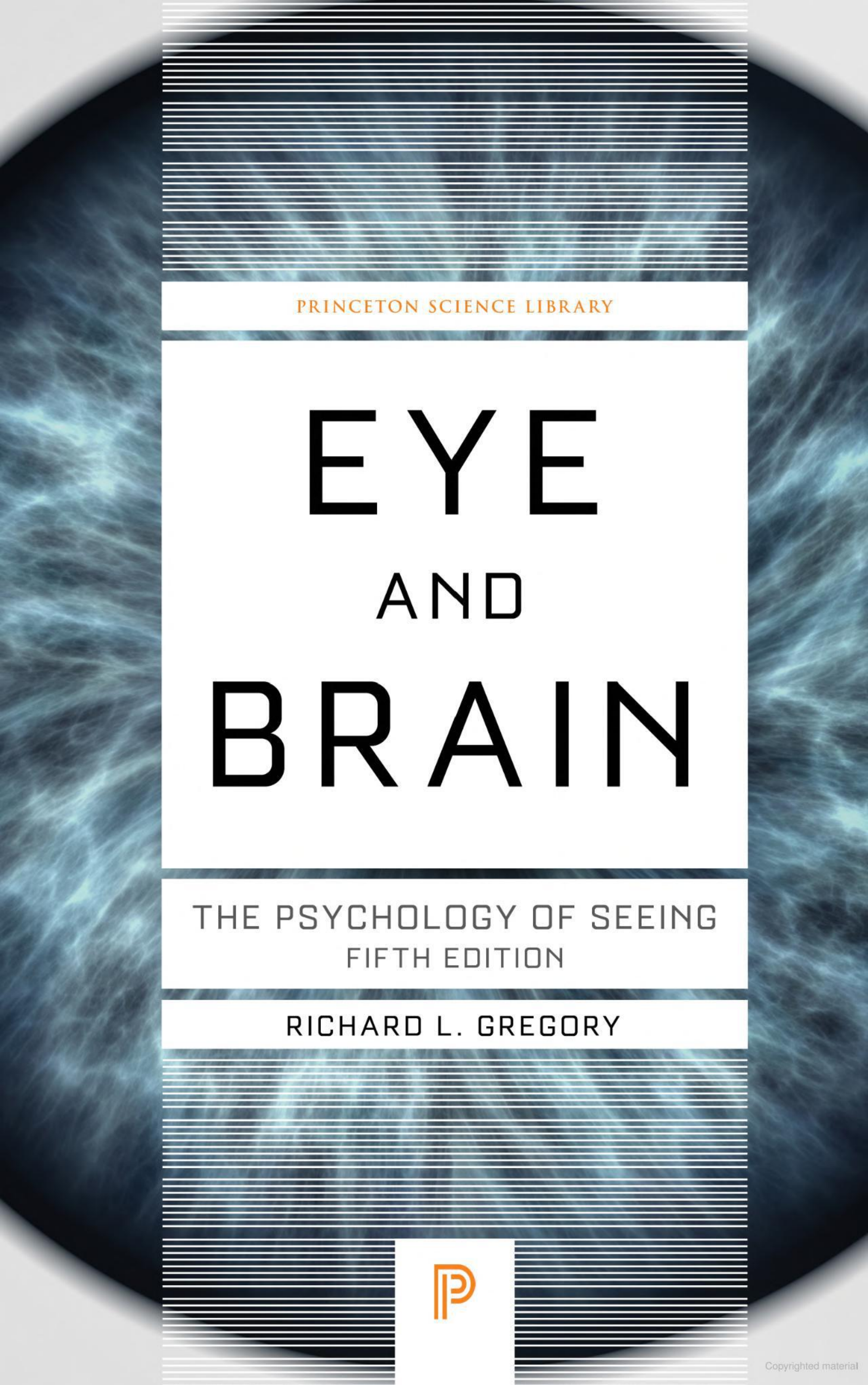

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EYE AND BRAIN

THE PSYCHOLOGY OF SEEING

FIFTH EDITION

RICHARD L. GREGORY

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Eye and Brain

The Psychology of Seeing

Fifth edition

by

RICHARD L. GREGORY

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PRINCETON, NEW JERSEY

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Pretext

This greatly rewritten edition of my first book started from the happy experience of giving lectures and running practical classes (very important!) at the University of Cambridge, England. It was a privilege to share the excitement of trying to explain what we see and how we see, including the strange phenomena of illusions, with generations of students. Many are now friends and colleagues, continuing to be fascinated by the gradually revealed wonders of eye and brain.

This book was not written for examinations or for any formal teaching course, though it has by now been so accepted, especially for psychology, physiology, the visual arts (including architecture), physics, and philosophy. This should not be surprising for perception is the basis of all our experience and understanding, in science and art and everyday life. The study of perception is indeed central to what used to be called by the splendid name—and still is in Scotland—`Experimental philosophy'. For questions and speculation enliven all interesting science.

This book is an *introduction* to the psychology of vision. It is written to be read easily, and to be enjoyed; but this does not mean that its subject is easy or that I have glossed over difficult issues. To take almost the first page: one has to think quite hard just why babies do not have to learn to see things the right way up, though the images in their eyes are upside down. (And why do we see ourselves right–left reversed in a mirror, yet not upside down?)

This is an introduction for solo take-off to reflect about how we see. No one else can altogether see or think for us. I can only hope that this book will be useful and entertaining.

