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Stereo and serial sniffing guide navigation to an odour source in a mammal

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Integration of bilateral sensory information is fundamental to stimulus localization in auditory systems and depth perception in vision, but the role of stereo olfactory cues remains obscure. Here it is shown that blind, eastern American moles combine serial sampling with bilateral nasal cues to localize odorants. Blocking one nostril causes moles to err in the direction of the open nostril with strongest effect within 4–5 cm of the stimulus. Nostril block does not severely disrupt more distant navigation towards odorants in a T-maze nor prevent animals from ultimately locating the odour source. Crossing inputs to the nostrils using plastic tubes causes a local repulsion from the stimulus, whereas uncrossed tubes do not disrupt localization. These findings show that mammals can make use of bilateral chemosensory cues combined with serial sampling to localize odorants and offer insights into the relative contribution of each strategy during different stages of natural search behaviours.

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It has been suggested that either serial sampling of odorants at different locations or simultaneous sampling from two places could guide chemotaxis^{1–5}. Of these two possibilities, the possible contribution of simultaneously compared bilateral cues during odorant localization has been a topic of much historical interest and recent investigation^{6–17}. Evidence for bilateral comparisons in humans comes from degraded scent-tracking abilities during unilateral nostril blockade or a fused airway¹⁸, but other studies suggest that nostril-specific odorant localization by humans requires trigeminal stimulation^{13,16}. Studies of trained rats found that bilateral sampling was necessary for determining the side from which an odorant arrived¹⁰, and investigation of neurons in the rodent anterior olfactory nucleus reveal the neural circuitry that could underlie bilateral comparisons⁹. More recent investigations show that rats can efficiently follow a scent trail and that this ability is degraded when a single nostril is blocked¹⁹. However, there is little information about the role bilateral nasal comparisons may have in localizing discrete odour sources based on concentration gradients.

This question is addressed here by exploiting the discovery of exceptional olfactory behaviours in blind eastern American moles (*Scalopus aquaticus*). Eastern moles have degenerated mechanoreceptive organs compared with other moles²⁰, tiny eyes hidden below fur and skin, and small ears tuned to low frequencies²¹. Thus, they were expected to perform poorly in localizing prey, compared with other moles with more elaborate mechanoreceptive arrays²². In surprising contrast, eastern moles had the ability to move rapidly and directly towards prey (earthworm segments) while moving their nose in an apparent serial sniffing behaviour. To investigate this ability, an experimental chamber was designed that allowed monitoring of sniffs while filming search behaviours with a high-speed camera (Fig. 1). The chamber had two subsections, one that served as a holding point, and the other containing a semicircular array of 15, 1-cm diameter wells (one well containing food) located 8 cm from the entry point. This experimental chamber eliminated airflow that might disturb olfactory gradients,^{23,24} allowed non-invasive sniff monitoring with a pressure transducer, and simulated the closed environment of the mole's natural underground habitat. The results of these studies show that the eastern American mole,

uses a combination of bilateral chemosensory cues as well as serial sampling to localize odorants.

Results

Radial arena and nostril block. Each trial was initiated by removing a bar that blocked the entrance to the chamber containing the food item. After 10–15 acclimation trials, moles were proficient at moving toward the prey item after a brief sampling period and typically located the food item in less than 5 s. The cross-point in degrees along the semicircle (Fig. 1) and the first well explored with a nose dip were measured to gauge accuracy. In 20 trials in each of two animals, moles were 100% accurate in searching the appropriate well first (as indicated by a nose dip into the well) and crossed the border of the 8-cm distant semicircle within an average of 1° of the centre of the prey item. Although eastern moles' eyes are tiny and hidden below the fur, additional animals were tested under 950 nm infrared illumination and performed equally well.

Analysis of sniffs relative to nose movements revealed a search strategy that is likely fundamental to mammalian olfactory behaviours^{25,26}—the sniff cycle was coordinated with movements such that the nose typically decelerated and paused (often touching the substrate) as a sniff was initiated, revealing a serial spatial sampling strategy coordinated with mechanosensory sampling (see Supplementary movie 1).

