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Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds

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Petrels, albatrosses and other procellariiform seabirds have an excellent sense of smell, and routinely navigate over the world's oceans by mechanisms that are not well understood. These birds travel thousands of kilometres to forage on ephemeral prey patches at variable locations, yet they can quickly and efficiently find their way back to their nests on remote islands to provision chicks, even with magnetic senses experimentally disrupted. Over the seemingly featureless ocean environment, local emissions of scents released by phytoplankton reflect bathymetric features such as shelf breaks and seamounts. These features suggest an odour landscape that may provide birds with orientation cues. We have previously shown that concentrated experimental deployments of one such compound, dimethyl sulphide (DMS), attracts procellariiforms at sea, suggesting that some species can use it as a foraging cue. Here we present the first physiological demonstration that an Antarctic seabird can detect DMS at biogenic levels. We further show that birds can use DMS as an orientation cue in a non-foraging context within a concentration range that they might naturally encounter over the ocean.

Keywords: procellariiform seabird; dimethyl sulphide; navigation; orientation; Antarctic

1. INTRODUCTION

A variety of animals are thought to navigate extreme distances using olfactory cues, but how they do it is a mystery (Wallraff 2004). Progress in our understanding of olfactory navigation has been hampered by at least three major obstacles: (i) identifying a potential odour cue that can provide spatial information that could be useful for navigation; (ii) establishing a physiological sensitivity to the odour cue; and (iii) demonstrating that the odour can be used as an orientation cue within a reasonable concentration range. Working with procellariiform seabirds, we have previously identified dimethyl sulphide (DMS) as a biogenic cue that contributes to the natural olfactory landscape over the ocean (Nevitt *et al.* 1995, 2004). DMS is a scented compound produced by phytoplankton that has been studied extensively in the context of global climate regulation. Thus, unlike other biogenic odours, considerable

information is available about its distribution across the world's oceans. For example, mesoscale spatial patterns of atmospheric DMS are known to reflect bathymetric and oceanic features including shelf breaks, seamounts and oceanic frontal zones (Berresheim 1987). Moreover, these odour features are not ephemeral, but can persist for several days or weeks, and show seasonal predictability suggesting that they might provide cues for orientation if seabirds can detect them. This study is the first to establish that a procellariiform seabird can physiologically detect DMS. We further show that birds can use DMS as an orientation cue in an unfamiliar context at concentrations that they might normally encounter at sea.

2. MATERIALS AND METHODS

We performed our experiments on Ile Verte (49°51' S, 70°05' E, ~1 km dia.) in the gulf of Morbihan in the Kerguelen Archipelago. We chose Antarctic prions, *Pachiptila desolata*, for this investigation because at-sea studies indicate that prions respond to (Nevitt *et al.* 1995) and naturally associate with DMS (Nevitt 2000), suggesting that they can smell it and potentially use it as an orientation cue. Experiments ran from 17 to 28 January 2004, midway through incubation (between 15 and 25 days in; incubation lasts for roughly 44 days) when prions could easily be retrieved from burrows for experimentation. Birds were banded prior to the study to identify individuals. Each study was tested only once.

(a) Physiological experiments

To test odour responsiveness, we monitored changes in heart rate upon exposure to DMS. Testing was done during daylight hours at ambient temperatures (10–14 °C) in a remote field hut built for experimentation. The field hut was positioned approximately 200 m southeast of the study colony and 100 m up an embankment from the sea.

For each experiment, a bird was carefully removed from its burrow and transported to the hut where it was weighed and fitted with two superficial electrocardiogram electrodes (coated with water-soluble conducting gel) at the base of the neck and on the rump. The bird was then carefully attached to a supporting beam using an ACE bandage, and transferred to a ventilated acoustically isolated chamber. The bird's beak was then positioned in a hand-blown glass ventilation tube. This tube provided the bird with a constant air stream (1500 ml s⁻¹). A second continuous (10 ml s⁻¹) air flux delivered DMS or control stimulus via a system of bypasses (Benvenuti *et al.* 1992). Thus, the main air stream could be mixed either with odour or blank (control). When not in use, we shunted this second air stream to an exhaust. We monitored heart rate using a modified Vetronics ECG monitor (ERM-8010).

