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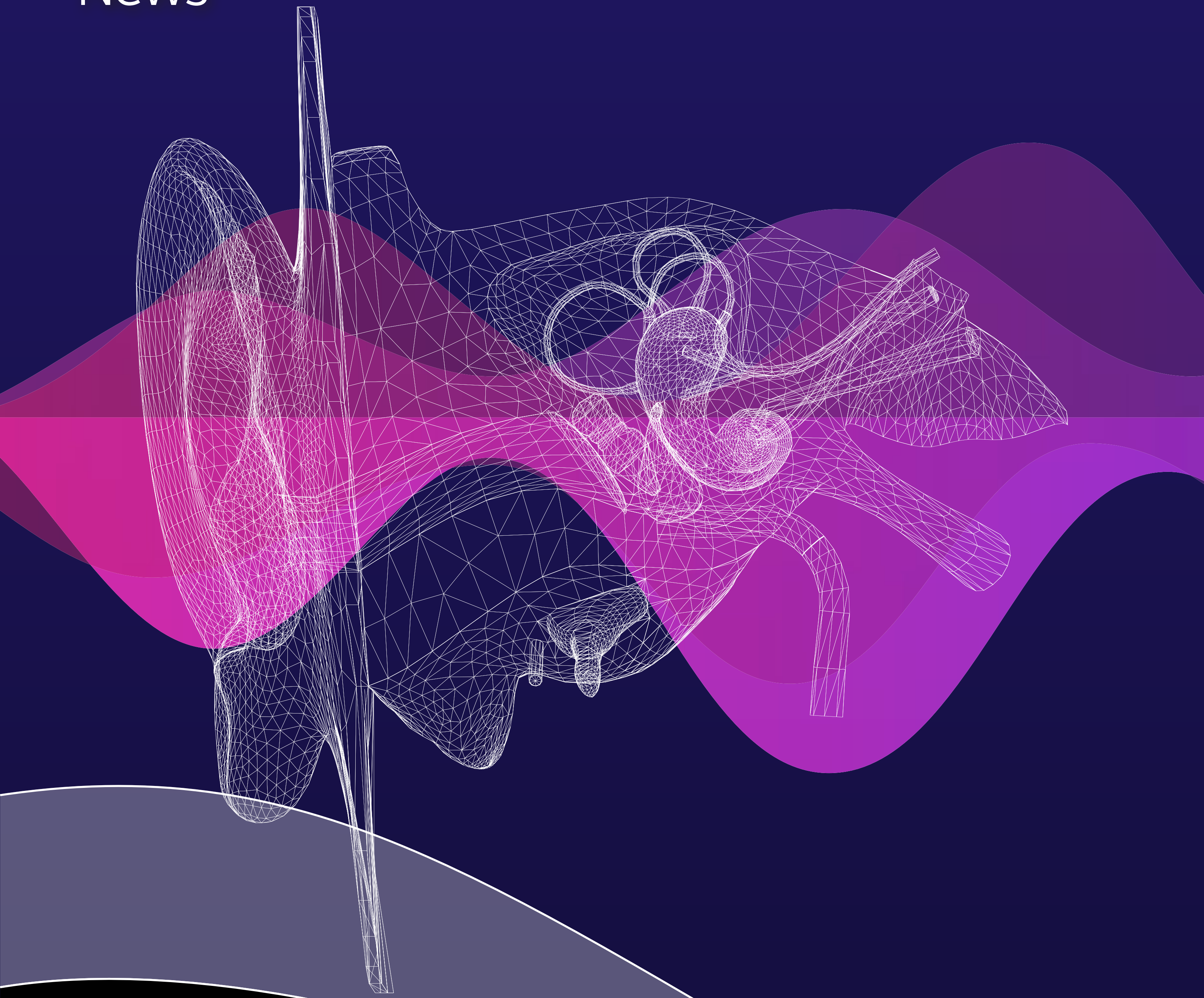