The accuracy of the moles and relatively direct path often taken towards food after an initial period of sniffing suggested the possibility that bilateral olfactory cues might supplement serial sampling to provide directional information. To examine this possibility, either the left or right nostril was temporarily blocked with a short piece of plastic tubing under isoflurane anaesthesia in four moles. Ten food-localization trials, matched in position to 10 pre-block trials, were then performed. In each blocked case, the mole was substantially and consistently biased to the side of the unblocked nostril (Fig. 2a–f and see Supplementary Movie 2). The average cross-point was skewed between 8 and 21°, and each case was statistically significant (P -value between 0.01 and <0.001, see Fig. 2). In the unblocked pre-trials, the moles were 100% accurate in exploring the food well first, whereas in the

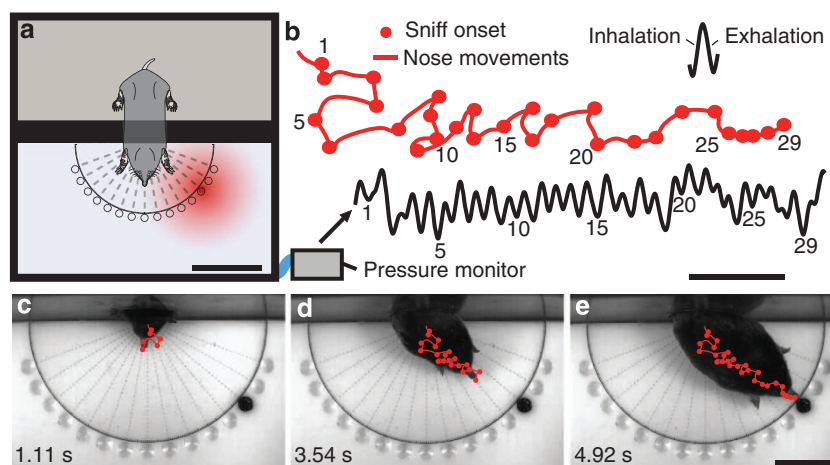


Figure 1 | Experimental chamber for radial search paradigm. (a) A plexiglass, 28-cm square chamber divided into two sections, was used for the first set of experiments. A holding chamber (top) was separated from the testing chamber containing the food and accessed through a small hole that was blocked by a vertical bar until each trial started (not shown). The box was accessed between trials by removing the lid, which sat on walls coated with vacuum grease to form an airtight seal. Eastern moles are small mammals typically weighing between 50 and 90 g. (b) An air-pressure monitor recorded respiration, and sniffing correlated with the time stamps of frames captured from high-speed video allowing nose movements (lines) to be correlated with sniffs (circles). Supplementary Movie 1 shows sniffs correlated with nose movements. (c–e) Example of mole search behaviour and nose movements correlated with sniffing. Trials were initiated approximately 1 min after food placement and trials usually lasted 5–10 s. Scale bars, 8 cm in **a**, 1 s in **b** and 4 cm in **c**.

