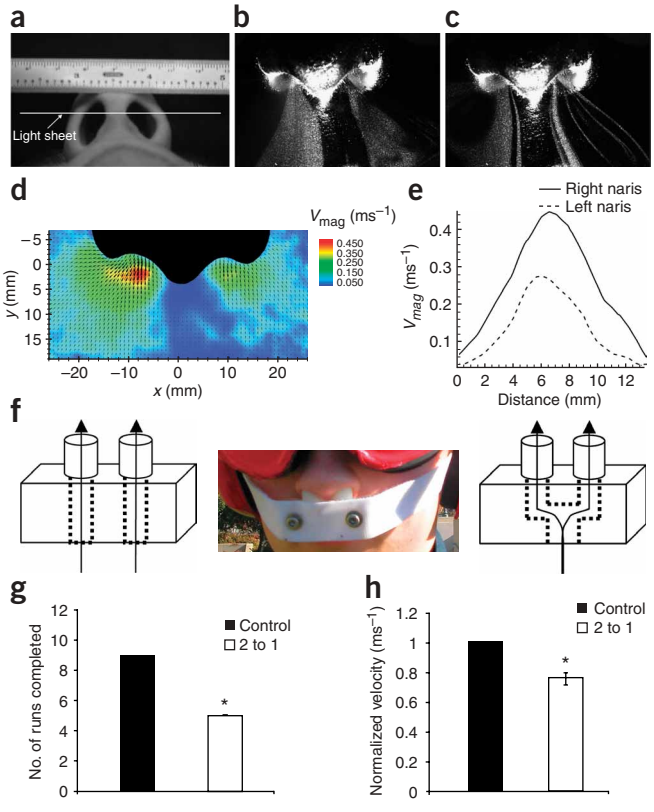

Figure 3 The two-nostril advantage in sampling and tracking. (**a**) The PIV laser light sheet was oriented in a coronal plane intersecting the nostrils at their midpoint. (**b**,**c**) PIV images of particle-laden inspired air stream for two example sniffs. (**d**) A contour plot of velocity magnitude of the inspired air stream into the nose of the subject sniffing at 0.2 Hz. (**e**) Velocity profiles of the right and left naris; abcissa indicates distance from the tip of the nose to the lateral extent of the naris. (**f**) Schematic diagrams of control prism (left) and non-spatial prism (right). Arrows show the direction of sniff airflow. Center, prism worn by subject. Inlet ports are located on bottom surface of prism; screws are located on front surface. (**g**) Subjects completed fewer trials using non-spatial prisms as compared to control prisms. (**h**) Subjects were significantly slower tracking with non-spatial prisms than with control prisms. Error bars, s.e.m.

significantly slower (24% reduction in speed, $t_{1,4} = 4.9967$, $P = 0.0075$, **Fig. 3h**) using the non-spatial prism than with the control prism. In Experiments 4 and 5 taken together, 18 subjects who completed a total of 52 tracks were both faster and more accurate when they were able to make comparisons across spatially offset nostrils.

Poor olfactory abilities in humans have been attributed to the reduction in olfactory receptor repertoire apparent in primate evolution[9]. However, demonstrations of keen primate olfaction[10] have challenged the causal relationship between receptor repertoire size and olfactory abilities[11] and the classical definitions of microsmat and macrosmat[12]. Here we found that not only are humans capable of the demanding macrosmatic behavior of scent-tracking, but they spontaneously mimic the tracking patterns of macrosmatic mammals. Using this model enabled us to address the key question of whether mammals use inter-nostril comparisons to aid scent-tracking.

Our results suggest that, although comparison of sequential samples alone can subserve tracking, there was an added benefit to simultaneous sampling at the spatially offset locations provided by the two nostrils. Neural and behavioral mechanisms that may subserve this behavior have been revealed in recent studies indicating that immobile rats[13] and humans[14] require bilateral input to localize odor sources within a single sniff. However, these past results—obtained in highly artificial settings with immobilized animals—did not show whether such differences were relevant to natural spatial behavior. Here we find that mammals performing a scent-tracking task, freely able to move their nose and sample the olfactory environment in real time, reap added benefit from sampling via their two spatially offset nostrils.

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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