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Michael Francis Land.
12 April 1942 — 14 December 2020

Elected FRS 1982

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Abstract

Michael (Mike) Land made lasting contributions to physiological optics of diverse animals and to understanding how animals and humans move their eyes. He combined a keen interest in natural history and evolution with elegant and accessible mathematical accounts of optics and vision. In the early part of his career he discovered focusing mechanisms based on reflection in scallops and compound eyes, and elucidated the evolutionary and functional relationships between spatial resolution and absolute sensitivity in eyes. Starting with studies of how spiders and flies use eye and body movements to track and intercept moving targets, Land went on to apply similar principles to human visuo-motor behaviour. He described where we look during routine tasks, such as making tea, and in more exacting conditions like driving and playing cricket. He showed how eye-movements are tailored top-down for a given task, and found that typically we foveate each location a fraction of a second before each action. Finally, he suggested how behaviour and awareness are anchored to an internal representation that incorporates egocentric and allocentric frames of reference. Land's deep curiosity about the living world led him to discover visual principles of in an unexcelled diversity of creatures.

Early years and schooling

Mike Land was born in Plymouth during the Second World War as the middle of three children. His parents Frank William (1911-1990) and Nora (nee Channon; 1910-1985) were mathematics teachers. Nora was from North Yorkshire while Frank Land, the son of a postmaster from Devon, had taught mathematics at Hampton Grammar School while completing his PhD. During the war Frank Land joined the Navy, where, fortunately, a sports-injury prevented him from joining HMS Hood on its final voyage in May 1941; instead he taught navigation at the Britannia Royal Naval College, Dartmouth. After the war Frank Land moved into teacher training, first in London, and then in 1950 as a Senior Lecturer in Education at Liverpool. In 1960 he published a popular book on *The Language of Mathematics* and took a Chair in Education at the University of Hull.

From 1950 to 1958 the Land family lived in Birkenhead, Cheshire. Mike had an elder brother Tony (1938-2021) and a sister Janet (b. 1947). At Birkenhead School he was head chorister and took piano lessons. He had a fine baritone voice and acquired a lifetime enthusiasm for ancient music, playing several period instruments. Mike was keenly interested in plants - his own rockery area in the garden was planted with specialist alpinists - and he enjoyed botanising in the nearby Welsh Hills. Mike became a Queen's Scout, attending an international jamboree, and travelled to Greece and the Faroes with the school Naval Cadets. He was a keen photographer, building a dark-room in the attic with home-made equipment. He took Russian as an extra sixth form subject as he had a year to spare. His brother Tony recalled that in the 1950's Mike temporarily lost interest in plants, "as they didn't move", and they went together to watch shorebirds on Hilbre Island. Eventually he opted for zoological studies.

Personal life

Mike married Judith Drinkwater in 1967; they had a son Adam and divorced in 1980. In 1980 he married Rosemary (nee Clarke). Rosemary and Mike had two daughters: Kate (b. 1981) and Penny (1983-2003). They moved to an Arts and Crafts house overlooking Lewes in East Sussex. Mike enjoyed the steep chalk garden, leaving space for a wild lizard orchid (*Himantoglossum hircinum*) whose flowering he celebrated with an annual party. In 2015, when poor health made gardening difficult, Rosemary and Mike moved to the nearby village of Ringmer. Mike died on the 14th December 2020 from the combined effects of lung disease and coronavirus.

Student years in Cambridge and London

Mike entered Jesus College in Cambridge in 1960, and in 1963 he took a first in Natural Sciences, with the Part-II (final year) in Zoology. Lectures by Carl Pantin (FRS 1937) gave him a life-long fascination with the invertebrates, especially marine species, and he looked for a PhD project in invertebrate neuroscience. At that time gifted students such as Mike Land first devised a PhD project and then approached a supervisor. Mike decided to investigate vision in the scallop (*Pecten maximus*), and started his doctoral studies in 1963 with John Gray (FRS 1972) at University College London. In 1966 Gray left UCL to serve the Medical Research Council, so the thesis was completed under the supervision of Andrew Huxley (FRS 1955; PRS 1980-85).

For his doctoral work Mike planned to work out how the visual signals from the scallop's many eyes are integrated by the nervous system, leading to the contraction of a single muscle that closes the shell in response to threat. He never pursued this plan, however, because to his surprise Mike noticed a minute image of his own face in each of the scallop eyes he peeped into. He realized that the eyes contain an imaging mirror rather than a lens, and thus made his first discovery [1]. Mike referred to this as good luck, but it was exceptionally good science, as few others would have seen the implications of the tiny, reflected images. Mike recognized a new imaging principle in animal eyes, whereby the curved mirror forms an image at one of the two retinas in the scallop's eye (Figure 1a), while the second deeper lying retina receives a blurred image. The optics and the neural responses suggested that the first retina warns the scallop to close its shell when it detects the movement of approaching predators, while the blurred image is used for orientation when the animal swims, which it does by clapping its shells.

So, Land dropped studying neural processing and instead asked how the sensory input, the eye, supported the scallop's behavioural responses. For the rest of his career Mike followed the same principle of relating visual input to behaviour, without scrutinizing in detail the neural networks that connect them. This strategy allowed him to compare visual systems across the animal kingdom.