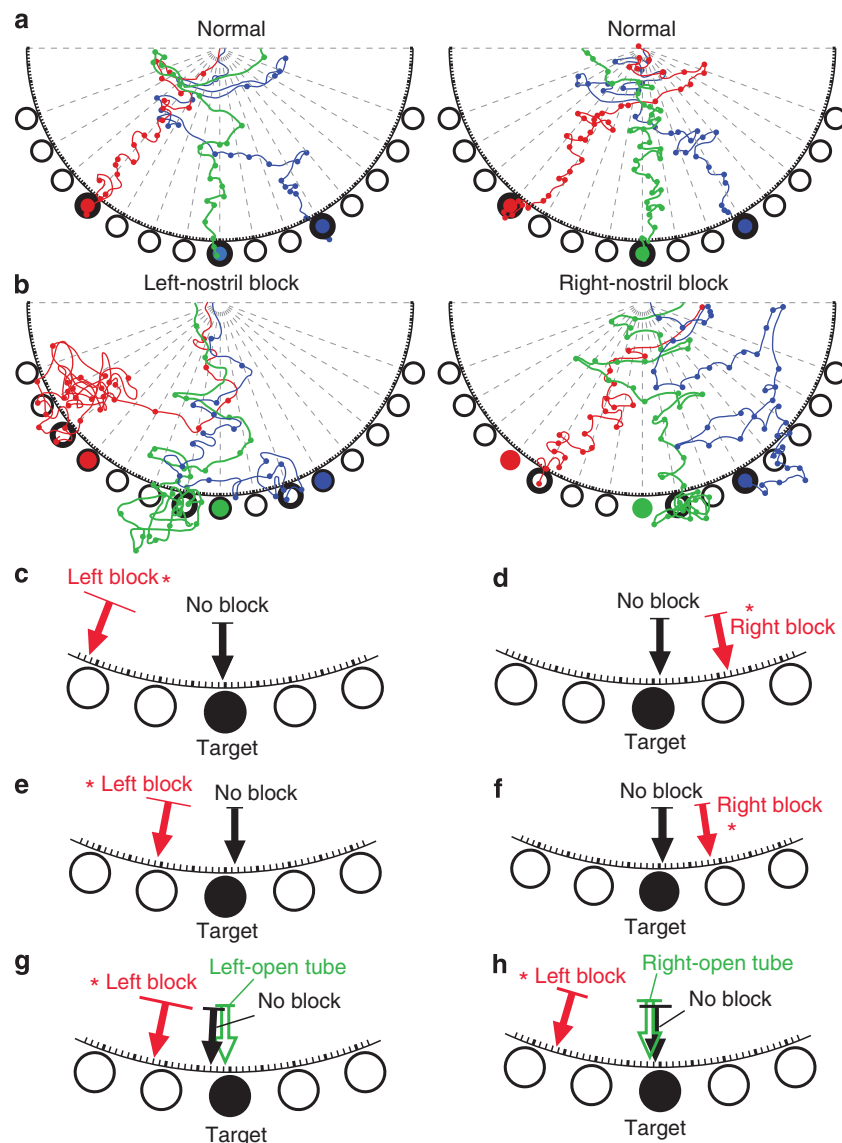


Figure 2 | Search behaviour under normal and nostril-block conditions for radial search paradigm. (a) Normal search behaviour from two moles (animal no. 2 on left and animal no. 1 on right). Colour of the trace matches target well colour for each trial. Circles indicate sniffs. The first well explored with a nose dip is indicated by bold outline. (b) Examples of search behaviour for left- and right-nostril block for cases shown in a. Left nostril block biased search to the right, whereas right nostril block biased search to the left. Coloured well indicates target (food) location; bold outline indicates the first well explored. Trace is illustrated until a well was explored, but moles continued to search and found the food in nearly every trial. (c–f) The mean cross-point (relative to target) for the tip of the nose along the semicircle of wells for normal and blocked conditions for four different animals (10 trials for each animal). For c (animal no. 2), mean unblocked cross-point was 0.4° and mean left block was 21.6° . For d (animal no. 1), mean unblocked cross-point was -1.0° and mean right block was -11.6° . For e (animal no. 3), mean unblocked cross-point was -1.5° and mean left block was 10.9° . For f (animal no. 4), mean unblocked cross-point was -0.5° and mean right block was 8.4° . (g,h) Results from two additional animals (10 trials for each condition) with the addition of an 'open-tube' control (green arrow). For g (animal no. 16), the mean cross-point was 3.0° for unblocked, 0.9° for the open-tube condition and 12.0° for the left-nostril block. For h (animal no. 15), the mean cross-point was 0.9° for unblocked, 1.7° for the open-tube condition and 16.4° for the left-nostril block. Under nostril-block conditions, moles were consistently and significantly biased in the direction of the open nostril (Watsons–Williams F-test, a circular statistic), but the open-tube condition was not significantly different from the normal condition. *P*-values for c–h are $P < 0.001$, $P < 0.001$, $P < 0.004$, $P < 0.001$, $P = 0.01$ and $P < 0.001$, respectively. Video of all 10 trials for blocked and unblocked condition for animal no. 1 and 2 is provided in Supplementary Information.

blocked trials, the moles first explored the wrong well—towards the open nostril—70% of the time. Importantly, in every trial the mole still located the food item, but with a longer latency than the unblocked condition.

The same experiments were then conducted in two additional moles, but also using a single piece of open plastic tubing in a nostril as a control for 10 trials (separate from the nose-block trials), to ensure that the plastic tube alone did not influence search behaviours independent of airflow (Fig. 2g–h). In these

cases, there was no obvious or statistical difference between the normal condition and the single open-tube condition, whereas in the blocked nostril condition, the bias to the open nostril was again obvious and statistically significant.

Simulated tunnel and T-maze with blocked nostril. To simulate conditions similar to an underground tunnel with less predictable distance to the food, a larger array of 144 smaller (5 mm