The bird was allowed to adjust for approximately 30 min, or until the heart rate stabilized (350–480 bpm). We then averaged heart rate at 1 min intervals for 15 min to establish a measure of variability in resting heart rate. Next, we delivered either an odour or blank stimulus for 30 s while heart rate was continuously recorded. Records were averaged at 1 min intervals for 2 min immediately following stimulus onset. The procedure was repeated for one odour and one blank on a total of 10 birds. The order of presentation was balanced among test subjects such that five birds received the odour first and five birds received the blank first. To minimize handling stress, we tested each bird only once and returned it to the colony within one hour of collection. The procedure seemed to have no long-term deleterious effects: the morbidity rate was zero and the rate of nest abandonment among birds used in experiments was indistinguishable from that of the background population of prions at Ile Verte.

To evaluate the cardiac responses to test stimuli, we examined the differences between heart rates before and after odour stimulation using established methods (Benvenuti *et al.* 1992). We first calculated the confidence interval for natural fluctuations in the resting heart rate before either stimulus was applied. We then noted whether changes in resting heart rate fell outside this confidence interval following odour or control stimulation.

Because empirical measurements of DMS were not practical to take at Ile Verte, the apparatus was designed so that headspace concentration, C_H , could be estimated using previously established methods (Dacey *et al.* 1984). The secondary air stream passed through a flask containing either DMS (100 ml, 10 μM) or distilled water. We assumed an equilibrium coefficient, K , of 15–20

corresponding to a temperature range of 10–14 °C, at 1 atm. Here, $C_H \approx 10 \mu\text{M}/15$ to $10 \mu\text{M}/20 \approx 0.5$ to $0.6 \mu\text{M l}^{-1}$. This concentration was diluted by 150 ($10 \text{ ml min}^{-1}/1500 \text{ ml min}^{-1}$), to a level of $3\text{--}4 \text{ nM l}^{-1}$ at the birds' bill.

(b) Behavioural experiments

We next determined whether individual prions would orient to DMS in a non-foraging context. Here we presented birds with DMS in an opaque PVC Y-maze positioned near the lab hut. We reasoned that if DMS constituted a familiar orientation cue, then birds should respond to it in a novel context. Thus, in a Y-maze set up, prions might recognize DMS as a familiar sea-smell, and be motivated to orient to it as a possible exit out of the maze.

The Y-maze design has been described elsewhere (Bonadonna & Nevitt 2004). In brief, the maze was constructed from opaque PVC wire housing and had three symmetrical arms. One arm was used as the starting point and was fitted with two trap doors that formed a temporary holding compartment for the test subject. The end of each odour choice arm was equipped with a separate compartment for the stimulus, in this case a Petri dish (5.5 cm diameter) containing either DMS ($1 \mu\text{M ml}^{-1}$, 4 ml) or control solution. This compartment was also accessible via a trap door to the outside. At 20 cm from each end, a CPU cooling fan (Globe Fan Technology Co. Ltd., product number S05010, Taiwan) was mounted on a second partition to provide a low-noise controlled airflow (9 CFM ; 2431 min^{-1}) through each choice arm. Thus, the bird did not have direct access to either Petri dish, but was in contact with air flowing over each dish at a constant rate. The maze was washed thoroughly with methanol (70%) after each trial to remove any odour residue; odour stimuli were alternated between arms for each trial and frequently exchanged with fresh solutions. These procedures eliminated possible biases between either the choice arms themselves or their relative positions with respect to physical features in the environment.

