
Preface

Almost 30 years ago, the celebrated German biologist Rüdiger Wehner published a landmark paper in the *Journal of Comparative Physiology* entitled “Matched filters – neural models of the external world” (Wehner 1987), and with it ushered in an entirely new way of understanding how peripheral sensory structures and sensory neural circuits have evolved to deal with complex, constant and seemingly infinite sensory information. The essence of his message was that any given species *does not* deal with all of this information – in fact *cannot* deal with it – at least not with the overwhelming majority of it. Instead, Wehner recognised that sensory systems rely on “matched filters” to extract the most pressing sensory stimuli that are crucial to the animal’s chances of survival and reproduction, and to suppress or even reject other stimuli. By matching the properties of neurons, circuits and sensory structures to the characteristics of the most crucial sensory stimuli that need to be detected, these stimuli can be directly and reliably extracted for further processing. Moreover, this extraction can be done with a minimum of neural tissue. To sense “the world through such a matched filter”, to quote Wehner himself, “severely limits the amount of information the brain can pick up from the outside world, but it frees the brain from the need to perform more intricate computations to extract the information finally needed for fulfilling a particular task”. An example of a classic matched filter can be found in the ears of certain species of moths, which are tuned to the high frequency sonar pulses of the bats that hunt them, and perceive little else. For these moths no other sound embodies the same danger or requires a behavioural response of the same urgency, and their entire auditory investment – from the morphology of the ear to the physiology of the auditory neural circuits – is devoted to the detection and analysis of that one narrow range of sonic frequencies (see also Chap. 4 by Römer in this volume).

In the years that have followed Wehner’s landmark contribution, it has become increasingly apparent that brains and nervous systems are energetically extremely expensive and that the cost of maintaining a nervous system represents a substantial fraction of an animal’s total energy budget. The main reason for this expense is the cost of maintaining the resting potential of neurons in readiness for electrical signalling. The resting potential, which is usually many tens of millivolts negative relative to the external cellular medium, is maintained (and restored following signalling) by active ion pumps that use energy from ATP molecules to pump sodium and potassium ions across the neuronal membrane against their passive

electrical and concentration gradients. This energetic cost is substantial and is incurred even in the absence of signalling. The extra cost of signalling is simply added to this (Niven et al. 2007). Thus, during evolution, nervous systems have been under pressure to become as lean and as efficient as possible (Sterling and Laughlin 2015), and not surprisingly this fact is inextricably linked to the evolution of matched sensory filters. To requote Wehner above, because matched filters “severely limit information picked up by the brain”, the energetic costs that would have been associated with coding superfluous information are effectively eliminated. And “freeing the brain” not only frees it from the need to perform intricate computations, it also frees it from the significant energetic costs that would have arisen by possessing the neural circuits necessary to make these computations. Simply put, matched filtering saves energy by stripping away unnecessary energetic investments and efficiently redirecting the remaining energy to where it is needed most.

Matched sensory filtering thus has two main evolutionary advantages: firstly it substantially enhances an animal’s ability to detect and analyse ecologically crucial sensory stimuli, and secondly it does so with the most efficient use of the animal’s limited energy supply. In this book we hope to showcase these advantages across the senses, in both vertebrates and invertebrates, and to show how matched sensory filtering is intimately linked to the ecologies of animals. This “ecology of sensing” – with its inherent use of matched filters – provides some of the most beautiful and remarkable products of natural selection that can be found in the natural world, and many of these are described in the pages that follow.

The nine chapters of this book are arranged according to the evolutionary origin of the different senses of animals. Chemoreception – the sensing of chemicals related to smell or taste – is the most ancient sense in the animal kingdom and even occurs in single-celled organisms. Many animals, such as insects, can detect important olfactory stimuli with remarkable sensitivity and at a millisecond time scale. In their review on insect olfactory systems, Riffell and Hildebrand explain how the insect peripheral and central olfactory systems filter meaningful chemical information from a noisy environment full of “unimportant” chemical components. Important olfactory information is perceived by a combination of active and passive processes, during which neural plasticity plays an essential role.