Biological mirrors

The discovery of eyes with imaging mirrors highlighted an interesting question: how can biological tissue act as a mirror? Commonplace mirrors are made from glass coated with metal, but biological tissues cannot deposit metal. Mike showed that instead, biological mirrors have layers of alternating high and low refractive index materials, which reflect a fraction of the incident light at each interface [2]. Layers a quarter of a wavelength thick achieve high efficiency by constructive interference, giving a coloured

mirror, while white reflectors are produced by stacking interference reflectors tuned to different parts of the visible spectrum. The silvery mirrors (“argentea”, see Figure 1a) in scallop eyes are formed by layers of guanine crystals separated by water, and Mike’s thorough theoretical analysis still stands. Mike’s doctoral work inspired his supervisor Andrew Huxley (1968) to apply the methods of Rayleigh and Stokes to write ‘A theoretical treatment of the reflexion of light by multilayer structures’. Huxley’s analysis helped establish Land’s future work on multilayer reflectors [6]. These publications have been influential in the development of the new field of biophotonics. He revisited multilayer reflectors several times, studying the silvery sides of fish and cephalopods, coloured stripes in tiny fish and the scales of jumping spiders.

Time in Berkeley

After completing his PhD in 1967 Mike took a fellowship at UC Berkeley sponsored by Gerald Westheimer (FRS 1984), who wrote to us recalling:

“Mike Land first came to Berkeley as Miller Fellow, intended for highly promising young scientists to spend two years as researchers in established laboratories to be looked over for possible future faculty appointments. His nomination was the result of the paper he had just published on the scallop eye, about which I had wondered ten years earlier when I first saw the tiny globes lining the mantle. I couldn’t imagine how they would be image-forming and thought that their optics might be an intriguing retirement project decades hence. But here Mike had shown that indeed an image was formed on a retina, and moreover by means of the posterior eye surface acting as a concave mirror! This discovery of a unique application of geometrical optics in the Animal Kingdom, already known to have used so many other optical tricks, revealed just the kind of mindset that fitted the thrust of the physical and chemical sciences that characterized forward-looking biology programs then.

“When he started his own research in Berkeley, Cambridge and UCL trained, Mike productively interacted with the lively bunch of graduate students and post-docs, showed an added dimension: appreciative of but not, like many of us, mesmerized by the intellectual brilliance and virtuosity that was the hallmark of British physiology and biophysics of the time. Instead, he was motivated by an abiding love of and curiosity about living things, in their own right and not just as substitutes or substrates for experiments to illuminate and/or improve the human condition. His influence, even as a beginning post-doc was felt

immediately when he helped include a section on comparative neuroscience (starting with the jellyfish) in the first undergraduate neurobiology course then developed in Berkeley.”

Mike found at Berkeley a remarkable group of vision scientists including Horace Barlow (FRS 1969), Jack Pettigrew (FRS 1987), Colin Blakemore (FRS 1992), Bill Levick (FRS 1982), Ken Nakayama and Barrie Frost, many of whom shared interests in natural history and the evolution of visual systems. Westheimer had suggested that Mike work on jumping spiders, and he continued:

“Working alone in a small room with minimal, mainly borrowed equipment, Mike embarked on the exploration of the visual system of two species of jumping spider (*Phidippus johnsoni* and *Metaphidippus aneolus*) collected from redwood tree groves. The research, culminating in a series of now classical papers in the *Journal of Experimental Biology*, examined the optical and anatomical structures of the many eyes of the spiders, and included functional analyses of the connecting nerves and attached muscles. Mike quickly became a valued member of the burgeoning neuroscience community in Berkeley, so when a faculty slot opened as Assistant Professor of Physiology, he was immediately appointed. He thrived in the free and fertile atmosphere of the 1970 Bay Area ambience, but within a few years, family health issues, and the fresher and more open culture that had meantime developed in the UK motivated him to return to his home country.”

Mike mostly studied the largest pair of eyes, the principal eyes of the jumping spiders, which have a peculiar and narrow movable retina attached to muscles. Looking at the fine structure of the retina, Mike identified no less than four layers of photoreceptors at different distances from the lens [3] (Figure 2a). To understand the optical consequences of this unexpected arrangement he built an ophthalmoscope for spider eyes. An ophthalmoscope views the photoreceptors in object space, revealing how they map onto and sample the external world in units of visual angle, and showed that the principal eyes were suited to distance estimation, polarization vision, and potentially colour vision.

Mike wondered how the attached muscles move the jumping spider’s retina [4]. As the lens is part of the exoskeleton it is immobile, but by moving its retina the spider can accomplish the equivalent of eye movements. With the ophthalmoscope and by direct viewing of the retina through the (partly transparent) dorsal exoskeleton, Mike observed saccades that bring targets to the centre of the retina, scanning eye movements for target analysis, and visual fixation of moving targets. The saccades were

particularly interesting, in part because they allowed the spider to distinguish prey from a conspecific mate or competitor [5]. This work on eye movements revealed similarities between humans and spiders that suggested common principles across the animal kingdom [4,10,25]. Because high resolution vision evolved independently in vertebrates and spiders, evolution must have ‘discovered’ these principles independently. Later, Mike’s interest in eye movements spurred investigations with wide impact on vision science.

Back to England

In 1971 Richard Andrew and John Maynard Smith (FRS 1977) invited Mike to join the School of Biological Sciences at the University of Sussex. Maynard Smith had foreseen the rise of the interdisciplinary subject we now know as Cognitive Science, helping to recruit early leaders including the experimental psychologists Christopher Longuet-Higgins (FRS 1958) and Stuart Sutherland, and the philosopher Maggie Boden. Land joined a group interested in the brains and behaviour of non-human species – an area of study which has developed into the field of neuroethology. Also at Sussex was the MRC Vision Unit led by Herbert Dartnall, which studied animal visual pigments.

