Inside JEB is a twice monthly feature, which highlights the key developments in the *Journal of Experimental Biology*. Written by science journalists, the short reports give the inside view of the science in JEB.

Inside JEB

NEUROSENSORY ECOLOGY IN THE JEB

It is often difficult to imagine how other people perceive the world, let alone other species, so when Ken Lukowiak was approached by The JEB's Editor in Chief, Hans Hoppeler, to draw together reviews discussing Neurosensory Ecology, he decided to steer clear of the usual sensory topics. Taking an alternative perspective, Lukowiak identified scientists who wish to understand how other creatures perceive the world through sensory systems that we can only imagine.

Edited by Ken Lukowiak and Janis Weeks, the articles in this issue of *The Journal of Experimental Biology* touch on acoustic and balance systems, visual perception in low light, olfaction, magnetoperception and predator–prey interactions. Several articles also discuss the evolution of sensory systems and the complex processing systems which ultimately extract information from sensory stimuli.

SENSORY REALMS IN THE OCEANIC ENVIRONMENT


Picture by Gregory B. Cunningham

Ken Lukowiak remembers the first time he met Gabrielle Nevitt on the bus coming home from a conference in Cambridge, UK. She described her work on procellariiform seabirds, such as albatrosses, and compared their sense of smell to that of the salmon; 'Nevitt looks at the world differently' says Lukowiak. Since their first encounter in 1995, Nevitt has gone on to study a wide range of oceanic creatures and in her current review (p. 1706) discusses the role of olfaction in navigation, foraging and recognition of individuals. Nevitt explains how her approaches have been informed by field studies of bird diets and observation of both chick and adult behaviour. Describing the 'olfactory landscape' perceived by birds on vast scales, Nevitt says that 'the olfactory landscape reflects oceanic and bathymetric features where phytoplankton accumulate and an area-restricted search for prey is likely to be more successful'. She then describes how the birds combine olfactory and visual cues while foraging over smaller distances, before discussing the role of olfaction in chemical communication, pointing out that 'some species can distinguish familiar individuals by scent cues alone'.

Moving from the aerial realm to the aquatic, Paul Nachtigall from the University of Hawaii and his colleague, Alexander Supin from the Russian Academy of Sciences, describe their work on the hearing processes involved in echolocation. Recording the sensory responses of a false killer whale to echolocation clicks, click echoes and simulated clicks, Nachtigall and Supin realised that, surprisingly, the brainstem auditory responses to the whale's click and its reflection were of 'comparable amplitude, in spite of the intensity difference' (p. 1714). The authors explain that the false killer whale reduced the sensitivity of its hearing by 40 dB while emitting powerful echolocation clicks. And when the team recorded the whale's hearing responses to objects at various distances from the mammal, they realised that the whale heard the echoes at the same intensity, even though the intensity of the echo from remote objects was almost 40 dB lower than the echo from a nearby object. Nachtigall and Supin also found that the whale adjusted her hearing sensitivity in response to object size. 'Overall, hearing during echolocation appears to be a very active process' the team conclude.

NOVEL SENSORY MODALITIES FOR NAVIGATION AND OTHER BEHAVIOURS


Picture by Kenneth Lohmann

Remaining with the aquatic theme, Ken Lohmann describes his work on oceanic creatures and the strategies they use to overcome the challenges of migrating in an environment devoid of visual landmarks and light (p. 1719). According to Lohmann, species that migrate over colossal distances rely on cues unavailable to terrestrial organisms, such as ocean currents and wave motions, and water-borne chemical cues. Lohmann explains that some species also use the earth's magnetic field to determine their orientation in combination with a magnetic map to determine their location.

Focusing on salmon and sea turtles, both famed for their ability to return to their birthplace after lengthy ocean migrations, Lohmann points out that they probably rely on 'navigational systems composed of two different suites of mechanisms that function sequentially over different spatial scales'. According to Lohmann, sea turtles probably navigate the open oceans by following magnetic maps, resorting to specific, but unidentified, local cues as they close in on their beach destination. Returning salmon home in on their birth river by following distinctive local chemical cues, but how they locate the correct river mouth after years at sea is unclear.

While aquatic creatures rely on their senses for navigation, foraging and negotiating their environment, they must also sense water oxygen levels to ensure survival. Although most aquatic species can relocate to the surface when oxygen becomes scarce, developing snail embryos remain secured to pond foliage in egg cases. Jeffrey Goldberg and his colleagues describe how developing snail embryos begin tumbling in their egg cases early in development. Surprisingly, the same behaviour can be stimulated by the neurotoxin 5,7-dihydroxytryptamine (5,7-DHT) suggesting that serotonin is the neurotransmitter that excites the embryo's tumbling behaviour (p. 1729). But why do the embryos 'tumble' consuming significant amounts of valuable ATP, when ATP levels may become compromised as oxygen levels fall? Goldberg suggests that the embryo's tumbling response to hypoxia is a respiratory behaviour where the embryos behave like stir-bars, mixing the egg capsule fluid to ensure oxygen delivery to the embryo. Unravelling the neural circuit which controls the embryo's tumbling behaviour, Goldberg describes how a serotonergic sensorimotor neuron (ENC1) senses oxygen levels and drives the tumbling response.