The question **'How do we see?'** may be approached from many points of view. Having approached it in one way we may, through change of insight, come to see it very differently. A classical account is that perception is the passive pick-up of information from the world, the brain having rather little to do. *Eye and brain* takes the very different view, that the brain (or mind) is highly active—constructing perceptions from hardly adequate information from the senses. On this view, illusions of many kinds take on remarkable significance, as

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phenomena well worth studying and trying to understand. Illusions have generally been written off as annoying and sometimes dangerous, but essentially trivial. A main theme of this book is to explain such phenomena of vision—which bridge art and science—as a way of discovering quite a lot about how perception works. It turns out that there are several very different kinds of illusions. Some are due to upsets of the physiology of the nervous system; others, very differently, are like incorrect hypotheses in science—due to inappropriate assumptions, or misplaced knowledge. The first kind of illusions may be compared with computer hardware errors; the second kind with bugs of software—though it does not follow that the brain is just like a digital computer.

How similar perception by machines is, or ever will be, to our own, is a topic of ever-growing interest as this new technology advances. In it, we see modern technology linked to ancient questions of philosophy—perhaps to find solutions even to why we are conscious.

Eye and brain first appeared in 1966, as the first volume of an imaginative series, World University Library, conceived by the distinguished London publisher Lord Weidenfeld. Each volume was lavishly illustrated, and translated into a dozen languages. This book owes a great deal to the original artists, Audrey Besterman and Mary Waldron, who drew so intelligently from my back-of-an-envelope doodles. Almost all of these first pictures are retained in this present much enlarged edition, together with others from *The intelligent eye* (1970), which is now out of print, and a large number of new pictures.

The second, third, and fourth editions (1972, 1977, 1990) of this book added new discoveries and ideas, though its structure remained essentially unchanged. The last 20 years have seen rapid growth of research. The brain sciences, including many kinds of studies of perception, have become a major international scientific endeavour, which has captured some of the greatest scientists from other fields—notably Francis Crick, who with James Watson and colleagues transformed how we think of life itself, through the discovery of the structure and significance of the DNA molecule.

This new edition is rewritten and greatly expanded. I hope it remains readable. It is, indeed, a considerable worry to tamper with a book that has been unusually successful over 30 years. It is a curious, and enjoyable experience, to criticize one's much earlier self and try to make use of the added experience and new ideas of one's later life.

Phenomena of illusion continue to be a major theme. Here is a new attempt to make sense of them, with a suggested classification. For any science, classification is extremely important. It seems high time

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to classify visual phenomena, by appearances and according to theoretical understanding, and this should be stimulated by seeing connections and differences more clearly. This is very much in the same spirit as Mendeleev's periodic table of the elements.

There is now, in this book, a lengthy discussion on the new work on seeing what babies see, and what and how they learn. This concludes with a short section on forgetting how to see: visual agnosia.

Studies of how motion is seen have always been important, but have now greatly advanced with the introduction of computer graphics. Unfortunately these phenomena cannot be demonstrated in a book. I would like to have included more on these experiments, particularly of Stuart Anstis and V. S. Ramachandran at UCSD in California; but perhaps these will have to wait for a new medium. We have, however, added 3-D red–green stereo, so that previously hidden phenomena may now be seen.

Attempts to give vision to machines remain of great interest, with a recent change of emphasis from digital computers to analogue processors, especially interactive neural nets. This is still in a state of flux, and it remains unclear just how far electronics can encapsulate visual brain function. As this is inherently technical, and has not yet yielded quite the dramatic results that were hoped for some years ago, regretfully I have not given it much space here.

Over the last few years there has been a remarkable burst of interest on consciousness, especially how sensations (*qualia*) may be explained. It remains unclear how or why they are caused, or what, if anything, they do. Although none of us know the answers, a few hints are suggested at the end of the book. The study of perception has been ongoing for at least 2000 years, and has accelerated from the work of Helmholtz in the last century, to the use of entirely new techniques, including imaging functions of the brain, with PET and NMR scanning. These promise new understanding of how physiological processes give cognition—understanding and perception. We may hope that later editions of this book will be able to report more fully on these extraordinarily exciting developments, just appearing over the horizon of what we can see.

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Plates

In the plate section at the back of this book there are red–green stereo pictures designed so that they appear three-dimensional when viewed through red–green spectacles (with the red filter on the left). This gives an interesting new perspective on some classic illusions.

To order red–green spectacles, please contact David Burder, 3-D Images Ltd, 31 The Chine, Grange Park, London N21 2EA.

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1

Visions of vision

The eye is a simple optical instrument. With internal images projected from objects in the outside world, it is Plato's cave with a lens. The brain is the engine of understanding. There is nothing closer to our intimate experiences, yet the brain is less understood and more mysterious than a distant star.

We have only to open our eyes, and spread before us lies a banquet of colours and shapes, shadows, and textures: a pageant of rewarding and threatening objects, miraculously captured by sight. All this, from two tiny distorted upside-down patterns of light in the eyes. Seeing is so familiar, apparently so easy, it takes a leap of imagination to appreciate that the eyes set extremely difficult problems for the brain to solve for seeing to be possible. How does it work? How are ghostly images transformed into appearance of solid objects, lying in an outer world of space and time?