At Sussex Mike collaborated with Thomas Collett to study how flies track and intercept moving targets. They found that male houseflies (*Fannia canicularis*) pursue other flies by turning in the direction of the target at a speed that is governed by the target’s angular velocity [8] (Figure 3). They then turned to the large hoverfly, *Eristalis tenax* which hovers in beams of sunlight waiting for passing objects that might be mates, and found that peas shot from a pea shooter evoked the fly’s pursuit behaviour [12]. If a length of cotton thread was attached to the pea the trajectory was curtailed, revealing that the fly’s initial response is to compute an interception path. *Eristalis*’ precise return to its hovering station, after a fruitless chase, was then partly governed by nearby visual landmarks. Groups of the smaller hoverfly *Syrirta pipiens* behave naturally when placed in a large transparent box with flowers from which they can feed. Male *Syrirta* have a pronounced forward pointing acute zone with a resolution 2-3 times greater than in the rest of the eye. The flies’ interactions in the box are intriguing [9]. Males pursue females using body saccades when the female is far from the male’s midline, and by smooth pursuit when the female is imaged on the acute zone. Should a female land on a flower, the male hovers briefly and then darts towards her, turning when close so that he lands parallel, head to head and tail to tail. If the chased fly is another male, the two briefly track each other, oscillating in antiphase, before separating.

Exotic eyes from the sea

In 1975, Mike's friend Peter Herring invited him to join his first of several cruises to the North Atlantic on the *RRS Discovery*. Here, the shape of the facets in compound eyes of the deep-sea shrimp *Oplophorus spinosus* caught Mike's attention [11,13] (Figure 1b). These shrimps and some other decapod crustaceans have perfectly square facets, unlike the hexagonal facets of most compound eyes. These square-faceted eyes have a clear zone between the ommatidial optics and the light-sensitive rhabdoms at the bottom of the eye. Clear zones are a feature of the superposition type of compound eye, where light from many facets is combined to form an image. Superposition eyes were thought to work as miniature Keplerian telescopes, but with such optics square facets make no sense. *Oplophorus* had no components that could act as the lenses of a Keplerian telescope; instead, under each square facet Mike found an equally square box of flat mirrors. An array of mirror boxes can act much like the Keplerian telescopes in classical superposition eyes: light from any given point in space can enter many facets and then be converged to a single point on the retina. Because shrimp superposition optics are realized by reflection rather than refraction Mike had discovered a new type of imaging, which he called "reflecting superposition", renaming the classical principle "refracting superposition". Realizing that this was a major discovery, Mike wrote a paper for *Nature* [11], but as he was finishing his paper, he learned that Klaus Vogt in Stuttgart had almost simultaneously found the same mechanism in crayfish. In 1975, Vogt had published a short note about the discovery in *Zeitschrift für Naturforschung*. In 1976 *Nature* published Mike's paper, referring to Vogt's note. Later Vogt (1977) published his full account. The two accounts were in perfect agreement, but Mike always gave the credit to Vogt because he published first.

The *RRS Discovery* cruises gave Mike access to mesopelagic invertebrates with unusual and interesting eyes that begged for explanation. He wanted to compare the eyes and vision of the diverse creatures that were brought on board and to explain the many cases where a given problem had found different solutions in closely related animals, or similar solutions in distantly related animals. For example, mesopelagic crustaceans such as euphausiids (krill) and hyperiid amphipods both have double compound eyes with very different dorsal and ventral parts [14, 22]. The upward-looking dorsal part is enlarged giving it acute vision for spotting silhouettes against the comparatively bright downwelling light. The ventral part is smaller with lower resolution, and is used for detecting bioluminescent animals against the dark background. Mike's work on the hyperiid amphipod *Phronima*, where long light-guides connect the image-formed by its giant dorsal eye to a small and distant retina, was particularly original [15].

At sea, Mike found scanning retinas similar to those of jumping spiders. These included the unique and remarkable eyes of heteropod snails, which have a single fish-like lens that focuses onto a strip retina that continuously scans across the image, taking about a second to cover the visual field [17]. This gives the snail high-acuity vision at a small fraction of the cost of building and running a full-size retina. The copepod *Labidocera* has a similar system. Copepods lack the lateral compound eyes of other crustaceans, and only have median eyes, called nauplius or frontal eyes. These usually comprise two to four shallow pigment cups without imaging optics, but *Labidocera* has evolved a pair of imaging eyes with spherical lenses and a scanning strip retina with five photoreceptors under each lens [21]. The similarity in eye design and function between heteropods and *Labidocera* is striking, although the snails are probably looking for prey, whereas the crustacean is looking for mates.

Developing a general theory of visual optics

Since the 1940s there had been much work on the physical limits of vision: some dealt with the limit to spatial resolution set by diffraction due to wave nature of light and others with absolute sensitivity restrictions due to limited photon capture and retinal sampling. The emerging nomenclature and formalism in this field was often inaccessible to biologists who lacked a background in mathematics and physics. With fortunate timing, Mike was invited to contribute to the influential book series, *Handbook of Sensory Physiology*. Mike took the opportunity to offer a general synthesis of the limits of vision, explaining visual optics and its application to morphology and physiology. Published in 1981, the *Handbook of Sensory Physiology* chapter [16] was entitled “Optics and vision in invertebrates”, but the theoretical parts included vertebrate eyes, and did much to make sense of the diversity of animal eyes. It was a masterpiece, becoming the theoretical foundation of visual optics in part because anyone could follow Mike’s full account of the underlying physics. Compromises between resolution and sensitivity became understandable, removing the mysteries of how eyes are tuned to nocturnal and diurnal lifestyles or how resolution is optimized over the visual field. For decades thereafter the literature on visual optics simply referred to Mike’s Handbook chapter, and rarely to the earlier work. Later Mike expanded on this work, writing a book with Dan Nilsson, *Animal Eyes* [34], published in 2001 with a second edition in 2012.