DMS solution was prepared in ethylene glycol (4 ml ; $1 \mu\text{M ml}^{-1}$); control solution contained ethylene glycol only (4 ml). Ethylene glycol was used because this compound is lightly scented, so birds had to discriminate between two scented compounds rather than between the presence or absence of odour. Second, DMS is much more soluble in ethylene glycol than in water. In an open system, this situation is preferable because gas flux is reduced and evaporation rate can be used to calculate stimulus concentration in the maze. Thus, the evaporation rate ($\sim 0.1 \text{ ml h}^{-1}$ or 1.7 nM min^{-1}) diluted by air flow in the maze (2401 min^{-1}) suggests that prions were presented with an average stimulus concentration of less than 10 pM during experimental trials. This concentration is undetectable to humans and falls well within estimates of biogenic emissions encountered at frontal zones close to the ocean surface where seabirds fly (Berresheim 1987; Sciare *et al.* 1999; Nevitt 2000).

As in earlier experiments, prions were captured and tested one at a time. Each bird was away from its nest for a maximum of 30 min and, as with the physiological experiments, we noted no deleterious effects on breeding success. Based on their relative mass, test subjects tended to be well fed (body mass (mean \pm s.e.): $152.7 \pm 3.7 \text{ g}$), and most of them had only recently returned from lengthy (~ 12 day) foraging trips.

To begin an experimental trial, a bird was removed from its burrow, transported to the maze and then placed in the entryway for a 5 min acclimation period. An inner trap door was then lifted for the bird to make a choice. Birds tended to stay in the intersection prior to choosing, and could be heard sweeping their heads back and forth as if sampling each arm. We assessed arm choice by the sounds of the bird walking in the maze, without disturbing the bird. We scored a positive choice if the bird travelled halfway down an arm and stopped for at least 2 min; however, most birds stopped at the end of the arm and remained there. No-choice birds either never settled down or sat quietly in the entryway, facing backwards towards the exit. These birds were removed from the maze after 15 min.

3. RESULTS

(a) Physiological experiment

We found that DMS ($3\text{--}4 \text{ nM}$) triggered a consistent increase in heart rate at the 0.01 confidence level for 10 out of 10 birds tested. By contrast, control stimulation never elicited a measurable change in heart rate, even within a less conservative confidence estimate of 0.05 (figure 1a). To our knowledge, this is

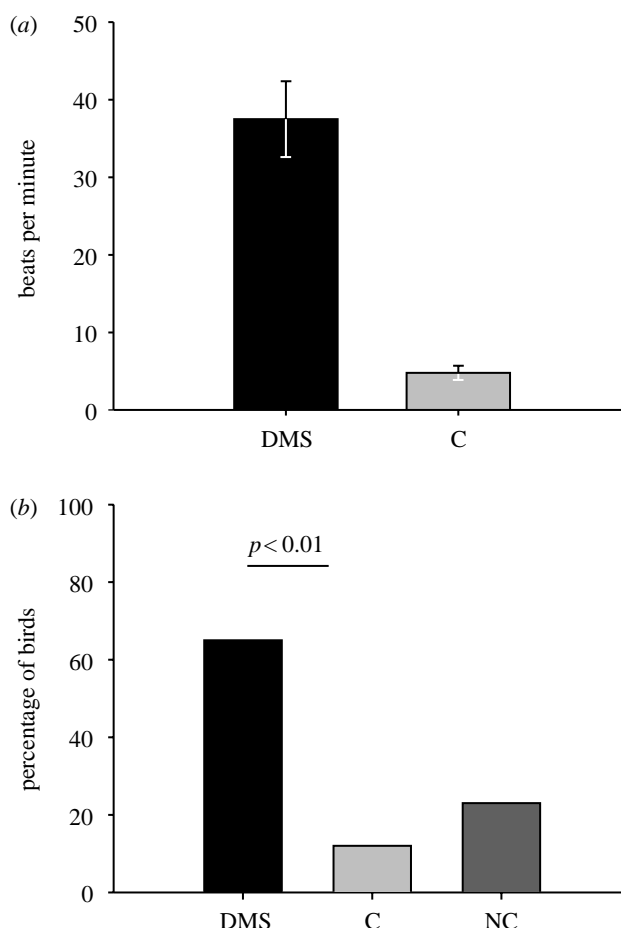


Figure 1. Physiological and behavioural responses to DMS. (a) Mean change in heart rate (expressed in $\text{beats min}^{-1} \pm$ s.e.) across 10 prions tested in response to DMS or control (see §2). (b) Orientation to DMS in a Y-maze. Each histogram shows the percentage of birds that chose DMS, control (C) or did not choose (NC) in Y-maze tests performed at Ile Verte.

the first report of an unconditioned somatic response of a bird to an identified biogenic odour at concentrations appreciably less than $1 \mu\text{M}$ (Roper 1999).