Having discussed snail embryo behavioural responses to low oxygen levels, Eric Warrant from the University of Lund describes the adaptations of insect visual systems to the extremely low light levels encountered at night. According to Warrant, a nocturnal lifestyle is highly attractive for insects that wish to avoid predators, parasites and encounters with competitors for blooms. But how have the relatively insensitive apposition visual systems of fast moving wasps and bees compensated to allow the insects to function in low light (p. 1737)? Warrant explains that the ocelli and compound eyes of nocturnal insects are relatively large compared with their diurnal counterparts and the photoreceptors have a higher sensitivity due to their slower response times. Unfortunately, the increased sensitivity also amplifies visual background noise, but Warrant explains that background noise can be reduced by summing the input from several photoreceptors. He suspects that lamina monopolar cells couple channels together in groups to improve nocturnal insects' visual sensitivity.

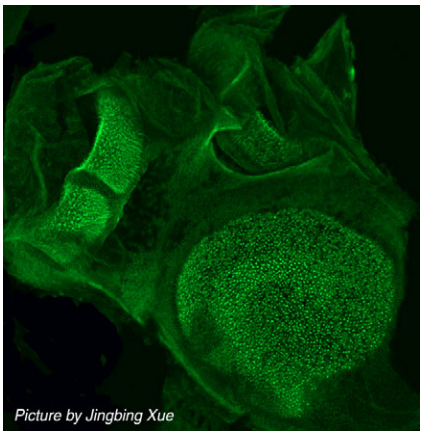
DETERMINING FRIEND *VS* FOE THROUGH SENSORY CUES


Picture by Ken Lukowiak

While many senses are key for negotiating and interpreting a diverse range of environments, the ability to detect predators is key for the survival for any species on the menu. But how do prey species respond to a predator's presence if they haven't seen a predator for many generations? Ken Lukowiak explains that lab based *Lymnaea stagnalis* snails have been free of predation by crayfish for more than 250 generations since they were gathered from a Dutch polder in the 1950s. Could the molluscs recognise threatening crayfish scent after 50 years of isolation? Amazingly, when Lukowiak and his team exposed the lab snails to water that had housed a colony of crayfish, the snails behaved defensively (p. 1747). They had retained the ability to recognise their predator despite half a century of isolation from the crayfish, and Lukowiak is keen to 'determine at the neuronal level how such instinct is both mediated and maintained'.

Having detected the presence of a predator, most quarry take evasive action such as curling up in a shell or taking cover. Another strategy, used by the cuttlefish, is to blend in with the background, and cuttlefish do this by adjusting 'behavioural components' on their skin to change their appearance. But before a cuttlefish can vanish into its surroundings, it must first interpret them. Daniel Osorio and his colleagues, Emma Kelman and Roland Beddeley, discuss how cuttlefish responses to 2D visual patterns have been measured, showing that the cephalopods respond strongly to light features and well defined edges to generate 'disruptive' camouflage patterns (p. 1757). Having established key 2D visual features that elicit a response from the cuttlefish, the team go on to describe the effects that 3D surfaces have on cuttlefish pattern selection, showing that the cephalopods respond strongly to visual depth by shading their own disruptive patterns. The team suspect that cuttlefish initially classify visual environments according to simple 2D cues, before assessing the environment's contrast and adjusting its camouflage accordingly.

SENSORY ENCODING IN HEARING AND BALANCE


Picture by Jingbing Xue

Governed by a set of fluid filled vestibular organs situated in our ears, balance is a sense that many take for granted past our early years; but not Ruth Ann Eatock. She is fascinated by the regularity of nerve signals generated by rodent vestibular systems and what they can teach us about sensory encoding. Describing factors that may influence the regularity of neuronal firing, such as the physiology and morphology of nerve contact with movement sensitive hair cells, Eatock goes on to discuss the different ion channels found in neuron sub-populations which, coupled with the different modes of hair cell drive, are responsible for the different firing patterns that have been identified (p. 1764).

Moving from the mechanosensory hairs in the ear's balance system to the mechanosensory hairs that detect sound vibrations, William Roberts and Mark Rutherford explain that 'mechanosensory hair cells in the ears are exquisitely responsive to minute sensory inputs, nearly to the point of instability' (p. 1775). The team show how mechanosensory hair signal transduction has both linear and non-linear properties, responding to soft sounds almost linearly, 'but close to instability' they say. They go on to explain that the non-linear responses may protect the system from becoming unstable as oscillations grow, ensuring that the system functions over a large dynamic range.