Time in Canberra

In 1982 Mike was elected to the Royal Society, and from that year to 1984 he took his young family on a two-year fellowship to the Department of Neurobiology of the Australian National University (ANU) in Canberra. The ANU was intellectually booming with the presence of people from across the globe, such

as David Blest, Joe Howard, Simon Laughlin (FRS 2000), Dan-Eric Nilsson, Daniel Osorio, Allan Snyder (FRS 1990), and, Mike's host, Adrian Horridge (FRS 1969).

From his earlier work, Mike knew that the photoreceptors, which form the "pixels" of the visual image in eyes, are sometimes visible through an ophthalmoscope. With the aim of continuing work on spider eyes, Mike constructed a new, versatile ophthalmoscope from a Spindler and Hoyer optics kit. He did use it for spiders, but his curiosity led Mike to other species. Notably, viewing a snake retina with Allan Snyder, he for the first time observed a vertebrate retinal cone mosaic through the eye's own optics [20] (Figure 2b; see also Jagger 1985). This method has since become routine, but at least for humans requires pupil dilation and adaptive optics to correct aberrations (Liang *et al.* 1997). Comparing spiders, snakes and insects [19,20], Mike was struck by the differences in image quality. In snakes and some spiders the photoreceptors were distinct and clearly separated, whereas in other animals they appeared to blur into each other so that their array was only barely visible through the ophthalmoscope (and hence the animal's own optics). This showed that some retinas 'under-sample' the image, resulting in clearly visible receptor arrays, some use 'matched sampling' and yet others 'over-sample' so the array is blurred. With oversampling the optical image quality limits resolution, but when retinas under-sample the receptor array is limiting. Mike explained the differences as adaptations for rapid motion vision, vision in dim light and maximizing image contrast.

In Canberra, together with Dan Nilsson and Joe Howard, Mike discovered afocal optics in butterfly eyes [18] (Figure 1c). Like most diurnal insects, butterflies have apposition eyes, where the photoreceptors in each ommatidium receive light exclusively from its own facet lens, but butterflies evolved from moths which have superposition eyes, where each photoreceptor receives light from many facet lenses. Superposition optics produce a brighter image and are common in nocturnal animals. Moths have a miniature Keplerian telescope in each ommatidium, which is formed by the facet lens together with a graded index lens in the underlying crystalline cone. As in all superposition eyes, each ommatidium produces an upright image, in contrast to the tiny, inverted image produced in each ommatidium of an apposition eye. This fundamental difference made it difficult to understand how apposition eyes could evolve gradually into superposition eyes or vice versa. This puzzle was resolved when Land, Nilsson and Howard [18] found that the ommatidia of butterfly apposition eyes contain an extremely powerful second lens, with a focal length of a few microns, which together with the facet lens forms a Keplerian telescope and an afocal ray path. They also gave a wave-optics explanation showing that the ommatidial optics of

butterflies were an excellent and unexpected alternative to the standard type of apposition optics that previously had been demonstrated in flies, bees, and horseshoe crabs.

Back in Sussex

By the mid-1980s Mike, memorably described by Qasim Zaidi as “the Marco Polo of vision”, had investigated the visual optics, eye movements and visually guided behaviour in more animal groups than anyone before him. He had a talent for writing in a style that anyone could appreciate and understand, and from the mid-1980s to the end of his life he wrote more than 60 reviews and commentary papers on various subjects, mostly as the sole author. These articles, alongside the text *Animal Eyes* (2001, 2012) [34] co-authored with Dan Nilsson will last far into the future. One of his final publications was the lovely memoir *Eyes to See* [36] which offered a personal view of the “astonishing variety of vision in nature”. Although he made many intricate and innovative studies in diverse animal species, he never lost sight of general principles.

Soon after returning from Canberra Mike was attracted by stomatopods in which the normal compound eye is divided by a distinctive midband of up to six rows of enlarged ommatidia. Stomatopods move their eyes with jerky saccades and rotations, which Mike compared to the then familiar IBM ‘golfball’ typewriter heads, suggesting that the midband is scanning across points of interest [23]. Mike was joined by a research student, Justin Marshall, and by Tom Cronin on sabbatical from the University of Maryland Baltimore County, who was already working on these vicious crustaceans. Together they started unravelling the unique colour and polarization vision of stomatopods [27], and the field has flourished ever since.

A new direction: human eye movements

Having worked on eye movements of spiders, insects [7], crustaceans [23,25], and even a deep-sea snail [17], Mike realized that the eye movements of these animals had much in common with those of humans [9]. In the early 1990’s, he began to study our eye movements from the point of view of a behavioural biologist. As Mike pointed out, humans have the advantage that they can tell you what they’re experiencing. To begin this project he designed a robust and head-mounted eye-tracker, based on a small video camera and simple optics, for visualizing the eye as it moved.

Mike spent the next two-and-a-half decades investigating how humans use their eyes in natural behaviour and what this tells us about visual cognition. The research was successful precisely because he began without specific hypotheses; he wanted to find out what happened and to use his findings to learn how we manage visual input to execute complex behaviours. Much of this work was included in his 2009 book with his former student Benjamin Tatler, *“Looking and Acting”* [32].