Sensory Systems Special Issue:
Delving into the physiology of sensation

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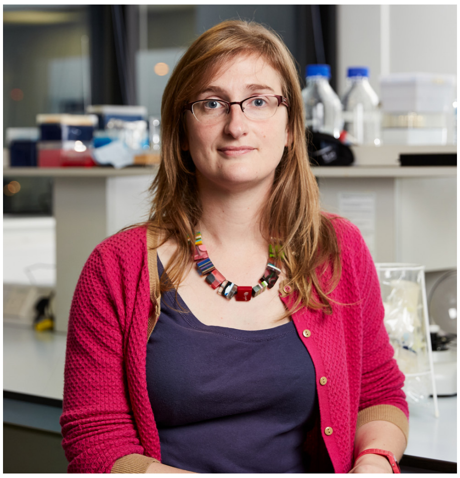
Why don’t we have whiskers?

What we can learn from mammalian whisker touch sensing



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I am a sensory biologist, specialising in whisker touch sensing. My job is to try to understand what animals perceive from their whisker sensations. It is a challenging job, made even harder by not being able to draw parallels from my own experiences – while most mammals have whiskers, humans, along with rhinos and some species of apes and cetaceans, do not. Most whisker research has focused on laboratory animals, such as rats and mice, and some species of zoo animals, such as seals. It is only now that we are beginning to study whiskers comparatively (Grant and Goss, 2022). By looking at lots of mammalian species, we are starting to truly understand which species have whiskers and why. Therefore, we can start to answer the questions *why don’t we have whiskers?* And *why should we care about them?*

What are whiskers?

The whiskers I will focus on in this article are mystacial whiskers – the whiskers on the moustache area of mammals. There are lots of different types of whiskers, including around the jaw, chin, eyes and feet, but mystacial whiskers have garnered the most attention from researchers because they are the longest and can also be moved. However, we are only starting to understand what the mystacial whiskers can do and the function of the other types of whiskers are still poorly understood (Fig.1, Table 1).

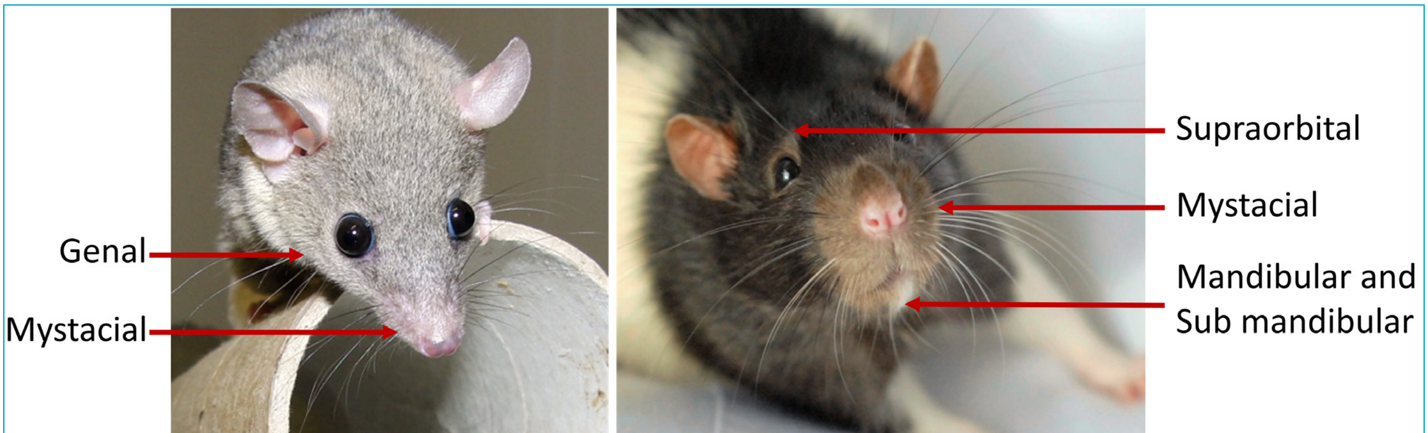

Figure 1. Different types of whiskers of grey short-tailed opossum (left) and brown rat (right) (photographs: Active touch sensing lab, University of Sheffield, Sheffield, UK)

Whisker	Location	Possible function
Genal	Cheek	Unknown
Mystacial	Moustache area	Guiding locomotion, foot placemants, foraging, exploration
Supraorbital	Above eyes	Unknown – possibly eye protection
Mandibular/submandibular	Jaw and under chin	Detection of self-motion i.e. speed
Leg/Foot	Leg/Foot	Guiding foot placements

Table 1. Different types of whiskers and their suggested functions.

