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Introduction : pretty and witty

(Ernst-Mayr-Lecture am 9. November 1999)

In: Berichte und Abhandlungen / Berlin-Brandenburgische Akademie der Wissenschaften (vormals Preußische Akademie der Wissenschaften) ; 8.2000, S. 307-310

Persistent Identifier: urn:nbn:de:kobv:b4-opus4-32248

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"If it could be demonstrated that any complex organ existed that could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down", so wrote Darwin, always a cautious man and a born sceptic, in his fundamental account on the origin of species. Indeed, what had perplexed him most and left him in a cold sweat, was the piecemeal evolution of a complex, integrated organ like the eye. Nevertheless, he finally reassured himself and claimed that even the human eye "may possibly have been acquired by the gradual selection of slight, but in each case useful deviations". His wife Emma, however, whom he had entrusted with his manuscript if he died, left a tell-tale note in the margin: "A great assumption / E.D.", she scribbled against her husband's claim. In today's *Ernst-Mayr-Lecture* Mike Land will show, vividly and courageously, that Emma's doubts were unjustified.

Of course, Darwin had the human eye in mind. But he would have felt even more uneasy had he known of the bewildering complexity and extreme perfection of the seeing organs in so-called lower animals far apart from human and non-human primates. Incredible as it may seem, there is geometrical beauty in the eyes of, say, such lowly creatures as deep-sea shrimps and night-flying moths; and it is to Mike Land that we owe much of our current understanding of this unsurpassed beauty in eye design, its functional significance and its evolutionary implications.

Educated at Cambridge, Mike started his career in optical physiology with a striking discovery. Most of us know scallops only from the *Coquilles St. Jacques*, and very few will have had the chance to enjoy the 60 beautiful blue eyes with which these animals are endowed. But when Mike, while doing his Ph.D. work at the University of London (UCL) – at the very same place, at which Darwin had lived before he moved to Downe – looked into one of these eyes, he was startled to see an inverted image of himself: not far at infinity, where proper dioptrics should have placed it, but deep in the scallop's eye itself. This chance observation finally led to the discovery of a novel optical mechanism, the mirror-box reflection-type of eye. It later stimulated engineers to apply it to the development of X-ray focussing and collimating devices used, for instance, in modern telescopes and in the etching technology of electronic circuits.

From London Mike moved to Berkeley where he enjoyed the notorious late sixties. He became a Miller Fellow at Gerald Westheimer's famous physiology and psychophysics lab. Again he struck gold, this time with a small spider, the retina of which moved actively within the eye, scanned the image and panned across the scene. This had never been seen in any more highly advanced animal, let alone in humans. But here, built into the front end of a jumping spider, there was what could be called a line-scan camera, in which visual information was taken in by the motion of a one-dimensional retina.

With these discoveries, Mike had immediately established himself as one of the leading optical physiologists. He would later receive the Alcon Prize for Vision Research and the Rank Prize for Opto-electronics. But at Berkeley he still was an entrepreneur, not to say some kind of maverick scientist, who ran across campus bashing trees in search for spiders, and then back in the lab exhibited extraordinary skills in mathematics and physics. He looked into his spiders' eyes through an ingenious, home-made ophthalmoscope, in which the retina, and any image formed on it, could be viewed through the optics of the animal's own eyes: a novel device, which was later adopted by one laboratory after another.

Quick, clever, original, and above all curiosity-driven, pretty and witty in designing his experiments, Mike represents the best in British research traditions: the use of simple, adequate, and elegant methods; the ability of never getting lost in details, nor in shallow over-arching theories; a hit-and-run kind of science rather than the more clumsy continental "systems building", which has the only advantage that one never gets dazzled by making a discovery; in short: relevance and elegance intricately intertwined.

Next, after his return to England, we see Mike attending cricket games (theoretically, at least). For in the meantime he had developed quite some interest in control theory, and hence wondered how a cricket fielder performed when trying to catch a high-ball. In terms of visual computation and motor control this is a tremendously tricky task. But with his quick grasp of the essential, and his love for insects, Mike immediately realized that some male hoverflies faced a quite similar problem when they chased females – and finally raped them in the air. From then on, he regarded manoeuvering flies as disembodied eye movements. He started to film such flies as they pursued an approaching projectile he had shot at them from a peashooter. Out of this analysis came an elegant algorithm, by which a male fly was able to foresee the female's flight path and to compute the proper interception course – and this might well be what human high-ball catchers do as well.