The research began with studies of car driving, when the body is fixed in the car seat, so gaze depends only on head and eye movements. As the driver is fully engaged in the task, there is little time for conscious input into eye movements; the behaviour is controlled by basic oculomotor mechanisms. Mike enjoyed driving, especially the Mazda Miata he bought a few years later, and living in a nation with winding country roads and narrow, busy urban streets must also have piqued his interest in this visual behaviour. Mike joined forces with David Lee of Edinburgh University to learn how drivers use their eyes when steering on the winding road up Arthur’s Seat in Edinburgh [24] where, eye tracker in place, they enjoyed driving a fully instrumented Jaguar car (on loan from Ford UK). They found that drivers fixated the apex of each upcoming curve, directing their vision along the line tangent to the edge of the road, and held this angle of view through most of each turn. Analysis of this viewing strategy showed that the angle of the tangent point relative to the car’s location is a function of the upcoming curvature of the road, allowing the driver to plan how to steer through each turn. Some years later, Mike had the chance to study the eye movements of a Formula 3 racing driver. While there were some differences in the visual strategies employed, many of the same principles of using vision to plan and guide steering and of keeping the eyes about a second ahead of the car were used when driving at 125 mph, just as when driving around Arthur’s Seat at 30 mph.

With the portable eye tracker’s utility proven, ball sports caught Mike’s attention. He realized that in some sports the angular velocity of the ball is too high for smooth tracking, so “keeping your eye on the ball” is impossible. With his graduate student, Sophie Furneaux, and Peter McLeod of Oxford University, Mike fitted tennis-table players and cricket batsmen with his eye tracker [26,29]. Strikingly similar eye-movement patterns were observed in both sports. The player judges the point where the oncoming ball will bounce and makes a saccade to that point about 200 ms before the ball arrives. In both games, once a player has the experience to predict the path of the ball after it bounces, a successful hit can follow. After Land and McLeod published their cricket studies in 2000 [29], they received reprint requests from several overseas cricket organizations – but not from any in the UK!

A key finding was that for driving and ball sports the first action taken is an eye movement, directed to a particular location (e.g. the tangent line of a bend or the bounce point of a ball). The command to move must be coupled with an instruction to look for something specific and is followed, typically within a few hundred milliseconds, by a second command to the motor system to execute a necessary action. Each task has its own specific eye movements and actions, which are almost always learned by experience and broadly consistent across individuals. Mike termed these movements and actions “the knowledge base of the oculomotor system” [31], which operates mostly below the level of consciousness. Overall, the top-down instructions to execute a single eye movement and the linked action are somehow encoded centrally in an “action schema” (Fig. 4).

Making tea

Mike wanted to learn how complex tasks are carried out by sequencing the single events of action schemata. The research, done in collaboration with fellow Sussex experimental psychologists Jennie Rusted and Neil Mennie, led to a now-classic study of making a cup of tea [28]. This is a nearly automatic, overlearned task for a typical Briton. Tea-making consists of about 40 to 50 individual actions, making the task complex but not beyond analysis. Unlike the simple schema of Figure 4, the action series is controlled by a higher-level “script” in memory [28]. Subjects wearing an eye-tracker made tea in an unfamiliar kitchen while being recorded by a fixed video camera imaging the work area and the subject’s movements. The recordings were analyzed for every body movement, eye movement, and related action.

Figure 5 shows a ~10s sequence taken from Mike’s own tea-making session, during which the electric kettle was located, picked up, moved to the sink (with the top being removed on the way), held while the correct tap was turned, and finally placed under the water stream to fill [28]. Strikingly, nearly all fixations were to task-related objects: in sequence, the kettle, the lid being removed, the sink, taps, and the stream of water. Actions occurred in similar sequences, each initiated by a body turn followed by one or more visual saccades to the object of interest and then a manipulation of the object.

The analysis revealed that four fundamental roles were executed by visual fixations: locating (finding an object), directing (during a reach, looking at the location where the hand will contact the object), guiding (leading two interacting objects to a proper relationship, such as a lid to a kettle or a teapot spout to a cup), and checking (looking to see that an action is being executed properly, such as monitoring the level of tea in a teacup). Each saccade was directed to the object about a half-second before the

commencement of the action, and the saccade to the next required object occurred about a half-second before the ongoing action was complete [28]. These observations led Mike to propose that the consistent relationship in space and time between vision and action is a fundamental unit of behaviour, which he called the Object-Related Act, providing the building blocks of complex actions. The relationships between gaze, vision, action and planning emphasize how vision and eye movements are part of a larger system for executing and supporting our behaviours. This observation has profoundly influenced research on vision and eye movements, highlighting the risks in studying these systems in isolation and the importance of considering natural behaviour. When Mike started to study human vision in natural behaviour he was one of very few taking this approach, which is now widely recognized as a key to understanding our vision and eye movements, and he is frequently cited in this context.

Mike envisaged that a high-level script sequences individual actions, each of which is adjusted for the particular environment of the task. As the task progresses, the eye movements necessary for its execution seem to be programmed in the oculomotor system's knowledge base – which is inaccessible to consciousness. Managing objects involves interactions between the gaze system (to look in roughly the right place), the visual system (to confirm the identity and orientation of the object specified for the task), and the motor system (to take the relevant action). These three subsystems, which reside in distinct brain regions, must themselves be controlled by a higher-level script that provides the instructions for each given task [30,31,32]. Besides all this, there must be a memory of the locations of required moveable objects (kettle, teacups) and fixed structures (sink, refrigerator).

Mike then asked how understanding the positions and movements of eyes during normal activity can provide a window into the brain [35]. Like others, he recognized that the mind constructs an inner model, which he called the “phenomenal world”. This world has a fixed orientation relative to the outer world, which is not displaced by eye, head or body movements. Somehow, the retinotopic views of objects in the outer world are mapped onto the phenomenal world to produce a simplified internal model (the “egocentric representation”) of the surroundings. This mapping is stabilized by efference copies of motor commands to the oculomotor system and neck positioning system, as well as by direct input from proprioceptors in extraocular muscles and the muscles that position the head on the neck. These and other inputs enable the brain to update its model continuously to represent the external world [33].