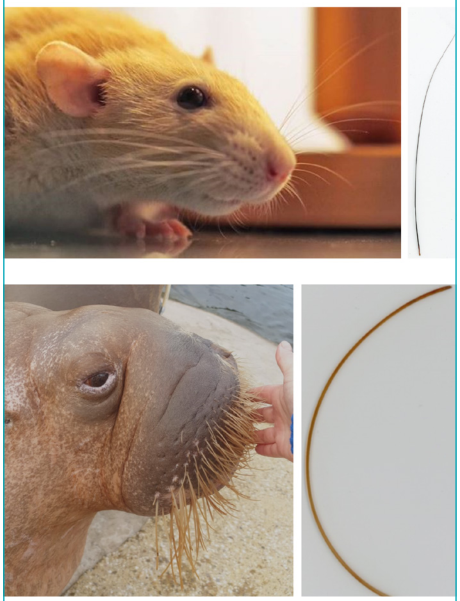

Figure 2. Top: A brown rat (Photograph: Maria Panagiotidi, University of Salford, Salford, UK) and an isolated rat whisker (26 mm long). Bottom: A Pacific walrus (photograph: Alyx Milne, Dolfinarium Harderwijk, Harderwijk, the Netherlands) and an isolated walrus whisker (74 mm long).

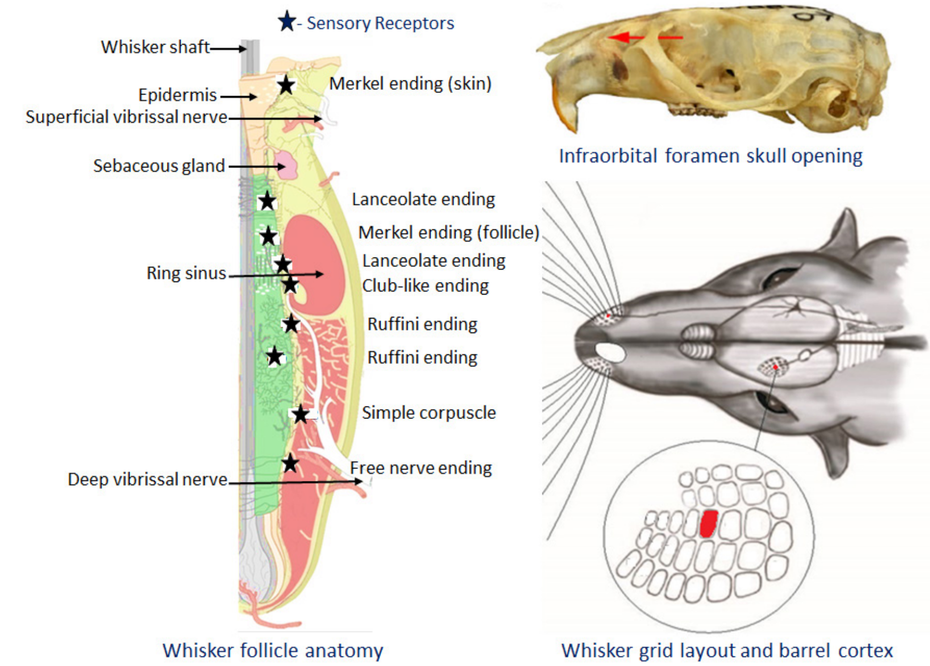

Figure 3. Left: whisker follicle anatomy (Diagram modified from Ebara *et al.,* 2017, Scholarpedia, under CC-BY-SA 3.0); stars correspond to sensory receptors with their nerve ending types labelled beside them. Each follicle is innervated by two sets of nerves – the deep and superficial. Most deep vibrissal nerves are myelinated, and most superficial nerves are unmyelinated. Right: infraorbital foramen and example topographic brain structures (Illustration: Geoff Goss, London South Bank University, London, UK).