From the beginnings of recorded questioning there have been several approaches to how we see. These are very different from current views. An essential problem was how distant objects reached eye and brain, while remaining out there in space. Two and half millennia ago, Greek philosophers thought that light shoots out of the eyes, to touch objects as probing fingers. A different notion at that time was that objects have expanding 'shells' like ripples from a stone dropped on a pool, but maintaining the object's shape to great distances. Called 'sense data' until quite recently by philosophers, they were supposed to be intermediaries—neither matter nor mind—between objects and perceptions. Both of these ideas were serious candidates before it was realized that in the eyes there are images of light, optically projected from the outside world onto the screens of the retinas. Optical images were unknown before the tenth century, and not until the start of the seventeenth were images discovered in eyes. At last it became clear that light does not enter or leave the brain, locked privily in its box of bone. All the brain receives are minute electrochemical pulses of

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various frequencies, as signals from the senses. The signals must be read by rules and knowledge to make sense. Yet what we *see*, and what we *know*, or believe, can be very different. As science advances, differences between perceived appearances and accepted realities become ever greater.

This is far beyond the common account that the eye is a camera; yet this is essentially true, though far from the whole story. It is the uncamera-like features of eyes and brains that most interest us here.

What is striking is the huge amount of brain contributing to vision, giving immense added value to the images of the eyes. Where does this extra richness for vision come from? By some authorities it is simply denied—they see perception as passive acceptance of what is out there, as a window facing the world. But this does not begin to explain how we see objects from the sketchy images of the eyes, even from sparse lines and crude dots of seemingly inadequate pictures. In ideal conditions, object perception is far richer than any possible images in the eyes. The added value must come from dynamic brain processes, employing knowledge stored from the past, to see the present and predict the immediate future. Prediction has immense survival value. It not only makes fast games possible in spite of the physiological signal delays from eye to brain, and brain to hand. Anticipating dangers and potential rewards is essential for survival—made possible by buying time from seeing objects distant in space.

This introduces a particular kind of way of thinking about perception. It is essentially the view of the nineteenth century German polymath—physiologist, physicist, psychologist—Hermann von Helmholtz (1821–1894) who described perceptions as 'unconscious inferences' from sensory data to what might be out there. This is the 'school of thought' accepted here, but there are others. Psychology is unusual among the sciences, in having doubts of its most basic assumptions, with very different alternatives held by different authorities. 'Active' and 'passive' accounts are extremely different ways of describing and explaining phenomena of vision. Few other sciences have such divisions in their basic ideas. There were equally dividing paradigms (as the American philosopher of science Thomas Kuhn calls them) at the time of Darwin, over whether there was evolution of species by natural selection or special creation of each species, but this is now resolved, by almost universal acceptance of evolution. However, although active, essentially Helmholtzian, accounts of perception are now dominant, this was not so a few years ago, and they are not universally held today.

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Paradigms of perception

It might be useful to outline some recent kinds of explanations:

Behaviourism was founded by John Broadus Watson (1878–1958) with his manifesto of 1913: 'Psychology as the behaviourist views it'. This set out to deny consciousness, at least as a ploy to make psychology scientifically respectable. Behaviourism was extremely influential in America until the 1980s, especially with the experiments and ideas of B. F. Skinner. It is based on the earlier work of the Russian physiologist Ivan Petrovich Pavlov (1849–1936) with his experiments on conditioned (or 'conditional') reflexes. Pavlov showed that, starting with an innate (inherited) reflex, such as salivating to the sight or smell of meat, dogs would come to salivate to any stimulus (such as a bell) presented at the same time or just before the food. It proved possible to build up chains of conditioned reflexes. For the behaviourists, it seemed that chains of conditioning would explain all learned behaviour, even language.

They listed innate reflexes observed in babies, and measured strengths of drives for rewards. So they developed a scientifically respectable-looking 'atomism' for describing complex behaviour from simple components.

Problem solving, at least for animals such as cats, was supposed to be by trial-and-error—without insight into the nature of a problem. Perception and behaviour were supposed to be controlled quite directly by stimuli, with modifications from internal states of drives such as hunger, so that with sufficient knowledge psychology should become a perfectly predictive science. This has not worked out. Watson's denial of consciousness makes psychology even more like physics; but for most of us today, it **threw the baby out with the bath water**.

Gestalt psychology was a very different rival school. Founded by a group of German scientists in the 1920s, the emphasis was on dynamics and 'holism'. Many of the Gestalt psychologists (entirely different from recent Gestalt therapy) fled from Nazi Germany under Hitler, to settle in America where they had a major influence.

A 'Gestalt' was a grouping of elements such that the whole is greater than the sum of its parts. Analysis into perceptual components was not supposed to be possible. An important concept was 'pregnance', roughly, 'pregnant with meaning'. Problem solving was supposed to

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be by 'insight'. A famous example is Wolfgang Kohler's chimpanzee Sultan; presented with a banana out of reach and a number of short sticks, he was described as looking at the sticks for several minutes, then suddenly joining two together to pull down the banana. Throughout there is an emphasis on sudden solutions, with sudden insights.

The Gestalt psychologists described visual perceptions as more than the sum of stimuli, organized according to various laws. These were mainly derived from subjective reports of how arrangements of dots are seen as patterns: which dots 'belong' together, form lines and so on, or are separate. This may seem vague, hardly 'scientific'; but the Gestalt laws of organization have turned out to be important for perception of sight and sound. They have been taken up by the artificial intelligence (AI) community, especially for programming computers to recognize patterns and objects. The laws include:

(1) closure—tendency for a roughly circular patterns of dots to be seen as 'belonging' to and forming an object;

(2) common fate—parts moving together, as leaves of a tree, seen as an object;

(3) contiguity of close-together features; and a preference for smooth curves.

The laws of organization were supposed to be inherited, but as they correspond to common features of almost all objects, learning could be involved, to give us all much the same visual organizations. Gestalt notions of brain physiology (electrical fields and so on) have been abandoned.