The internal model is constructed quickly, as demonstrated by the well-oriented activities carried out in the unfamiliar kitchen in the tea-making study, and can shift as a person moves through space to new

locations. Mike was interested in the means by which the egocentric representation remains stable during body turns and visual refixations. Two internal systems, not well understood, counterrotate the egocentric frame with head turns and corotate the retinocentric frame with eye movements, maintaining an inner representation of the world that matches the actual, fixed external world [35]. We take the seamless operation of both systems for granted, but without them we would constantly be disoriented in our actions.

Ultimately, Mike's interest in human eye movements, visual percepts, and actions led him to consider the nature of consciousness. While he never wrote a paper specifically on this topic, the final two chapters of his book *Eyes to See* [36] discuss his thinking on consciousness in humans and other animals, returning him to the start of his career to unite his work of diverse animals and visual systems. Mike posited an evolutionary scale of consciousness, related to visual competence and sensory awareness. While the rudimentary vision of his first research subjects, the scallops, provides no more information than that needed for an escape response, the complex, stealthy, and seemingly planned paths of jumping spiders approaching prey implied situational awareness. Mike's lifelong research with creatures whose visual abilities spanned much of the evolutionary spectrum allowed him an intuitive entry into their minds, ultimately unifying his outstanding, broad-reaching research interests.

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Figures and Figure Captions

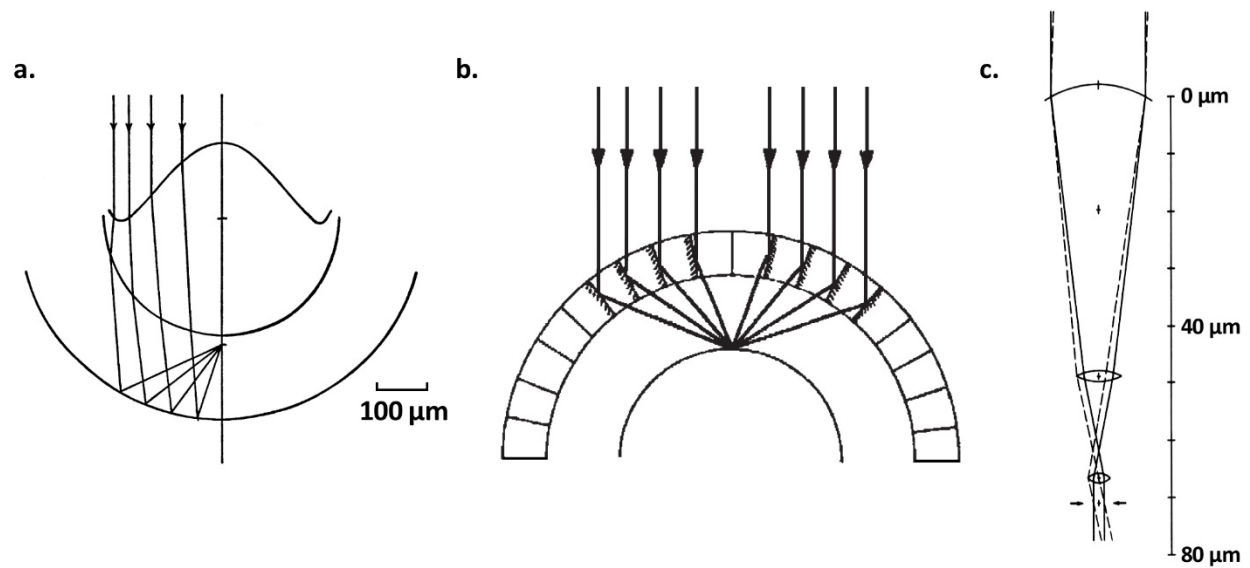


Figure 1

Three focusing mechanisms discovered by Mike Land and co-workers in animal eyes. a) The reflective argenteum in the eye of the scallop, *Pecten maximus*, forms an image without spherical aberration (From Ref [1]. Fig. 9); b) Reflecting superposition optics, based on corner-reflection in the square-faceted compound eyes of some decapod crustaceans (From Ref [11]. Fig. 1). c) Afocal optics in the compound eye of the butterfly *Heteronympha merope*. The ommatidial optics are modelled by a refracting cornea surface and two thin lenses ($f = 37$ and $5 \mu\text{m}$). The ray path is that of a telescope and is shown here by marginal rays entering at 0° (continuous) and 2° (dashed) to the optical axis. The rhabdom connects to the cone at the exit pupil (arrows) of the telescope. The second lens in the crystalline cone has a focal length of about $4 \mu\text{m}$. (From Ref [18]. Fig. 3)