In the seventies this way of looking at problems of control theory was quite unusual, at least compared to what then could have been called the Holy Grail of biocybernetics, a renowned Max Planck Institute, which had also made the fly its main experimental guinea-pig. At this institute, a senior Professor used to explain to each visitor that the fly's visual behaviour could be described best by a set of differential equations. One day, when Mike had become the victim of such a pontifical blackboard lecture, and had apparently not generated enough enthusiasm for this approach, the Professor asked him: "Dr. Land, don't you understand what I am trying to explain to you?" – "Of course, I understand", Mike replied, "but I don't like it". Shortly thereafter, at a memorable Dahlem Conference in Berlin, the debate between the senior and the junior scientist resulted in a clash of opinions, and came to an end. Later, in the evening, I took the picture shown in Figure 1 (the left-hand picture) of victorious Mike.

Some 15 years later Mike changed his field of research and his everyday appearance as well (see right-hand picture in Figure 1). By now he was a Professor at the University of Sussex at Brighton, and a Fellow of the Royal Society. Technologically, he had invented a light video-based, head-mounted device to monitor

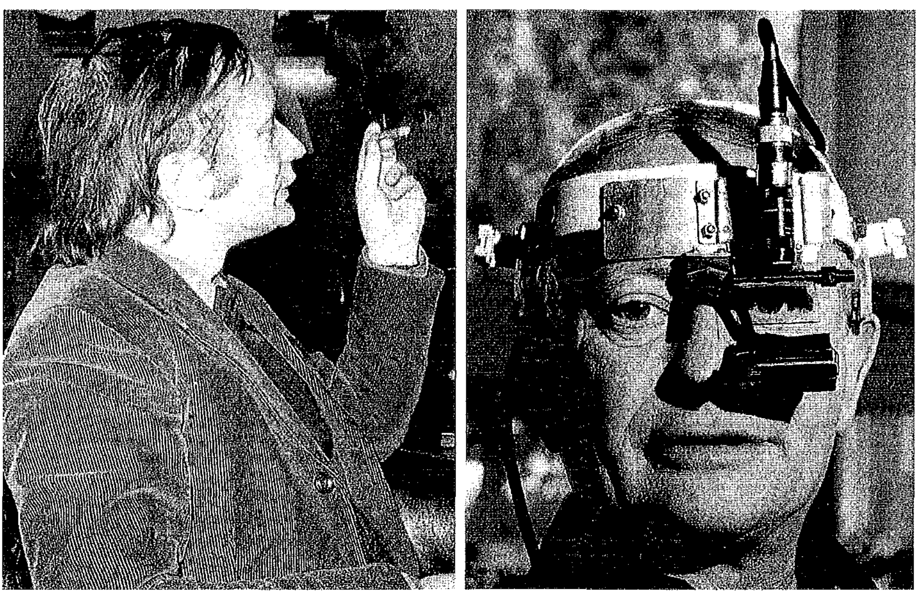

Figure 1
Mike Land, 1977 and 1998

his own eye movements, or the eye movements of any person he was interested in. This cyber-space type of equipment, which leaves its wearer completely free to do ordinary things like reading newspapers, reading music, driving cars, or playing ball games, makes it possible to record simultaneously the observer's eye movements and the observed scene. Armed with his gadget Mike moved from the cricket field to the racetrack and figured out what visual cues and computational rules racing (and normal) drivers use to steer their courses.

However interesting this kind of research might be – and however disclosing, if one used Mike's device to study mate choice among, say, disco dancers – let us now return from eye movements to the eye itself: the topic of this evening. Why are there so many types of eye? Is each type perfectly attuned to the personal circumstances of its owner, or are there evolutionary constraints impeding the most efficient solution? And finally, can we trace back all these different types of eye to one common ancestor? About a year ago, just across the street, in the *Konzerthaus*, the molecular biologist Walter Gehring gave a *Pour le Merit Lecture* on the evolution of eyes. It was the same title as that of today's *Ernst-Mayr-Lecture*, but a different topic, and a completely different kind of reasoning. Walter Gehring argued that common master genes governed the ontogenetic development of all kinds of eye, and made them all homologous structures. But these master genes might well turn out to be the slaves of morphogenetic and functional constraints: common old genes, but diverse new eyes. Is this the message Mike Land will finally convey to us this evening? Let's see. One message, at least, is clear at the outset: In the century to come molecular biology will answer all questions concerning life – except for the interesting ones. And these are the topics Mike Land is now going to talk about.