Cognitive psychology, in its various forms, denies that perception and behaviour are controlled by stimuli, emphasizing the importance of general background knowledge and more-or-less logical thought processes. How far these apply to perception is controversial. Generally, visual perception has been thought of as quite separate from cognitive problem solving, but this can be questioned. However, Hermann von Helmholtz did think of visual perceptions as unconscious inferences, and so related perception to thinking.

The Cambridge psychologist Kenneth Craik (1914–45) put forward the notion that the brain works with physiologically existing functional 'internal models' of perceived and imagined objects and situations. This is now generally modified to a more symbolic account; but the notion of *representing* by the brain is accepted as central to cognitive approaches.

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The intelligent eye

This philosophy, or paradigm, is largely derived from Helmholtz. It is, that visual and other perception is intelligent decision-taking, from limited sensory evidence. The essential point is that sensory signals are not adequate for direct or certain perceptions; so intelligent guessing is needed for seeing objects. The view taken here is that perceptions are predictive, never entirely certain, *hypotheses* of what may be out there.

It was, perhaps, the active intelligence of perception that was the evolutionary start of conceptual problem-solving intelligence. When, a generation before Freud, Helmholtz called perceptions unconscious inferences he was much criticized—for how could blame or praise be applied to unconscious perceptions, and actions? We are still puzzled by these issues.

There are many traps along the way of exploring Eye and Brain. It is important to avoid the temptation of thinking that eyes produce pictures in the brain which are perceptions of objects. The pictures-in-the-brain notion suggests an internal eye to see them. But this would need a further eye to see *its* picture—another picture, another eye—and so on forever, without getting anywhere. Early this century, the Gestalt psychologists held that perceptions were pictures inside the brain: supposed electrical brain fields copying forms of objects. So a circular object would produce a circular brain field. Presumably a house would have a house-shaped electrical brain-picture, though this is far less plausible. A green object having a green brain-trace is ridiculous. This notion, known as isomorphism, led to supposing that properties of brain fields produce visual distortions (like bubbles tending to be spherical), visual phenomena being explained by their supposed mechanical or electrical properties. There is no evidence for isomorphic brain traces.

We now think of the brain as *representing*, rather as the symbols of language represent characteristics of things, although the shapes and sounds of language are quite different from whatever is being represented. Language requires *rules* of grammar (syntax), and *meanings* of symbols (semantics). Both seem necessary for processes of vision; though its syntax and semantics are implicit, to be discovered by experiment.

Some puzzles of vision disappear with a little thought. It is no special problem that the eyes' images are upside down and optically right–left reversed—for they are not seen, as pictures, by an inner eye.

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As the image is not an object of perception, it does not matter that it is inverted. The brain's task is not to see retinal images, but to relate signals from the eyes to objects of the external world, as essentially known by touch. Exploratory touch is very important for vision. It matters that touch–vision relations remain unchanged. When changed experimentally (with optically reversing prisms, or lenses or mirrors) then a problem is set up, and special learning is required. No special learning is needed for a baby to see the world the right way up.

The Gestalt psychologists made some excellent suggestions, realizing that the visual system has to solve some very difficult problems, which arise right at the start. How does the mosaic of retinal stimulation give perception of individual objects? (This also applies to hearing, especially of speech. We can only distinguish separate words in familiar languages). The visual separations of objects are not given simply by borders of light on the retinas. Separations into objects is given by various rules, and by knowledge. Sharp borders are rather rare, except for line drawings, which are not typical and present their own problems.

The tendency to group elements into wholes was investigated by the Gestalt psychologists, with patterns of dots. Their experiments suggested various rules of organization for object creation. This was a much more useful idea than isomophism, and it has turned out to be important for programming visual computers, though this development is in its infancy. We can see something of dynamic grouping in an array of dots (see Figure 1.1). The dots are equally spaced, but there is a tendency to 'organize' them into columns and rows. We can see in ourselves active try-outs for organizing visual data into objects. With more complexity, groupings and re-groupings can become more dramatic (Figure 1.2).

If the brain were not continually trying out organizations of data, for searching for objects, such as faces, the cartoonist would have a hard time. In fact all he or she has to do is to present a few well-chosen lines and we see a face, complete with an expression. This essential process of vision can, however, go over the top to make us see faces in the fire, galleons in the clouds, or the Man in the Moon. Vision is certainly not infallible. This is largely because knowledge and assumptions add so much that vision is not directly related to the eyes' images or limited by them—so quite often it produces fictions. This can be useful, as images are inherently inadequate, but visual fictions, and other illusions, worry philosophers seeking certainty from sight.

How did such complex processes for representing things start?

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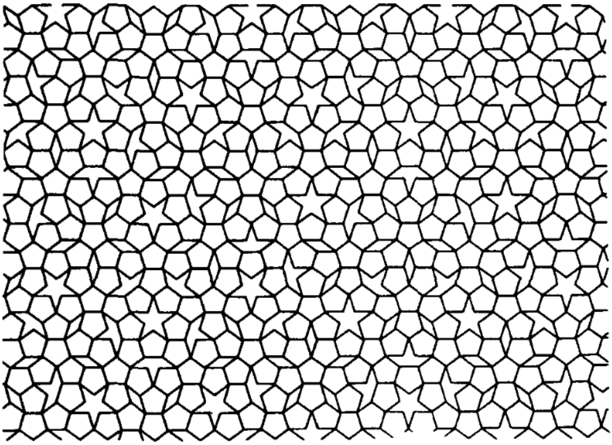

1.2 These circles form intricate ever-changing patterns through the dynamics of vision.

Many reflexes still protect us (such as blinking to a puff of air on the eye, or to a sudden loud sound) and reflexes are essential for the maintenance of body functions such as breathing and digestion. But gradually, through evolution, direct control from outside objects has been largely replaced by more and more indirect representations of objects and situations. This has the huge advantage that behaviour can be appropriate to properties of objects that are not and often cannot be signalled by the senses. Thus we pick up a glass to drink not simply from stimuli, but from knowledge of glasses, and what they may contain. By contrast, a frog surrounded by dead flies will starve to death, for though they are edible it does not see them, as they do not move.

