

Figure 2 | Vertical position of, and force exerted by, a 27-kg load carried by a hiker walking at 5.6 km h⁻¹. **a**, The displacement of the load (*L*) with the locked backpack (left panel) is equal to the displacement of the frame (*F*) plus the displacement of the load relative to the frame (*R*). Vertical movement of the load (*L*) with the suspended backpack (right panel) is reduced because the load moves down in the frame (*R*) to compensate for the upward movement of the frame (*F*). **b**, The large vertical displacement of the locked backpack (left) requires large accelerative forces (AF) — the difference between the total vertical force and the weight (red dotted line) to be exerted on the load by the frame; the load, in turn, exerts large forces back on the walker. With the suspended backpack (right), therefore, little accelerative force is required. The double-support and single-support ('inverted pendulum') phases of walking are shown for the first step.

backpack is equivalent to walking with 21.7 kg in the locked backpack in terms of metabolic cost, so — for a given metabolic rate — the suspended backpack enables a substantially heavier load to be carried (a mean of 5.3 kg ± 3.4 kg more, $n = 6$; see table in supplementary information). These findings show that a passive device can make the energetic cost of carrying loads more economical^{1,6,7}.

The large weight of backpacks carried by children is internationally recognized as a public health problem^{8–10}. Lower peak vertical forces during load carrying could reduce muscle and orthopaedic injury. Total peak vertical forces are even more harmful during running, reaching more than three times the static force of the load. The suspended backpack cuts the vertical oscillation of the load from 77.8

to 26.0 mm ($P < 0.001$, paired t -test, $n = 5$; see table in supplementary information), reducing accelerative forces by 86% (s.d. ± 8%, $n = 5$) and total peak vertical force by 60%, thereby greatly easing discomfort. Being able to run with this backpack, rather than being forced to walk, would be particularly useful to emergency personnel who need to carry equipment rapidly to disaster sites.

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OLFACTION

Underwater 'sniffing' by semi-aquatic mammals

Terrestrial species that forage underwater face challenges because their body parts and senses are adapted for land — for example, it is widely held that mammals cannot use olfaction underwater because it is impossible for them to inspire air (sniff) to convey odorants to the olfactory epithelium^{1–5}. Here I describe a mechanism for underwater sniffing used by the semi-aquatic star-nosed mole (*Condylura cristata*) and water shrew (*Sorex palustris*). While underwater, both species exhale air bubbles onto objects or scent trails and then re-inspire the bubbles to carry the smell back through the nose. This newly described behaviour provides a mechanism for mammalian olfaction underwater.

High-speed video recordings of star-nosed moles reveal that they continuously emit and re-inhale air from their nostrils while foraging underwater (Fig. 1; for videos, see sup-

plementary information), indicating that they could be 'sniffing' odours while submerged. To test this idea, moles were trained to follow an underwater scent trail that was randomly laid on either of two paths leading to food (for details of methods, see supplementary information). Trails were laid in a channel covered with a steel grid that allowed the air bubble to pass through it, contact the scent trail, and be re-inhaled, while at the same time preventing contact with the mole's star nose (see video in supplementary information).

The five moles tested on an earthworm scent followed the underwater scent trails to reach a reward with an average accuracy of 85% (ranging from 75% to 100% correct for the 20 trials used for each mole; Fig. 2a), and the two moles tested on a fish scent followed the smell with 85% and 100% accuracy, respectively (see supplementary information).



Figure 1 | Star nose of the mole (*Condylura cristata*) breathing air while underwater. Bubbles are of comparable size to 'sniff' volumes above water in small mammals.

