thousand papers and grants begin with the assertion that this is a big question in need of resolution. But we've been working on this question for a hundred years and are (from my perspective) no closer than we were a hundred years ago to a consensus as the resolution of this 'big question'. I don't think that there are many big discoveries in the history of biology where, if you look back at them you could say the scientists who made the discovery were addressing a big question. It seems like far more often the big discoveries come from knowing some organism or feature of an organism really well and then combining that deep knowledge and inquiry with some insight that spans fields. My guess is that the next big discovery is far more likely to come from someone studying, say, the behavior of squirrel sperm, than gunning for the next big question.

If you could ask an omniscient higher being a scientific question, what would it be? I'd like to know about the dimensions of life. How small it gets, how deep in the Earth. Where else in the universe life exists. The most unusual organisms we have yet to detect, or the most unlikely biology. I'd like to see a cabinet of curiosities compiled by someone who knew where the best stuff was kept. I guess I'd also like to know if there are rules by which life or existence more generally works that we are still missing. We've got natural selection. We have the laws and regularities of ecology. We have genetics and epigenetics. But surely we are missing something. What is it that we are missing? There are also the practical concerns as well. Most of the challenges society faces need to be resolved with better education, better policies and better collective decisions, not necessarily more or newer science. But in those places where more or newer science is needed, what are the critical insights. Where, for example, are the new antibiotics? The new medicines? Which species should we be studying to best help humanity. The answer is almost certainly not mice, rats, and fruit flies though I'd love to hear as much from someone who could see it all.

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Book review

Space in the brain

Brian L. Day

Making Space: How the Brain Knows Where Things Are
Jennifer M. Groh
(Harvard University Press, Cambridge, MA; 2014)
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Without assuming any prior knowledge of neurons, sense organs or neural communication, Jennifer Groh succeeds in explaining the fundamental problems faced by the brain in deciphering all things spatial in her new book *Making Space: How the Brain Knows Where Things Are*. How does the brain work out what things are and where they, and we, are? By deliberately avoiding obfuscatory technical language and through clever use of analogy, Groh opens up this tricky subject to the layperson. Indeed, this enjoyable book has something to offer every reader, including those with a grounding in neuroscience. Concepts are presented faithfully with clarity and wit, and although easy to digest, they are not oversimplified. The book is primarily about the brain making sense of space, but there is a surprise package at the end. Here, Groh throws caution to the wind and openly speculates about the even more mysterious brain function of abstract thinking. Could it be, she asks, that this mysterious process somehow utilises the neural building blocks used for spatial analyses? In the same easy-to-read style as the more mainstream bulk of the book, Groh makes a compelling case.

To achieve all of this, Groh has to cover a lot of ground, but it never feels dry or heavy going. This accomplishment is partly down to the skilful way the need-to-know neuro-facts are inserted between fascinating stories. Some of these are historical stories that describe the way ideas have changed and developed over millennia. For instance, we learn that the ancient Greeks were unable to agree on the fundamental issue of whether

the eyes see by emitting or by receiving material, a conundrum that apparently was not resolved until the 11th century. Some of these stories reflect on key and often surprising experiments, such as getting ants to walk on stilts to see if they use a form of step-counting to navigate home, which it seems they do. Other stories describe intriguing brain phenomena, such as single neurons in the human hippocampus that respond to pictures as well as names of specific individuals. We are reliably informed that one such neuron was found to respond to a variety of photographs of the actress Jennifer Aniston as long as her ex-partner Brad Pitt was not in the scene!

A good part of the book is spent on the nature of the sensory signals that the brain uses as its raw material — signals that come from the eyes, ears and skin, which tell the brain about things outside the body, and signals that arise from sensors in muscles and balance organs, which tell about body movements and body shape. Because the brain relies heavily on visual information when analysing what things are, Groh pays a lot of attention to this sense, and describes how the visual system is organised to determine boundaries between things. To do this, she discusses the optics of the eye, the remarkable cascade of events that occur to transfer light energy into meaningful neural signals, and the subsequent neural processing that goes on at the back of the eye and beyond.

When analysing *where* things are, it is explained how the brain uses multiple senses in parallel not only to detect the thing's presence but also to provide an appropriate reference frame to establish its location. For example, the location of an object that touches the skin of a hand can only be worked out if the positions of the corresponding wrist, elbow, shoulder and rest of the body are also known.