These brain representations are far more than pictures. They include information of what various kinds of objects may do, or be used for. For behaviour to be appropriate in a wide variety of situations requires a great deal of knowledge of the world. Knowledge must be selected and accessed within a fraction of a second to be useful for perception, or the moment for action (or survival) will pass. So the intelligence of vision works much faster than other problem solving. This may be why perceptions are quite surprisingly separate from generally more abstract conceptions, and may disagree. Thus, one experiences an illusion, though one knows it is an illusion and even what causes it. Illusions tell us a great deal—sometimes, as I shall show, more than we would wish to know!

Here, I have introduced the kind of approach to vision which is

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developed in this book. This may be called an *indirect* and *active* account. Not all authorities will agree with it. The alternative—that perceptions are directly from the external world—was argued most strongly by the American psychologist James J. Gibson (1904–1979), at Cornell University. His experimental work, especially on moving and stationary gradients for depth perception (Figure 9.18), is justly celebrated. Gibson considered that seen depth and form are determined by patterns such as these, from what he calls the 'ambient optical array' of light. Gibson's theory is a kind of realism, in which perceptions are supposed to be 'picked up' from the world, rather than created as representations. Realism has always been attractive to philosophers, as it promises reliable perception, and so unquestionable bases for empirical knowledge. Given retinal images, and the complexities of the physiology of vision, as well as the richness of illusion (see Chapter 10), it is hard to see how this can be literally true. Gibson's essentially *passive* account is very different from the notion in this book, that perceptions are constructed hypotheses.

Phenomena of illusion are played down as embarrassments by *direct* theorists such as Gibson, but are grist to the mill, and evidence for, knowledge-based processes of perception. But if past experience, assumptions, and active processing are important, there can hardly be raw data for vision. Rather, we might say that perceptual data are cooked, by processes we shall look at here in considerable detail.

Perceptions as hypotheses

The indirectness of vision and its complexity are evident in its physiology. As much as half the cortex of the brain is involved, including rich 'down-going' pathways. Its activity is evident from physiological recordings and from many visual phenomena. These include ambiguities of various kinds, and our ability to see objects in a few sketchy lines of a picture.

Cartoons (such as Figure 1.3) bring out the importance and power of knowledge and assumptions for seeing more than meets the eye.

There are many well known ambiguous figures, which show that the same pattern of stimulation at the eyes can give rise to very different perceptions. There are three kinds (Figure 1.4): those which alternate as *objects* or *space* between objects (figure–ground); those which spontaneously switch in *depth;* and those which change from one *object* into a different object or kind of object.

We shall have a lot to say about visual ambiguities as these phenomena are intriguing and useful for teasing out kinds of processes of

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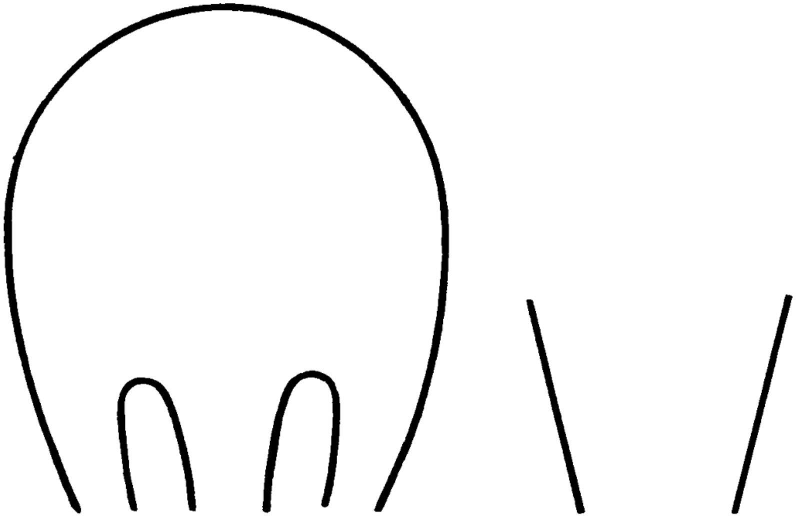

1.3 A joke figure—what is it? Just a bunch of meaningless lines? As soon as you see it as objects, it will suddenly appear almost solid, as objects not mere patterns. (The answer is given at the end of this chapter.)

vision. They are important in art, and they can present hazards in real-life situations such as driving and flying. The essential problem for the brain to solve is that any given retinal image could be produced by an infinity of sizes and shapes and distances of objects, yet normally we see just one stable object. So the usual lack of phenomenal ambiguity is even more remarkable than the brain's occasional failure to make up its mind.

A central notion here is that perceptions are *hypotheses*. This is suggested by the fact that retinal images are open to an infinity of interpretations, and from the observed phenomena of ambiguity. The notion is that perceptions are like the predictive hypotheses of science. Hypotheses of perception and of science are risky, as they are predictive and they go beyond sensed evidence to hidden properties and to the future. For perception, as for science, both kinds of prediction are vitally important because the eye's images are almost useless for behaviour until they are read in terms of significant properties of objects, and because survival depends on behaviour being appropriate to the immediate future, with no delay, although eye and brain take time to respond to the present. We behave to the present by anticipation of what is likely to happen, rather than from immediate stimuli.