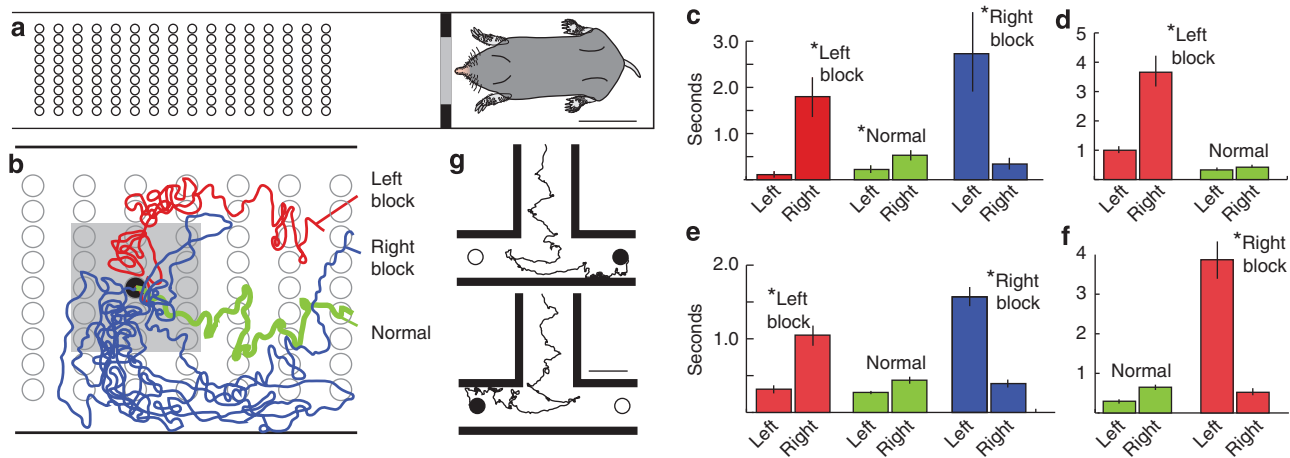


Figure 3 | Blocked and unblocked nostrils in the rectangular tunnel array. (a) In this paradigm, a smaller food item (earthworm segment) was placed in a smaller (5 mm diameter) well. (b) Under normal (green trace), right-nostril block (blue trace) or left-nostril block (red trace) conditions, the amount of time spent to either the left or the right of the food item within a 4-cm square (grey) around the food was measured for 10 trials for four moles. Left and right were with respect to the animal, which did not turn around in the arena during the trials. In two of the four moles, the side of the nostril block was switched and the animal was retested. In each case, the mole spent a much greater and significantly different amount of time on the side with the open nostril (two-tailed *t*-test). (c) Data from animal no. 5, showing normal and both nostril-block conditions. This animal was the only one with a statistically significant bias ($P=0.04$) under normal conditions (green), reflecting an approach most often from the right. Left (red) or right (blue) block biased the animal substantially to the open nostril and greatly increased search time to locate food (two-tailed *t*-test, $P=0.005$ left block, 0.017 right block). (d–f). Results from animal no. 6 (e), 7 (d) and 8 (f). In d, left block $P=0.02$; in f, right block $P=0.005$; and in e, left block $P=0.007$ and right block $P=0.002$. Bars are s.e. of the mean. (g) Examples of nose tracks for a mole in a T-Maze with the left nostril blocked (animal no. 14). Scale bar, 4 cm (in a and g).

diameter) wells was constructed and placed in a longer rectangular enclosure (Fig. 3). After 10–15 acclimation trials, data for 10 pre-trials and 10 position-matched nostril-blocking trials were collected for four additional moles. The time spent to either the right or the left of the prey item (Fig. 3b) was compared, and in two of the animals, the nostril block was switched and the animal was retested (Fig. 3c–f). In each case, the mole was significantly biased (Fig. 3) towards the side of the open nostril and the latency to locate the food item was greatly increased (see Supplementary Movie 3).

In both paradigms, the moles with blocked nostrils searched with a bias to the side of the stimulus corresponding to the open nostril. But they did not turn in circles and were not completely disoriented, suggesting that there is more than bilateral comparisons guiding orientation. In each case, the animal was able to orient towards the stimulus and was able to overcome the bias caused by the nostril block to find the food. Presumably, serial spatial sampling was largely unaffected by the nostril block and guided the longer-distance orientation of the mole. To further investigate this possibility, four animals were tested in a T-maze (Fig. 3g) before and after nostril block. The T-maze provided a structured choice between two opposing directions to reveal whether animals would turn in the direction of the blocked nostril at a distance from the odorant. High performance in the T-maze did not deteriorate with nostril block. After nostril block, one animal was correct in 100% of 10 trials, two animals were correct in 90% of 10 trials and one animal was correct in 85% of 20 trials (see Supplementary Movie 4).

Crossed airflow to the nostrils. To further investigate the role of bilateral cues, short polyethylene tubes were inserted (under isoflurane anaesthesia) to temporarily re-direct the airflow from the nostrils in four additional moles, two in the radial arena and two in the tunnel arena. Crossing the airflow from the two nostrils reverses potential bilateral sniffing cues but should have little effect on serial sampling. In this condition, the moles usually

could not eat the food item as a reward because the tubes blocked them from dipping into the wells. As a result, fewer trials were possible (5 trials each condition in radial array, 9 and 10 trials each condition in 144-well tunnel array). The moles were tested with both crossed and uncrossed airflow (Fig. 4). In the radial arena for the uncrossed condition, both moles rapidly located the food item in five out of five trials. Crossing the airflow had a dramatic effect—in this condition, no food item was located and the moles often searched on either side of the food (Fig. 4b, c). Results were similar in the tunnel array with small wells. Moles in the uncrossed condition repeatedly attempted to contact the food, stopping with the tubes located over the food. In the crossed condition, they searched more often on either side or missed the food completely—spending significantly less time with the tubes over a 1-cm square encompassing the food item in the course of the crossed trials (see Supplementary movie 5 for behaviour).