One other key concept explored in this book concerns the different ways space may be represented in assemblies of neurons and how this representation can vary according to the sensory system involved. For instance, we are shown how the location of a thing that is both noisy and visible is coded in radically different ways by the auditory and visual systems, so requiring very different types of brain processing to extract the spatial information. This leads Groh to ask — how are these different representations of the same spatial attribute combined by the brain? How is this language barrier bridged? The book does not really answer this question, which is fair enough given that it is a mystery that has yet to be solved. However, Groh does reveal that the brain sometimes makes mistakes when combining spatial information from different senses. These errors give rise to illusions, which in the case of sight and sound are routinely exploited by ventriloquists. But, as this book helps us realise, errors and illusions are also keenly exploited by neuroscientists, as they provide important and unique clues about how the brain works.

Be aware that this book does not offer a comprehensive deconstruction of the brain and its senses, but that is not its intention. Rather, it is a succinct attempt to convey a flavour of some of the issues surrounding the brain's analysis of a three-dimensional world. To do this, Jennifer Groh has knitted together very selective strands of knowledge acquired from many sources, including the 2014 Nobel prize-winning work on spatial cognition. In sum, it is a book written with the authority of an expert that can be understood and enjoyed by almost any curious person.

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Quick guide

Elementary motion detectors

Mark Frye

What is an elementary motion detector? An elementary motion detector (EMD) is a theoretical model devised to explain the minimal computations required to perceive movement from the activity of photoreceptors. An eye maps an image of the world onto a sheet of photoreceptors. Any single receptor has a narrow field of view, and responds to fluctuations in illumination over time within its narrow field, but cannot provide unambiguous information about the direction of movement of an image. For example, a receptor response might result from a bright spot in the visual scene moving into its field of view from above, below, left, or right. The direction of motion can only be detected by comparing the activity of at least two receptors. The EMD is one of several models that predict the minimal interactions between two photoreceptors required to detect directional movement of the visual scene from the pattern of activation at each.

What are the components of an EMD? The components of the EMD are roughly similar to any model for motion detection, grounded in the physical principles of movement. In its most basic form, the EMD model is composed of two spatially separated input channels such as photoreceptors, a time delay, and a nonlinear interaction such as multiplication. The *spatial separation* is important because a bright spot within the moving scene would stimulate the first input, followed by the second input, a comparison that provides a correlation in space so that any point in the scene activates the two receptors only if it is in motion. A *time delay* ensures that the signal arriving at the first input is correlated in time with the one arriving at the second input when the scene is moving. Delaying one input provides the added advantage that any correlation between the inputs occurs for image motion in only one direction — from the delayed toward the un-delayed side. For this reason, the EMD is often referred to as a 'delay and correlate' model. Finally, the two signals are *multiplied* to boost tightly correlated activity (Figure 1).

How was the model derived and explored? Bernhard Hassenstein and Werner Reichardt developed the model in the 1950s. They referred to it as a correlation model, and it has become commonly referred to as the Reichardt detector, the Hassenstein-Reichardt EMD, or simply the EMD. The model is simple and elegant, and its key operations are intuitive (Figure 1). However, the internal components, such as the spatial separation of the inputs, the temporal delay and multiplication, each constrain the performance of the EMD in ways that allow direct comparison of the model to the performance of neurons, neural circuits, or whole animal behavior. To explore these predictions, Hassenstein and Reichardt took a psychophysical approach in which they reasoned that visual reflexes are robust in any animal with sophisticated visual behavior. Motivated by pioneering work at the time on the visual behavior of other insects, they glued a beetle by its back to a stiff wire and suspended it within a large rotating visually textured drum. The tethered beetle clasped a lightweight ball that it could 'roll' with its legs, apparently fooled into thinking it was walking on the ground. By rotating the drum around the tethered beetle, and observing its ball rolling reactions, they were able to directly compare the behavioral responses to the predictions made by the model.

What evidence suggests that animal vision is based on the EMD? The model makes specific functional predictions that distinguish it from other theoretical models of motion vision. Consider a simplified visual scene made up of evenly spaced stripes. The EMD encodes the rate of stripes passing over the stationary input arms rather than the true velocity of the moving pattern — in other words, the model cannot distinguish a pattern of thin stripes moving slowly from a pattern of thick stripes moving quickly. A visual neuron or behaving animal that shows similar