Seeing a table, what the eye actually receives is a grainy pattern

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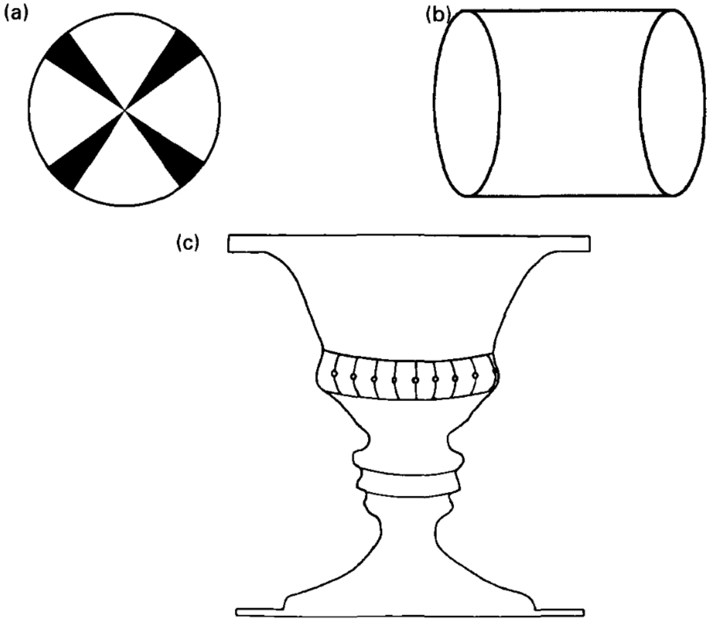

1.4 Kinds of ambiguities: (a) figure–ground switching (or object and space swapping), (b) depth flipping, (c) object changing.

which is read as wood—though it might be a plastic imitation, or perhaps a picture. Once the *wood* hypothesis is selected, behaviour is set up appropriately. People who live with plastic tables pretending to be wood do terrible damage to mahogany! Science and perception work by knowledge and rules, and by analogies. Figure 1.5 gives an archaeological analogy. Some of the holes in the ground might be ancient post holes; others might be rabbit holes, to be ignored. One group of archaeologists accepted close-together large holes as evidence for a grand entrance. These were altogether rejected by the other archaeologists. One group constructed a large rectangular hut: the other, a small rectangular hut and a circular building. 'Bottom-up' rules—holes being close together and forming straight lines or smooth curves, and 'top-down' knowledge or assumptions of what kinds of building were likely—affected the 'perceptions'. Both could have been wrong.

The visual brain has the same kind of problem for accepting or rejecting evidence from patterns of photons in the eyes. Seeing objects involves general rules, and knowledge of objects from previous experience, derived largely from active hands-on exploration.

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A central theme of this book is that perceptions are much like hypotheses of science. Hypotheses of science do not only have ambiguities; they can also have or produce, distortions, paradoxes, or fictions. It is interesting that all of these can appear as phenomena of perception. For under various conditions which can be set up and investigated, as well as in normal life, we can see distortions, paradoxes and fictions. With ambiguities, these turn out to be key phenomena for investigating and understanding perception.

The big difference between hypotheses of science and perceptual hypotheses is that only perceptions have consciousness. We will hazard a guess as to why this might be at the end of the book.

What is so special about human vision? We learn a lot from observing other animals; but only humans can draw or paint representations, and only humans have a structured language. It turns out that both pictures and language depend on imaginative use of ambiguities.

Our early human ancestors were able to represent and see mammoths and bison in sketchy lines and blodges on cave walls. It was presentations of alternative realities, and playing with fantasies through ambiguities, that released mankind from the tyranny of reflexes and tropisms of our distant ancestors. So humans took off from nature, into evocative art and questioning science, making civilization possible.

Why we are so biologically special, with our huge brain and knowing eyes, is beyond the range of this book and the ability of its author to answer.