Estimated range for bilateral cues. In the experiments described above, the food was moved to a different position for different trials for the obvious reason that moles might simply learn the food's location if it was always in the same place. In a new and different paradigm, food was always located in the same position to examine the paths that moles take to the food under less variable conditions. The moles were still biased to the side of the open nostril during nostril block in this paradigm (Fig. 5 and Supplementary Movie 6). Four animals were investigated, in each case with a control open-tube condition, normal condition, and both a left- and right-nostril block. For ease of comparison, only the control (open-tube trials) and the nostril-block trials are shown in Fig. 5. The results further emphasize the important role that stereo cues have in the search strategy, and at the same time suggest that the nostril block has its strongest effect beginning at a distance of 4–5 cm from the odorant (see Fig. 5 for statistics). As was the case for the other paradigms, the moles still located the food, suggesting that serial sampling provides sufficient cues for stimulus localization.

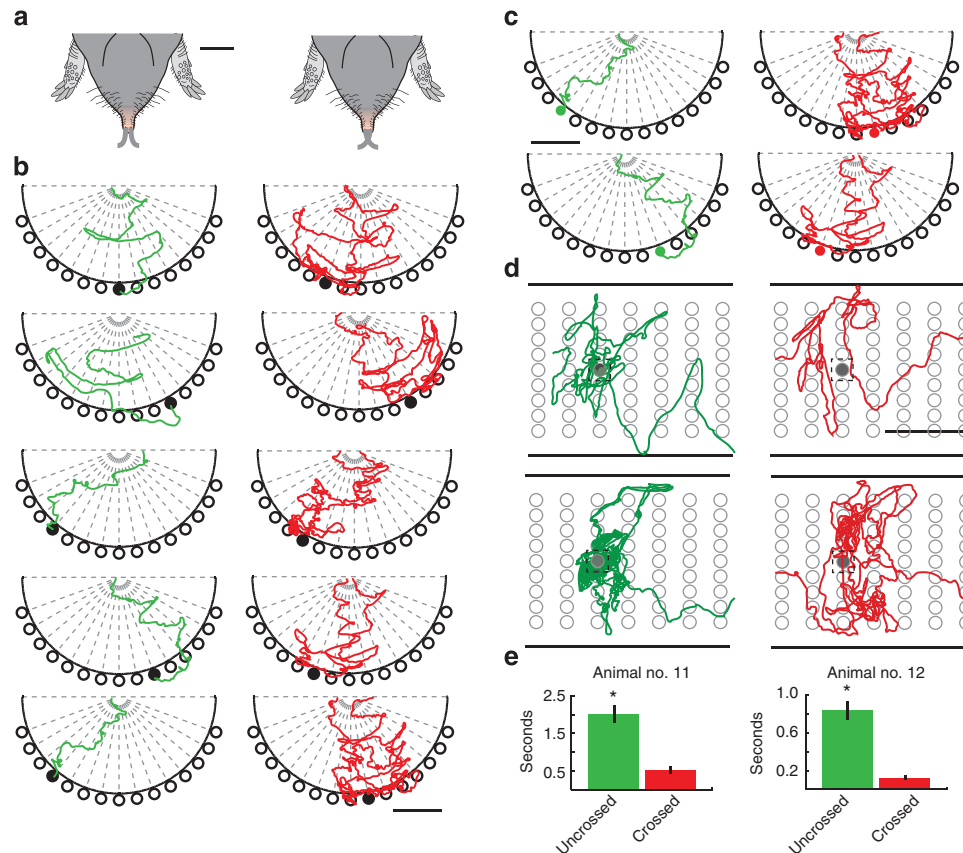


Figure 4 | Effect of crossed airflow. (a) In four moles, short, open polyethylene tubes were inserted into the nostrils to alter the airflow direction. Moles were tested in both uncrossed (left) and crossed (right) condition. (b,c) Examples of nose tracks for the uncrossed and crossed condition. For the two moles tested with the radial array, each animal quickly found the food (green traces) in five out of five trials for the uncrossed condition. In the crossed condition, the moles did not find the food in any of the five trials each, but often searched to the left and right of the food item (red traces) or completely avoided the food item. (d) In the 144-well array, moles in the uncrossed condition spent a significantly greater amount of time with the tubes over the food item as measured for a 1-cm square around the food well (dotted square). (e). Results for animal no. 11 (left) and 12 (right) in the 144-well array showing the amount of time over the square in d (two-tailed *t*-test, animal no. 11, nine trials for each condition, $P = 0.014$; animal no. 12, 10 trials for each condition, $P = 0.005$). Each trial was initiated when the animal came within 3 cm of the food item and continued for 10 s thereafter. The tracks and analyses used the position of the midpoint between the tube openings. Scale bars, 1 cm (a) and 4 cm (b–d).