Whiskers are similar in structure to hair and fur, although they are typically a little thicker and longer than other hair. Whiskers are made of keratin, and are flexible, tapered and curved (Fig.2) (Dougill *et al.,* 2020). These properties are likely to help them to deform and vibrate against different surfaces, which is better for sensing. Mammals that live in aquatic environments have thicker and stiffer whiskers than terrestrial mammals (Fig.2), probably to make sure they can be accurately positioned in high-drag aquatic environments (Dougill *et al.,* 2020).

How do whiskers work?

What really sets whiskers apart from other hair, such as fur, are their specialised follicles. Much like our hair, the whisker itself cannot "feel". Rather, the hair sits within a complex and sensitive follicle, called the follicle sinus complex (Ebara *et al.,* 2017). Each follicle is surrounded by large blood sinuses, which is why mystacial whiskers are sometimes called sinus hairs (Fig.3). The follicle is densely innervated by a variety of different nerve fibres (Fig.3) that can translate whisker vibrations into neural information. As the whiskers are deformed, such as by contact or water movement, these deformations are detected by the different nerve endings in the follicle and are conveyed as spike impulses to the brainstem (trigeminal nuclei). Properties of whisker deformation, such as which whisker was deformed, and the force, duration and direction of deformation are all useful properties that are detected and encoded by these nerves.

This information from the whisker follicle travels via the deep vibrissal nerve to the infraorbital nerve – a division of the trigeminal nerve. The infraorbital nerve passes through a small skull opening – called the infraorbital foramen – and into the brain

Whiskers can be moved in quite complex patterns too, including changing their spread, speed and position. It is thought that, much like our fingertips, whiskers are an active touch sensing system.