Key to Figure 1.3

Washer woman with pail

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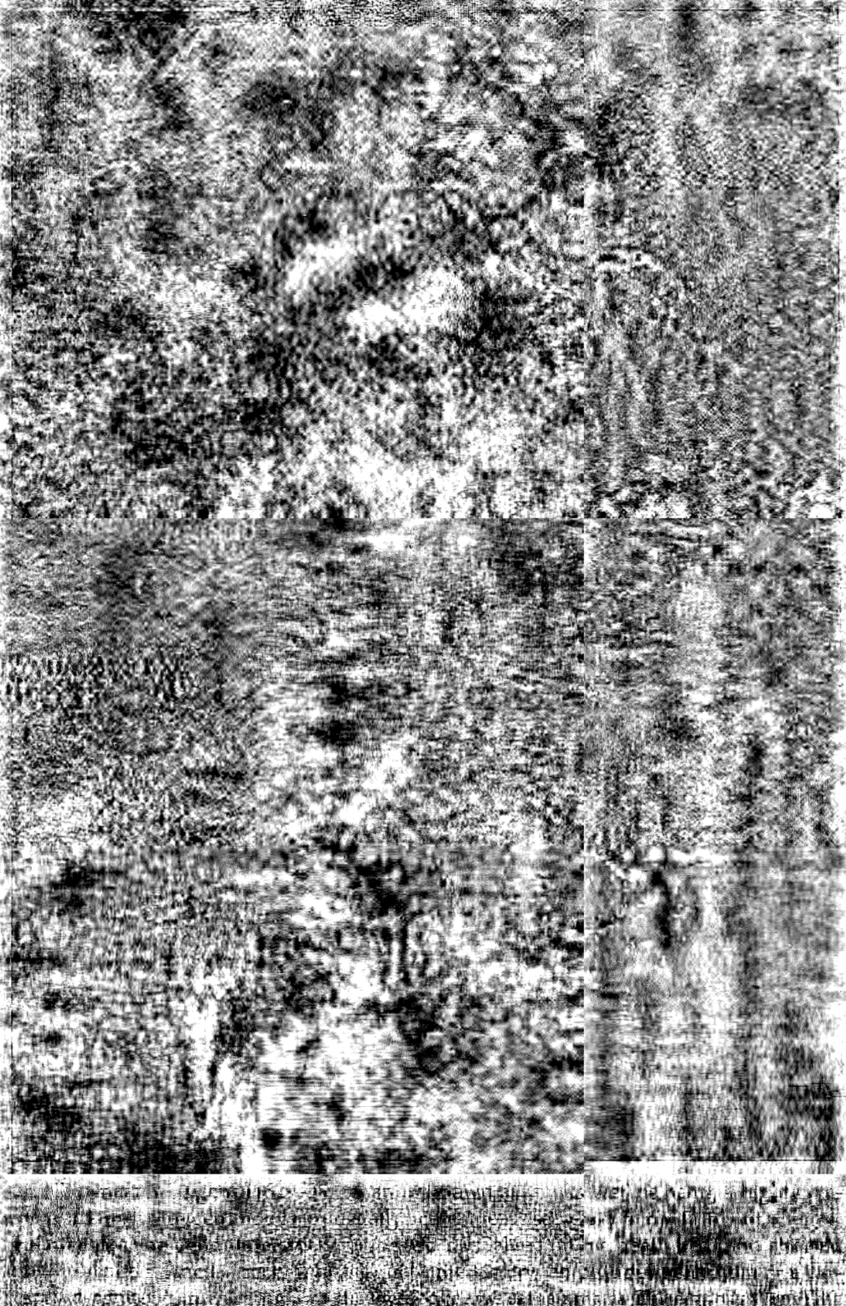

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contact with each other. Any disturbance, he suggested, would be carried in all directions through the packed spheres as a wave, and this wave is light.

The controversy over the nature of light is one of the most interesting in the history of science. A crucial question in the early stages of the discussion was whether light travels at a finite speed or whether it arrives instantaneously. This was answered in an entirely unexpected way by a Danish astronomer, Olaus Roemer (1644–1710). He was engaged in recording eclipses of the four bright satellites orbiting Jupiter, and found that the times he observed were not regular, but depended on the distance of Jupiter from the earth. He came to the conclusion (in 1675) that this was due to the changing time light took to reach him from Jupiter's satellites—the time increasing when the distance increased—because of the finite speed of light. The distance of Jupiter varies by about 300 000 000 km (twice the distance of the Sun from Earth), and the greatest time difference he observed was 16 minutes 36 seconds earlier or later than the calculated time of the eclipses of the satellites. From his somewhat faulty estimate of the distance of the Sun, he calculated the speed of light at 309 000 km per second. With our modern knowledge of the diameter of the Earth's orbit we correct this to about 300 000 km per second, or 3×10^{10} cm/s. The speed of light has since been measured very accurately over short distances on earth and is now regarded as a primary constant of the universe.

Because of the finite speed of light and, more important for terrestrial objects, the considerable delay while nervous messages reach the brain, we always sense the past. Our perception of the Sun is eight minutes late, and all we know of the furthest object visible to the unaided eye (the Andromeda nebula) is from before humans appeared on earth. For nearby objects, there is the neural delay of several hundredths of a second, which is significant for fast action.

The value of 3×10^{10} cm/s for the speed of light strictly holds only for a perfect vacuum. When light travels through glass, or water, or any other transparent substance, it is slowed down to a velocity which depends on the refractive index (roughly the density) of the medium through which it passes. This slowing down of light is extremely important. It is this that causes prisms to bend light and lenses to form images. The principle of refraction (the bending of light when passing through changes of refractive index) was first understood in 1621 by a Dutch mathematician at Leyden, Willebrod von Roijen Snell (1591–1626). Snell died at thirty-five, leaving his results unpublished. The French philosopher–mathematician René Descartes (1596–1650) published the law of refraction, or sine law, 11 years later, (Figure 2.4).

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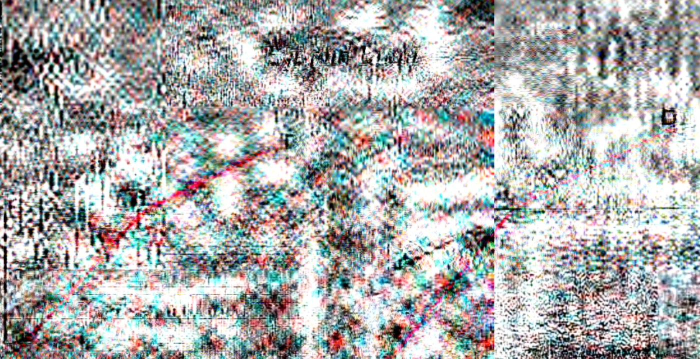