Various animal senses such as hearing, touch, whisking and several others (e.g. infrared perception in some insects) can be attributed to mechanoreception, involving sensory cells that respond to mechanical pressure or distortion. Mechanoreception is also a very old sense and, like chemoreception, even occurs in single-celled organisms. In this book, four chapters deal with matched filtering in the various senses based on mechanoreception. Friedrich Barth uses spiders’ sense of touch to explain the functioning of the large numbers of mechanoreceptive hairs on their exoskeleton. Even though natural stimulus patterns are frighteningly complex, spiders rely on a highly specialised sensory periphery to solve complex behavioural tasks.

Tactile facial hairs, called whiskers or vibrissae, are also used by many mammals. Grant and Arkley explain how, during active whisking, whisker

specialists can extract information about size, texture, shape and position by moving their whiskers over an object. Here again a great deal of processing is conducted by matched filters at the sensory periphery, with the spatial layout and properties of the sensors being matched to the problem at hand. In addition, a mapping of the peripheral arrangement of tactile hairs in the cortex allows for eloquent and economical processing of sensory information.

Two additional chapters on mechanoreception deal with audition, explaining how insects and certain vertebrates acquire sensory information using sound. Heiner Römer presents several examples of sensory matching in the acoustic domain of insects. By concentrating on only some aspects of a sound stimulus and ignoring the rest, insects can match the tuning of their receptors to the carrier frequency of the relevant sound or to the temporal parameters of songs. Economic filtering additionally occurs in the intensity domain and begins already in the peripheral receptors. Acoustic matched filters are also found in other animal groups, and Narins and Clark present examples in the auditory systems of several selected vertebrates. They point out how matched filters can be effective detection tools when examples of the desired signal are available a priori.

Visual matched filters have evolved for all aspects of life in both insects (described in Chap. 6 by Warrant) and vertebrates (described in Chap. 7 by Douglas and Cronin). In insects, the pressing ecological challenges and the overriding energy constraints of small brains and sense organs have led to an enormous variety and sophistication of visual matched filters in insect eyes. Vertebrates also show an enormous diversity of specialisations, including pigment filters, optical adjustments and retinal sampling variations. This plasticity, which is based on a single fundamental eye design, enhances the utility of visual perception in a particular habitat and simultaneously reduces the energetic costs of vision.

The last two chapters deal with the so-called sixth senses, those that fall outside Aristotle's original canon of five senses (sight, hearing, touch, smell, and taste). Infrared perception, absent in most animals, can be found in a few pyrophilous insect species and in some snakes, as outlined in Chap. 8 by Schmitz and colleagues. Despite their different functional principles, insect IR receptors all show the same built-in filter properties, which are based on a match of the absorption properties of the atmosphere and the chemical composition of the insect cuticle. Even electroreception in some aquatic vertebrates can be considered a sixth sense, with this sense probably already present in the earliest vertebrates. As von der Emde and Ruhl point out in their chapter (Chap. 9), weakly electric fish have developed a complex set of matched filters that match the properties of the incoming electrical signal to the properties of the peripheral sense organs. This matching allows electric fish to economically perceive objects in the near field. Interestingly, objects located at greater distances are perceived visually, again with eyes functioning as matched filters for specific visual stimuli.

This book provides a new and updated synthesis of sensory ecology in animals and builds upon the classic 2001 Springer volume *Ecology of Sensing*, edited by Friedrich Barth – one of our current authors – and Axel Schmid. By exploring sensory ecology in the context of matched filtering and energetic constraints, we

hope not only to honour Rüdiger Wehner's immense contribution to the field but also to highlight how the finite energy budgets of animals have been critically important in the evolution of sensory processing. We wish to thank our authors for their excellent contributions to this book and our editors and production staff at Springer for their patience and guidance as this book was being completed.

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References

- Barth FG, Schmid A (2001) Ecology of sensing. Springer, Berlin/Heidelberg/New York
Niven JE, Anderson JC, Laughlin SB (2007) Fly photoreceptors demonstrate energy-information trade-offs in neural coding. PLoS Biol 5(4):e91
Sterling P, Laughlin S (2015) Principles of neural design. MIT Press, Cambridge, MA
Wehner R (1987) "Matched filters" – neural models of the external world. J Comp Physiol A 161:511–531

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