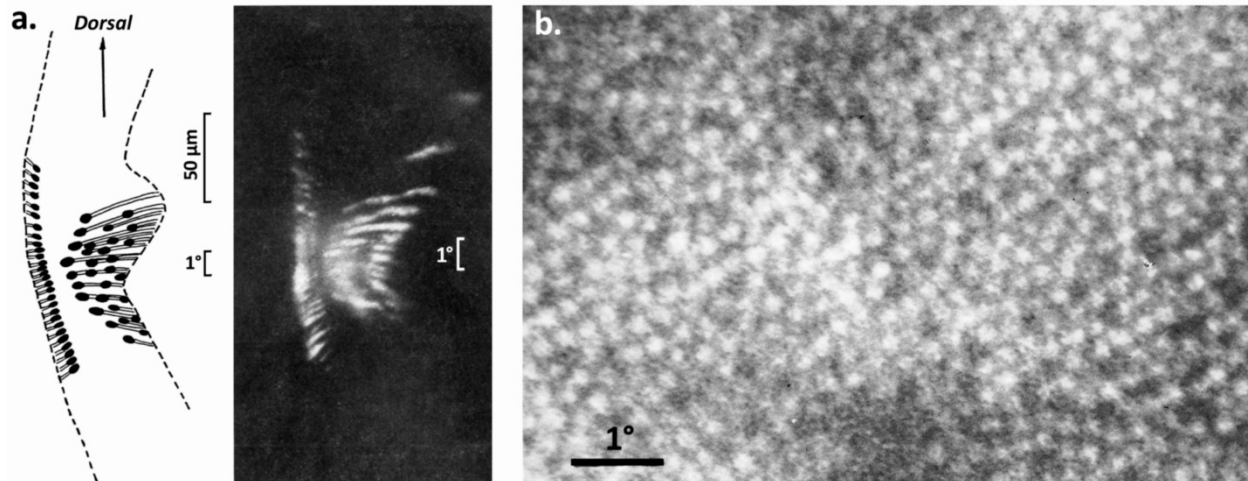


Figure 2.

Ophthalmoscopic images of spider and snake retinas. a.) *Left.* Drawing of layer 4 of the principal eye retina of the jumping spider *Phidippus johnsoni*, from the direction of the incident light. *Right.* Ophthalmoscopic photograph of the retina revealing the intermediate segments of the receptors of layer 4. (From Ref [3] Fig. 7.) b.) Photograph of the retina of the garter snake *Thamnophis sirtalis*. To our knowledge this was the first ophthalmoscopic image of a vertebrate retina, in which the receptors are imaged through the eye's own optics and pupil. The method has since become routine but usually requires adaptive optics. (From Ref [20]. Fig. 2)

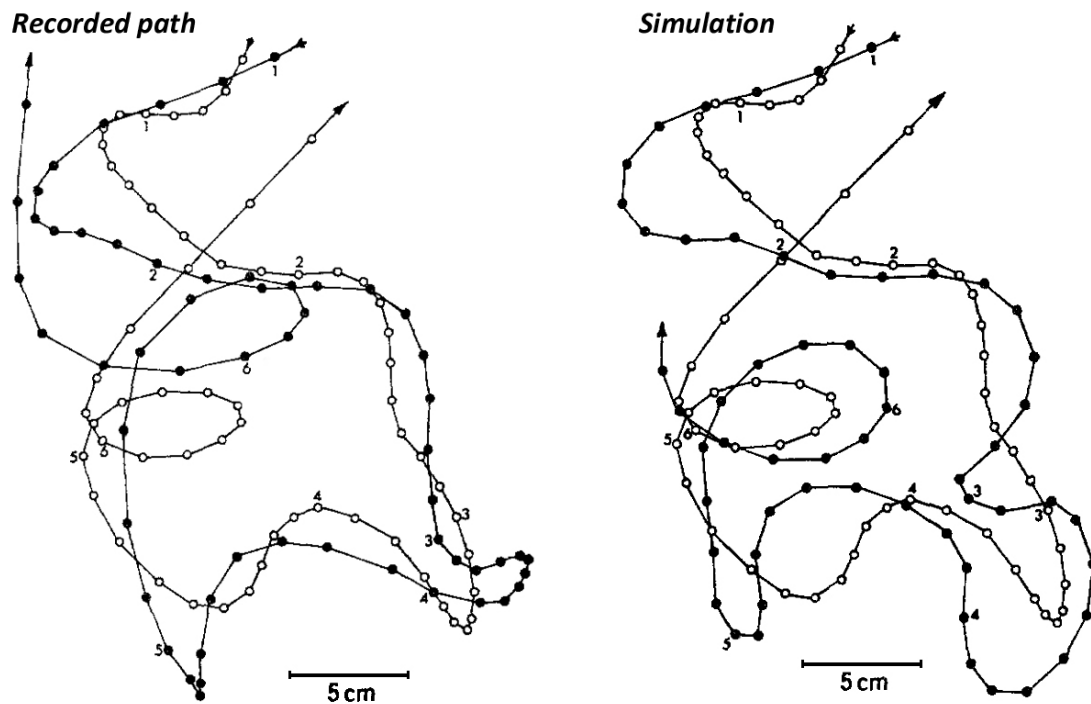


Figure 3.

Pursuit behaviour by male houseflies (*Fannia canicularis*). *Left*. The longest recorded flight paths of leading (solid circle) and pursuing (open circle) flies during the longest recorded chases. Flight paths are indicated by points at 20 ms intervals, with corresponding instants on the two paths numbered at 200 ms intervals. *Right*. Pursuit predicted by a model relating the angular velocity and location on the retina of the leading fly to the response of its pursuer (From Ref [8] Figure 11)

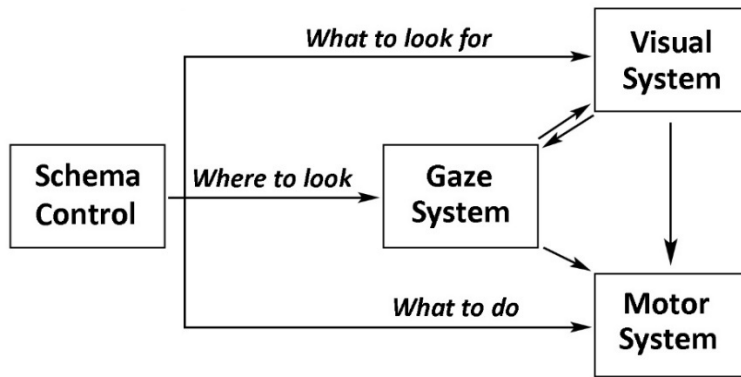


Figure 4:

An action schema. This diagram shows the subsystems proposed by Land and Tatler for the execution of an action. Arrows indicate the interactions. (From Ref. [32]. Figure 1.1)

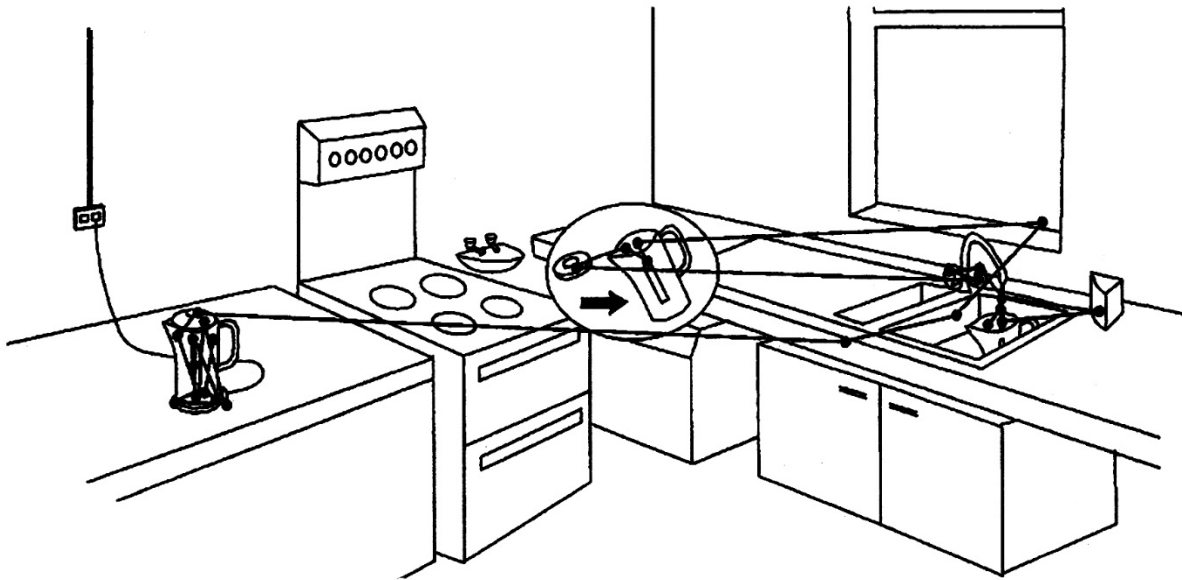


Figure 5.

Making tea. Mike Land's fixations displayed as black dots linked by lines that show saccades as he fills a kettle from the sink. Fixations are to task-related objects, and are stereotyped between individuals, implying a learnt sequence of eye-movements and actions (from Ref [28]. Fig. 2.)

Awards and Recognition

Fellow of the Royal Society (1982) (Council Service [Dates])
Frink Medal of the Zoological Society of London (1994)
Foreign Member of the Royal Physiographic Society of Lund, Sweden (1995)
Alcon Prize for Vision Research (1996)
Academia Europea (1998)
Rank Prize in Optoelectronics (1998)



Suggested Frontispiece (Royal Society Portrait)

Brief Author Profiles

Thomas Cronin



Tom Cronin did his doctoral research at Duke University, working on the photobiology of planktonic crustaceans. This work introduced him to the publications of Mike Land, whom he joined in 1989 for a sabbatical studying the eye movements of mantis shrimps. Mike later joined him for research at the University of Maryland Baltimore County, where Tom is a professor of biological sciences, and at the Duke University Marine Laboratory. These interactions led to a decades-long friendship with the Land family. Cronin's research concerns the visual ecology of a diverse set of animals, ranging from simple sponge larvae to whooping cranes and right whales, but most of his effort has centered on the very strange visual systems of mantis shrimps, generally in collaboration with one of Mike's former graduate students, Justin Marshall.

Dan-Eric Nilsson



Dan-Eric Nilsson is an emeritus professor of zoology at Lund University in Sweden, where he has spent much of his career at the departments of Zoology, and Biology. During his postdoc 1983-1984 in Canberra, Australia, he met Mike Land and the two started a collaboration on the optics of butterfly eyes. After the postdoc period he moved back to Lund University, where he founded the Lund Vision Group, and developed it to an internationally recognized centre for comparative vision research. His main fields of research have been visual optics in invertebrates and the evolution of eyes and vision. He continued to collaborate with Mike on the eyes of various invertebrates and they went jointly on a cruise with the RRS Discovery to the Atlantic in 1987 to work on vision in pelagic animals. Together with Mike, he also co-authored the book "Animal Eyes" 1st edition 2002 and 2nd edition 2012. His current research is focused on visual information in natural environments and how it controls the choice of behaviour.

Daniel Osorio



Daniel Osorio completed his PhD in Neuroscience at the Australian National University, arriving at the same time as Mike Land in 1982. His first project was a study of butterfly colour vision and pupil mechanisms with Mike and subsequently with Dan Nilsson. For this work he built an ophthalmoscope fitted to a goniometer, which allowed stimulation and physiological recording from single known ommatidia. After postdoctoral work in Cambridge and at the ANU, he moved to the University of Sussex as a lecturer in 1992, and has remained there since. He studies the psychophysics, evolution and function of colour vision and visual camouflage in a wide range of animals, including birds, insects, fish, primates and cephalopods.