Finally, the crossed nostril experiments were also repeated in this new paradigm. In two moles for 10 trials in each condition, the crossed nostrils impaired the mole's search behaviour (Fig. 6). As in the previous paradigms, the moles with crossed nostrils frequently searched back and forth or to the side of the food (see Supplementary Movie 7), often missing the food completely. Both the path length and the time taken to reach the food item (or the far side of the arena in the case of moles that missed the food) were significantly longer (see Fig. 6) for animals with the crossed nostrils compared with the uncrossed nostrils.

Discussion

The series of experiments described above indicate that bilateral cues from the nostrils have an important role in the animal's ability to localized odorants. Results are similar to findings in the auditory system, where bilateral timing and intensity cues have an essential role in stimulus localization. In early landmark findings in barn owls, Knudsen and Konishi^{27,28} found that plugging an ear resulted in mislocalization of sounds in the direction of the open ear (erring primarily in elevation because of owls' asymmetric ears). In the case of olfaction, it seems most likely that bilateral cues act primarily at close proximities to the stimulus under normal

conditions. This follows the expectation²⁹, and recent experimental confirmation⁸, that olfactory gradients are steepest near the odour source, providing a stimulus configuration where short-distance (inter-nostril) comparisons would be most informative. Figure 7 provides a hypothetical search strategy illustrating the relative roles of serial spatial comparisons and simultaneous bilateral comparisons suggested by the present results (gradient shape based on data in Louis *et al.*⁸). At a distance in a shallow gradient, large movements and serial sampling of different areas in space provide directional information. At closer proximity, where the gradient is steep, shorter movements and bilateral nasal comparisons provide additional cues. Blocking a nostril provides a consistent 'pull' in the direction of the open nostril, biasing the animal in one direction. Crossing the nostrils puts the two normally complementary cues in continuous, dynamic conflict as the animal moves back and forth searching for the stimulus, accounting for a greater disruption. Such a two-tiered search strategy sensitive to the slope of a gradient may be relevant to a wide range of species and ecological niches. The present results provide additional support for findings^{8–10,30,31} that suggest that the integration of bilateral cues found in visual and auditory systems also occurs for chemosensory systems to guide stimulus localization.