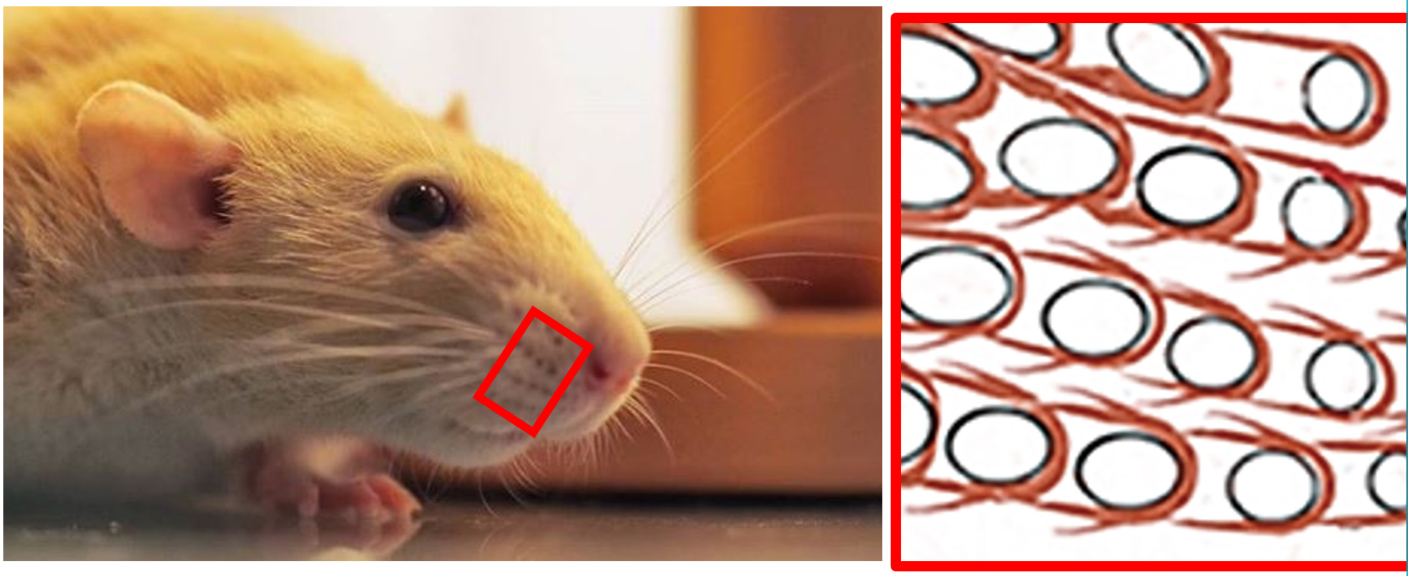

Figure 4. Whiskers and whisker intrinsic muscles. Left: Photograph of a brown rat (Photograph: Maria Panagiotidi, University of Salford, Salford, UK); Right: Magnified illustration of the whisker muscles within the red box from the photograph. Black circles correspond to individual whisker follicles. The brown sling muscles around every follicle are the intrinsic muscles. Follicles within the same row are coupled together via their intrinsic muscles.

(Fig.3). Whiskers can vary in numbers from 4 in porpoises, to around 300 in walruses and several thousand in manatees. Animals with more whiskers have a larger infraorbital nerve and foramen, since more whiskers tend to carry more sensory information. Therefore, the size of this skull opening is a good proxy of how sensitive an animal's whiskers are (Muchlinski *et al.,* 2020).

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Whiskers are arranged in a grid-like pattern on an animal's face, in rows and columns (Fig.3). In some species, this same pattern can be seen throughout the brain in physical structures called barrelettes in brainstem, barreloids in thalamus and barrels in cortex (Fig.3). This one-to-one mapping of whiskers to topographic structures in the brain has fascinated neuroscientists for decades as they are able to trace a sensory signal from an individual whisker follicle, all the way from the trigeminal complex through the brain to the cortex (Fig.3). This has established whisker touch sensing as a useful model for understanding sensory processing in the brain (Grant and Goss, 2022).

Whiskers do not just sense, they can also move. In most species, each whisker has its own individual intrinsic muscle (Fig.4), which contracts to move the whiskers forward. Some animals, such as rats and mice, move their whiskers forward and backward, almost constantly, in a process called *whisking*. This occurs at around 8 times per second in rats, and 25 times per second in mice, which are amongst the fastest movements that mammals can make! This muscle architecture is present across mammals, from marsupials to primates, but is absent in some species, including deer, horses, diurnal primates, apes and humans (Muchlinski *et al.,* 2013). Humans even have some vestigial muscle remnants just above our lips, in the moustache area, although they are probably not functional.

As well as simple scanning motions, whiskers can be moved in quite complex patterns too, including changing their spread, speed and position. It is thought that, much like our fingertips, whiskers are an active touch sensing system. They are moved across objects to focus on important (salient) features to identify and distinguish between objects. For instance, by feeling around the edges of things that are differently sized and stroking across the surfaces of different textures (Milne *et al.,* 2021), in much the same way that we would do with our fingertips.

Why don't humans have whiskers?

Perhaps the high sensitivity and mobility of our own fingertips means that they play a similar role to whiskers and is one of the reasons why humans don't need whiskers. Certainly, it is challenging to answer the question *why don't humans have whiskers*?

One way to approach the question is to look at the animals that have great whiskers – those with long, numerous whiskers, with large infraorbital foramen and lots of intrinsic muscles. These species tend to forage in dark, complex habitats, such as underwater (e.g. seals and sea lions) or be nocturnal, climbing specialists (e.g. mice and shrews) (Muchlinski *et al.,* 2020). Indeed, many small, quadrupedal mammals use their whiskers during walking and climbing to guide safe foot placements in the dark (Grant *et al.,* 2018). Therefore, perhaps being upright makes whiskers useless for us, as they cannot be positioned ahead

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of our movements to guide locomotion and foraging.