(b) Behavioural experiments

Of the 25 birds tested, 20 successfully made a choice. Seventeen oriented to DMS whereas three oriented towards control (binomial test, $p < 0.01$; figure 1b). Choices were typically made within 1.5 min (mean \pm s.e.: DMS: $67.6 \pm 12.5 \text{ s}$; control, $79.3 \pm 21.4 \text{ s}$). Five birds did not choose an arm but stayed in the entryway of the maze, facing the exit door to the outside of the maze. No-choice birds were removed from the maze after 15 min and returned to the colony.

4. DISCUSSION

The most detailed investigations of orientation by olfactory cues in birds have been done on pigeons, swifts and starlings (Wallraff 2004). While considerable evidence suggests that pigeons, in particular, can use olfactory maps to assist them in navigating over large (hundreds of square kilometres) spatial scales, olfactory orientation has often been challenged on purely conceptual grounds. Odours are assumed to be dynamic and ephemeral and not easily translatable

into spatial information useful for navigation. Elucidating a mechanism requires identifying tractable naturally derived odours that can be shown to occur along relatively stable or predictable spatial fields at concentrations that birds can smell (Wallraff & Andreae 2000).

Thus, the identification of DMS as a biogenic odour that is detectable to a procellariiform provides a fundamental advance in our ability to begin to understand how olfactory information might be used as an orientation aid at large (hundreds to thousands of square kilometres) spatial scales in these birds. Oceanic DMS constitutes the principal source of natural sulphur in the atmosphere. Because DMS is critical in the regulation of global climate, considerable effort has focused on understanding its production and patchy distribution, particularly in the southern oceans where primary productivity tends to be high. For example, spatial variability in surface seawater DMS concentrations has been documented in summer in the southern Indian Ocean in the Crozet–Kerguelen region. Here, the concentration profile shows spatially discrete peaks and valleys ranging in concentration from 0.9 to 35.8 nM, with maximum levels associated with series of discrete frontal zones and the Crozet and Kerguelen plateau regions (Sciare *et al.* 1999). Atmospheric background concentrations were not measured as part of this study, but correlate strongly with seawater concentration and with marine heterogeneity (Zemmelink *et al.* 2002). It is well established that emissions produce local elevations in atmospheric DMS (Dacey *et al.* 1984; Zemmelink *et al.* 2002), which are detectable within a few metres of the ocean surface where procellariiforms fly. An ability to identify or discriminate such features by scent could conceivably provide seabirds with spatial or positional information to assist orientation over a seemingly featureless ocean (Wallraff & Andreae 2000). This idea is attractive since it has recently been shown that several species of albatrosses (black-browed (*Diomedea melanophris*), waved (*D. irrorata*), wandering (*D. exulans*)) and white-chinned petrels (*Procellaria aequinoctialis*) do not require magnetic cues for orientation or navigation (Benhamou *et al.* 2003; Bonadonna *et al.* 2003, 2005; Mouritsen *et al.* 2003), suggesting that procellariiform seabirds must also utilise other senses (Nevitt 2000).

In summary, our research (i) identifies DMS as a biogenic odour cue that can provide spatial information over the ocean, (ii) establishes a physiological sensitivity to this odour cue, and (iii) demonstrates that DMS can be used as an orientation cue in an experimental context within biologically appropriate concentration parameters. Taken together, our work provides the most comprehensive demonstration to date that an animal can detect a naturally occurring odorant potentially useful for orientation and navigation over the world's oceans.

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