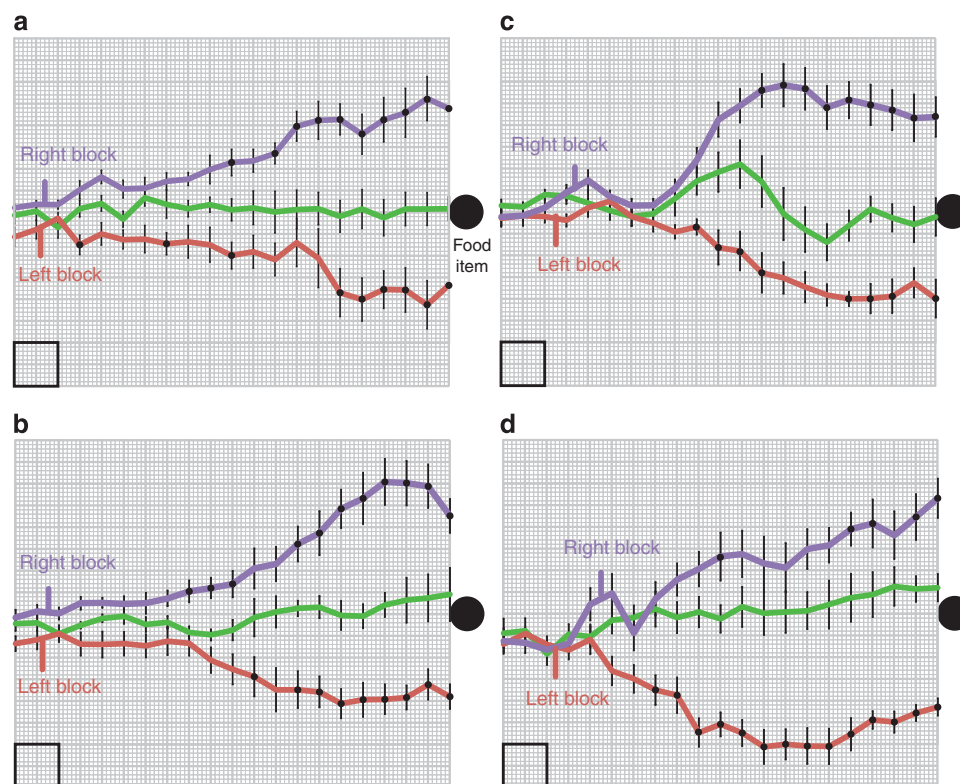


Figure 5 | Search paradigm with the food located in the same position for each consecutive trial. (a–c). Results of 10 trials for each of three conditions for four animals. Purple track is the average of 10 trials for the right-nostril block, red track is the average of 10 trials for the left-nostril block and green track is the average of 10 trials for an open tube in the left nostril as a control (see Supplementary Movie 6 for behaviour). Despite the uniform location of the food item in different trials, the animals were still biased to the side of the open nostril. Bars are s.e. of the mean. The filled dark circles mark points that were significantly different from the control open-tube condition using repeated measures analysis of variance followed by Tukey's HSD test for a 0.05 significance level. The dark square represents 1 cm². Animal no. 18, 19, 20 and 21, each correspond to panel a–d, respectively.

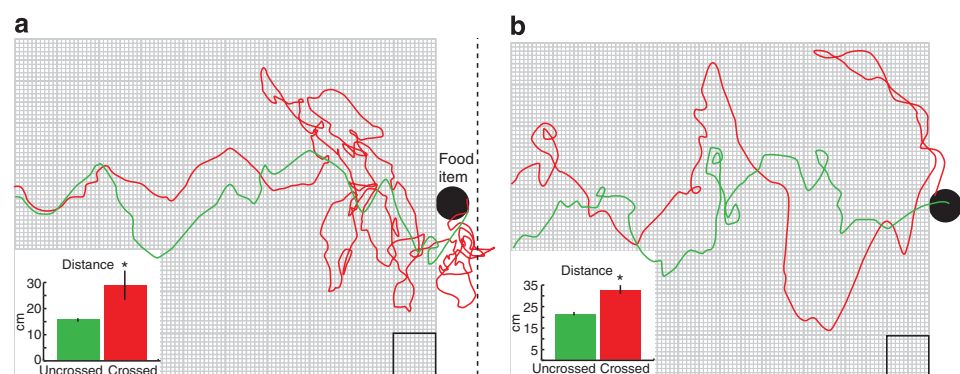


Figure 6 | Example of behaviour with crossed and uncrossed nostril tubes. (a,b) In the course of 10 trials for each condition, the distance travelled to reach the food (or a position 1 cm past the food as indicated by the dashed line) was significantly greater for the crossed nostril condition (two-tailed *t*-test, $P = 0.03$ for **a** and $P < 0.001$ for **b**). Time measurements are not shown as they were substantially equivalent to distance. The position tracked was the midpoint between the openings of the nostril tubes. The dark square represents 1 cm². Panel **a** corresponds to animal no. 19 and panel **b** corresponds to animal no. 20. (see Supplementary Movie 7). Bars are s.e. of the mean.

Methods

Specimens of *S. aquaticus*. Animals were collected in Davidson County under Tennessee Wildlife Resources Agency permit 1868. Moles were housed in plastic containers measuring approximately 60 cm long, 40 cm wide and 40 cm deep. These were filled to roughly 7 inches from the top with a mixture of commercially available potting soil and sphagnum. Dry leaves were added to serve as nesting material. The animals were fed commercially available nightcrawlers of the genus *Lumbricus*, supplemented occasionally with crickets and supplied with a water dish.

Experimental chambers. Experimental chambers were constructed of Plexiglass assembled with Weld-On fast set solvent (IPS Corporation, Gardena CA, USA). The length and width of the experimental chamber for the radial search paradigm

are shown in Fig. 1. The depth of the chamber was 9 cm. The white base material for holding the stimuli was composed of chemically inert polytetrafluoroethylene plastic, often used in the food industry as cutting boards. Grids and guides for scoring data were added to the base material by printing from Adobe Illustrator (Apple, Cupertino, CA, USA) onto 8.5 × 11 sheets of self-adhesive clear gloss (part no. IJG50 Chartpak, Leeds, MA, USA). After adhering the printed layer to the base material, a second clear layer of the same material was overlaid to protect the printout from repeated washing and cleaning in the course of the experiments. Small sections of earthworm were used as odour sources.