In addition, we notice that more diurnal or visual mammals have fewer whiskers, which are also less organised with fewer whisker muscles (Grant and Goss, 2022). Therefore, perhaps our reliance on other senses, such as vision, also make whiskers less useful for us. Odontocete cetaceans (such as dolphins) have very few, or no whiskers, with no intrinsic whisker muscles, as echolocation is instead an important sense for them. We also see that while nocturnal primates have whiskers and intrinsic muscles, diurnal primates have fewer whiskers with no muscles, and whiskers are entirely absent in some apes and humans (Muchlinski *et al.,* 2013). Being upright, relying on vision, and having sensitive and moveable hands and fingers, probably makes whiskers a less important sense for humans.

What can we learn from studying whiskers?

Neuroscientists use whiskers as a model to address fundamental questions around sensory processing in the brain. Most drugs and treatments are developed in laboratory rats and mice before human trials. We have found that measuring whisker positions and movements in these animals reveals impacts from disorders such as Motor Neuron Disease, Huntington's disease, Parkinson's disease, Alzheimer's disease, Cerebellar Ataxia, Somatosensory Cortex Development Disorders and Ischaemic stroke (Simanaviciute *et al.,* 2020). We notice that whisker movements can be impacted earlier than any other behavioural measure (including balance beam tests, swim tests and gait analysis). By looking at whisker movements in these animals, we may be able to detect diseases and treatment effects earlier.

As well as applications for human neuroscience and disease, whisker research is also driving technological innovation too. The aerodynamic shape of seal whiskers has been used to inspire wind turbine blades (Ahlman *et al.,* 2020). There are also many tactile whiskered sensors and robots being developed for a wide range of medical, industrial and environmental applications, such as underwater exploration of archaeological sites, autonomous inspection of off-shore wind and wave generators and environmental monitoring of ocean currents.

Why should we care about whiskers?

Whiskers can also give important insights in animal biology and evolution. Comparative studies looking at the infraorbital foramen of extant and extinct mammals suggest that the first mammals are likely to have had functional whiskers and even the ancestors of mammals, the therapsids, may also have had whiskers (Muchlinski *et al.,* 2020; Grant and Goss, 2022). In addition, the importance of whiskers to nocturnal and aquatic mammals in guiding their feeding and locomotion behaviours has huge implications for captive mammals. Sometimes whiskers can be lost, for example, rats and mice can engage in barbering, where a dominant animal removes the whiskers of their subordinate cage mates. I have seen this especially in some strains of female mice. Whisker removal reduces the social and locomotor functioning of an animal. It is extremely stressful and negatively affects brain development. Rats and mice without whiskers walk with a shrunken posture, struggle to balance and swim and do not engage in fighting; therefore, whisker barbering probably establishes a dominance hierarchy (Grant and Goss, 2022). Mother cats sometimes trim their offspring's whiskers, perhaps to establish a dominance hierarchy or to keep the kitten close to the nest. We need to make sure that whiskers are stimulated in captive animals that rely on their whiskers, perhaps by increasing tactile stimuli around their enclosures and designing feeding enrichment to encourage natural whisker movements (Grant and Goss, 2022). This might be something for all of us to try with our pets at home, especially if you have cats, rabbits, guinea pigs or hamsters – as these all have quite prominent whiskers.

As well as the direct applications of my whisker research, studying whiskers has also given me lots of surprises too. Did you know that in Guiana and bottlenose dolphins, their whiskers fall out and the remaining follicles then become electrosensors (Hüttner *et al.,* 2021)? And that the whiskers of all species that we have tested so far fit to the shape of an Euler spiral (Dougill *et al.,* 2020)? This is a shape whose curvature changes linearly with its length and was first described by Leonhard Euler in 1744.

I truly think that whisker science has the power to inspire us all by demonstrating the complex and ingenious innovations of the natural world. While it is still a challenge for us to picture how a rat whisker "feels" or how a dolphin electrosenses, we can wiggle our fingers around, think very hard, and try our best to understand it all.

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