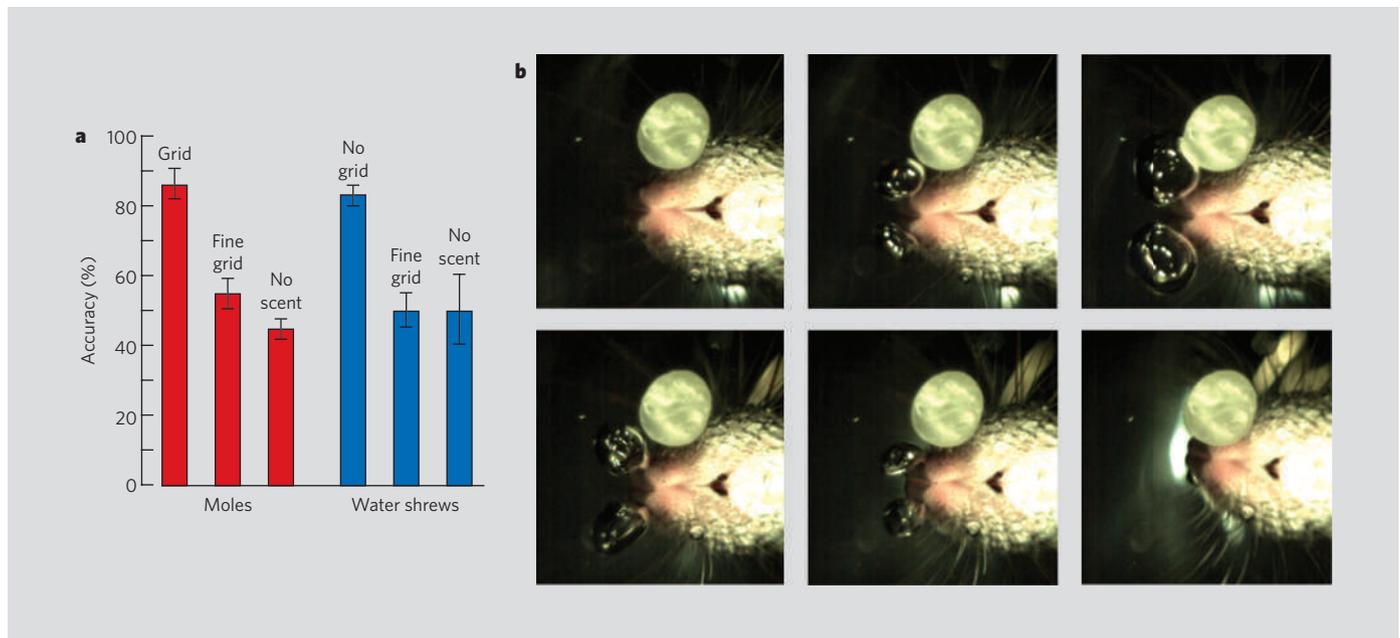


Figure 2 | Underwater olfaction in semi-aquatic moles and shrews. **a**, Results of tracking of scent trails (20 trials per experiment) by the star-nosed mole (*Condylura cristata*) and by the water shrew (*Sorex palustris*). Performance was significant ($P \leq 0.05$ s.e.m. is indicated for each bar) for moles (red bars) sniffing through a grid ($n = 5$) and for water shrews sniffing in the absence of a grid (blue bars, $n = 2$). Performance was at chance when bubbles were blocked with a fine grid ($n = 3$), or when the trail had no scent. **b**, Underwater sniffing by two water shrews. The bubble is in contact with a wax object (green). Top panels, expiration; lower panels, inspiration.

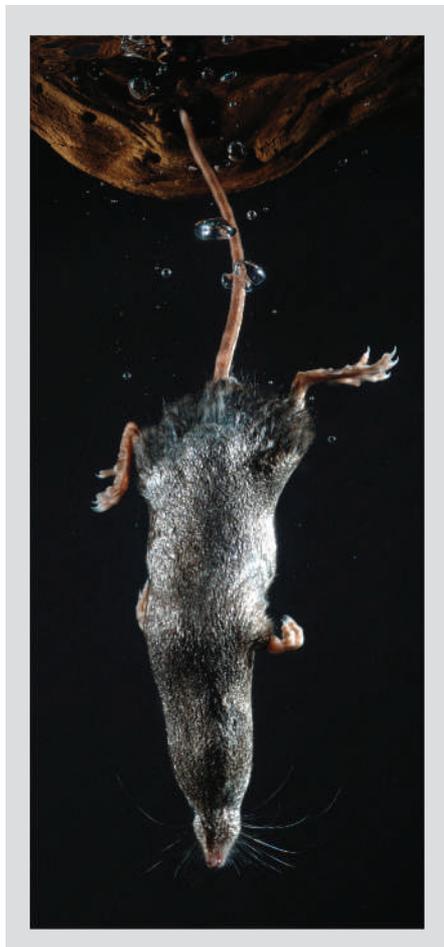


Figure 3 | A diving American water shrew (*Sorex palustris*). This semi-aquatic species has water-repellent fur and is the smallest mammalian diver.

Three moles were also tested with a grid of finer mesh that prevented bubbles from contacting the scent trail. Their performance dropped to chance (that is, 50% in a two-choice test), suggesting that close proximity or contact of the bubbles with the odorants was also at chance for two moles when there was no scent trail to follow (Fig. 2a).

Star-nosed moles therefore seem to have adapted their olfactory system for use underwater. To test whether other semi-aquatic mammals might show the same behaviour, I investigated whether the water shrew (Fig. 3) uses a similar strategy. Four water shrews were each seen to emit and re-inhale bubbles that were frequently in contact with objects before being re-inhaled (Fig. 2b, and see video in supplementary information).

Two water shrews were trained to follow an underwater fish-scent trail. No grid was used to prevent direct contact with the scent, because the nose of these animals does not physically permit sniffing through a grid; they depend on their whiskers, or vibrissae⁶, for exploratory contact, unlike the mole, which uses its sensitive star nose. One shrew was accurate in 80% of trials and the other in 85% of trials, and both performed at chance when a blocking grid or a no-scent trail was used (Fig. 2a). These findings show that water shrews are also able to use olfaction underwater.

Can the observed behaviour be classified as 'sniffing' underwater? The volumes of air that are expired and re-inspired (0.06–0.10 ml), the rate of airflow (5–6 ml s⁻¹), the frequency (8–12 Hz) and the context (while exploring an object or pausing) were all remarkably simi-

lar to sniffing, as described in air^{7,8}. Rats, for example, sniff at a similar frequency (4–12 Hz) and airflow rate (5 ml s⁻¹) and, corrected for body weight, by using comparable volumes of air (0.25 ml)⁹.

These results call for a reassessment of the assumption that olfaction is useless underwater and raise the possibility that air could be an intermediate substrate for odorant transport in other aquatic animals as well.

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