Video equipment. Experiments were filmed with a MotionPro HS-3 camera at 50 or 100 frames per second with two 19-led honeycomb stroboscopic illuminators

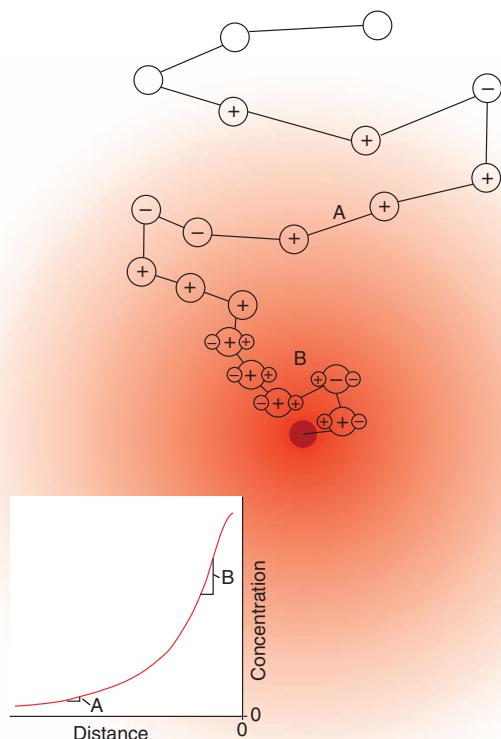


Figure 7 | Hypothetical contributions of serial and stereo olfactory sampling. Circles represent the location of sniffs and lines represent movement of the nose. Plus and minus in the large circles represent a comparison with the previous sniff during serial sampling. Small circles represent the contribution of bilateral cues close to the odour source where the gradient is steep. Lower left represents a hypothetical concentration gradient (drawn from data of Louis *et al.*⁸ for Fourier transform infrared spectroscopy after 2 min of diffusion).

(Integrated Design Tools, Inc.), and for infrared, using an IR-Flood Ultra-Covert 940 nm illuminator (Night Vision Experts, Buffalo, NY, USA). Video was transferred to a MacPro laptop using MotionProX (Integrated Design Tools, Inc.), and movies were created using Quicktime Pro (Apple, Cupertino CA, USA). For selected trials, respiration and sniffing were monitored using a PS-1000/A-004 differential transducer and a RESP-1 respiration monitor (CWE, Inc.) connected to a PowerLab 4/30 data acquisition unit using LabChart software (ADInstruments, Sydney Australia) while simultaneously recording camera TTLs (frame time-stamps) for correlation of video with recordings.

Behavioural experiments. Nostril blocks were made from Intramedic polyethylene tubing (Clay Adams) filled with President SEM casting compound (Ted Pella Inc. Redding, CA, USA) to close tubes. Open tubes were manually curved after exposure to hot water. Animals were briefly anesthetized with isoflurane until unresponsive for tube insertion. A cold metal mirror (Zwaardemaker mirror) was used to confirm airflow through the tube based on condensation. Trials were initiated by removing a blocking bar from the opening, separating the holding chamber and placing a small plastic cover over the hole from which the bar extended—approximately 1 min after the earthworm segment was placed in the well. For behaviour under normal conditions or with blocked nostrils, the position of the tip of the animal's nose was tracked. For trials with crossed or uncrossed tubes, the midpoint between the opening of the tubes was tracked. Manually traced tracks were scanned into Adobe Photoshop, sized and then placed into Adobe Illustrator to construct figures. Animals were removed between trials, and the experimental platform was cleaned. Significance was evaluated for animals in the radial area arena (Figs 1 and 2) using a Watsons-Williams F-test with the circular statistics program Oriana (Version 2; Kovach Computing Services, Pentraeth Anglesey, Wales, UK). Significant differences for animal tracks in Fig. 5 were assessed with a repeated measures analysis of variance followed by a Tukey's HSD test using a 0.05 significance level in JMP statistical software (SAS). Tracks in Fig. 5 were made by manually recording the position of the tip of the nose to the nearest millimetre as each half centimetre vertical grid mark was passed. Tracks for

animals in Fig. 6 were plotted from the time the midpoint between the nostril tubes crossed the first vertical line of the illustrated grid and continued until this point was over the food item, or passed the dotted line representing 11 cm on the x-axis (this is a conservative measure of the effect of nostril crossing, as some animals with crossed nostrils searched well beyond the 11-cm mark). All procedures were approved by the Vanderbilt University Institutional Animal Care Committee and are in accordance with the National Institutes of Health Guide to the Care and Use of Laboratory Animals.

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Author contributions

K.C.C. designed the experiments, conducted the experiments, analysed the data, constructed the figures and wrote the manuscript.

Additional information

Supplementary Information accompanies this paper on <http://www.nature.com/naturecommunications>

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