Staying with the sense of hearing, Don Caspary and his colleagues from Southern Illinois University School of Medicine discuss the neurological changes that accompany hearing loss in elderly animals. Caspary reviews the literature covering age related hearing loss, and attributes may of the problems that older animals encounter interpreting communication signals in noisy environments to the loss of inhibition by GABA and glycine neurotransmitters (p. 1781). They explain that the loss of inhibition probably affects temporal processing of auditory signals and the ability of elderly animals to localize sounds in the environment. The team concludes that these losses probably significantly affect the survival chances of elderly animals, pointing out that 'the impact of sensory aging on predator–prey relationships in a natural habitat has not been well studied'.

THE ADAPTIVE EVOLUTION AND PROCESSING OF SENSORY SYSTEMS

Having discussed the ecology of senses ranging from olfaction to balance and hearing, and aspects of the neurophysiology that underpin them, the collection of reviews moves on to consider the evolutionary influences that have shaped neurological systems. Jeremy Niven and Simon Laughlin review our understanding of the influence that energy limitations have had on the evolution of the neural system (p. 1792), with particular attention to vision. Explaining that 'some selective pressures act to increase the benefits accrued while others act to reduce the costs incurred', Niven and Laughlin point out that 'the nervous system is under selective pressure to generate adaptive behaviour' while incurring significant energetic costs. Outlining the energetic costs of information processing, and the costs incurred by $3Na^+/2K^+$ ATPase ion transport during neural activity and inactivity, Niven and Laughlin go on to give examples of efficient neural systems in insect vision, such as the combination of analogue and digital information transmission and 'saving wire' by placing brain regions close together to reduce axon length. Niven and Laughlin conclude by saying 'reducing energy expenditure can account for many of the morphological features of sensory systems and has played a key role in their evolution'.

Continuing with the visual theme, Adriana Briscoe reviews work on the evolution of the butterfly eye. 'The butterfly eye is a marvel of evolution' says Briscoe and adds that 'they are nearly as diverse as the colors of wings'. Explaining that much of the diversity can be attributed to variations in the distribution, spectral properties and number of visual pigments, Briscoe has analysed the expression patterns of the visual pigment proteins (opsins) from four butterfly families in parallel with the genes' phylogeny to reconstruct the ancestral butterfly eye (p. 1805). She describes how the ancestral eye, which most closely resembles the nymphalid eye, expressed combinations of UV and blue sensitive visual pigments in two of the eye's cells, with the remaining seven cells expressed long wavelength visual pigments alone. According to Briscoe 'visual systems of existing butterflies then underwent an adaptive expansion based on lineage specific blue and longwave opsin gene multiplications and on alterations in the spatial expression of opsins within the eye' giving rise to the butterfly eyes we see today.

Shifting focus from visual systems to the electroperception of weak electric fields by mormyrid and gymnotiform fish, Harold Zakon and his colleagues from the University of Texas investigated how both families have independently evolved their electric sense (p. 1814). 'The imprint of selection must reside in the genome' says Zakon. Knowing that the electric organ responsible for the fish's electric field is derived from muscle, Zakon and his colleagues focused on the expression of two Na^+ channels, originally found in muscle. The team found that both families have lost the Nav1.4a channel from muscle, but the channel has been retained by the electric organ. They were then able to estimate Nav1.4a evolutionary rates from electric and non-electric fish, and found that the rates of evolution were highest when the channel was compartmentalised by the electric organ and lost from muscle. Zakon concludes by suggesting that mutations in the channel are due to positive selection and the rate of evolution in the gene results from a change in the selection pressure exerted on it when its expression became restricted to the electric discharge organ.

Having detected a sensory stimulus, how does the nervous system process the signal to extract sensory information? This is the question that intrigues Gwen Jacobs and colleagues from Montana State University. Focusing on the cricket cercal system, which detects air movements eliciting at least 14 behavioural responses, Jacobs describes a range of neurological methods that have been applied by various labs to understand the structure and operation of this system (p. 1819). According to Jacobs, the cercal system 'captures a very well-sampled image of the air-current field surrounding the animal, and represents the image of that field as activity across a continuous map of that field in the terminal abdominal ganglion'. She points out that this representation is analogous to the way our visual field is mapped onto the visual cortex. Finally Jacobs outlines the computational operations carried out by the first-order sensory interneurons, to produce generalist information from the sensory input which can be processed to extract higher order information, such as feature recognition, by more specialised cells in higher levels of the nervous system.

CONCLUDING REMARKS

This collection of 14 outstanding reviews takes the reader throughout the realm of neurosensory ecology, from the behavioural responses elicited by sensory information to the details of the neural processing required to interpret complex sensory stimuli. Lukowiak and Weeks hope that the collection will open people's eyes to the range of sensory functions, many beyond our comprehension, that will continue to shed light on the way other creatures interpret the environment. Lukowiak says 'Just because we don't sense it doesn't mean it's not there. There are other sensitivities out there, and other animals use them to sense their environment and interact with it'. And he closes with a note of caution that we have to be careful of the harm our activities may cause other species, such as the possible damage caused to whales by human sonar activity. 'We have to be careful what we do in case we harm creatures that have sensitivities beyond our own' warns Lukowiak.

10.1242/jeb.019992

Kathryn Phillips
kathryn@biologists.com