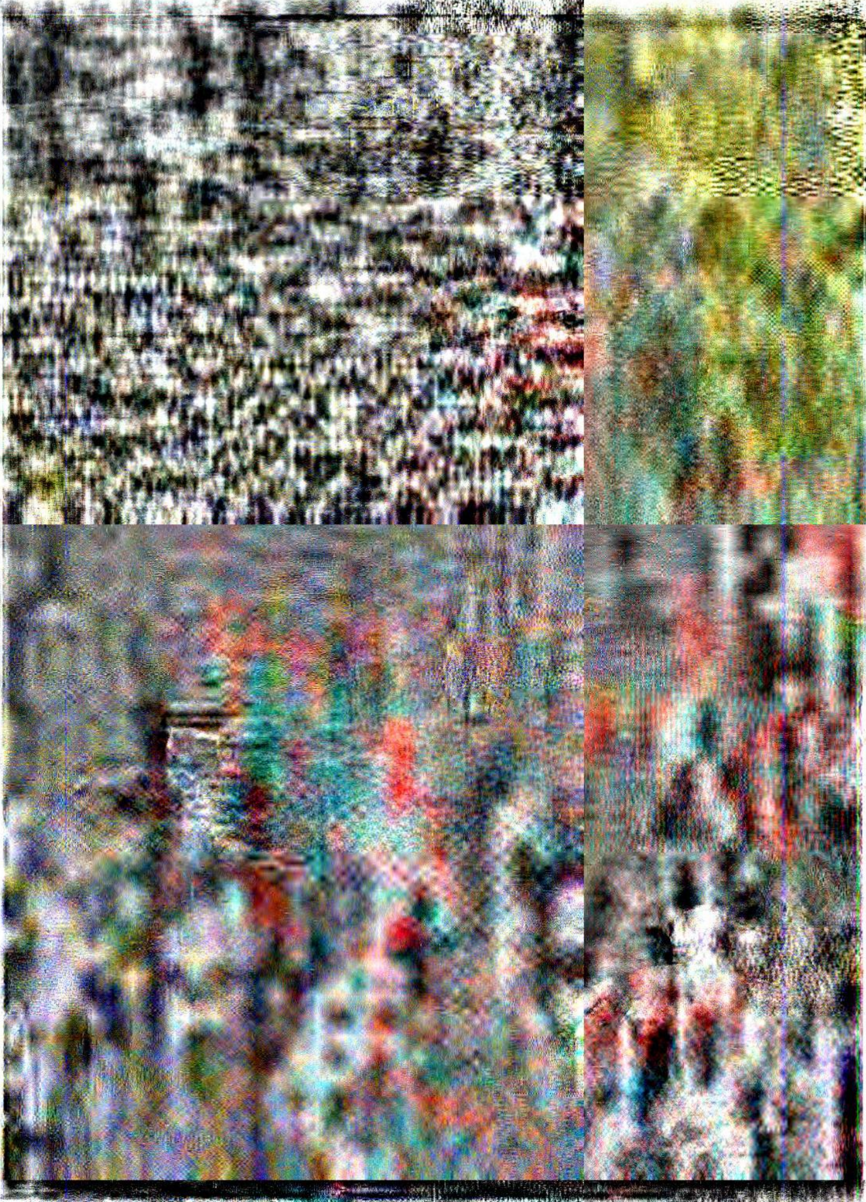

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The first experiment for measuring the number of quanta required for the eye to detect light was undertaken in 1942 by three physiologists, S. Hecht, S. Schlaer, and M. H. Pirenne. Realizing that the eye must be almost as sensitive as theoretically possible, they devised an ingenious experiment depending on probabilities, based on a function, the Poisson distribution. This gives the expected distribution of hits on a target. The idea is that at least part of the moment-to-moment variation in the effective sensitivity of the eye is not due to anything in the eye, or the nervous system, but to the moment-to-moment variation of energy of a weak light source when there are only a few quanta arriving. Imagine a desultory rain of bullets: they will not arrive at a constant rate, but will fluctuate. Similarly there is fluctuation in the number of light quanta arriving at the eye. So a given dim flash may contain a small or large number of quanta, and is more likely to be detected if there happen to be more than the average number in the flash. From lengthy experiments to build up 'frequency-of-seeing' curves, the number of quanta can be deduced from the steepness of the curves. So basic physics is important for vision.

The quantal nature of light is important for detecting fine detail. One of the reasons why it is possible to read only the largest newspaper headlines by moonlight is that too few photons fall on the retina to build up a complete image (within the time-span over which the eye can integrate energy, which is about a tenth of a second.) This is pure physics. Sometimes it is hard to establish whether a visual effect should be thought of as belonging to psychology, to physiology, or to the physics of light.

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3

Eye

In the beginning

How did eyes evolve? Through what stages did their incredibly sophisticated retinas, their receptors, lenses, irises, and controlling muscles develop? Isn't there a chicken and egg problem here? For what use is an eye without a brain to interpret its images?

The problem of how eyes developed, presented a challenge to the theory of evolution by natural selection which gave Charles Darwin, at the time of the publication of *The origin of species* in 1859, his famous 'cold shudder'. For Darwin's theory of how organisms evolve is very different from inventing and designing with human intelligence. When an engineer sets out to improve an instrument, he can go 'back to the drawing board' and make experimental models, most of which will not work well, if at all; but this is hardly possible for natural selection, for each step must confer some advantage on its owner. What use is a half-made lens? What use is a lens giving an image if there is no brain capable of making effective use of it? How could such a brain come about before there was an eye to feed it information? There is no master plan for evolution; no looking ahead, no experimental inefficient try-outs. Eyes and brains have come about through slow blind trial and error. To retrace the steps we must look for possible advantages at each stage—though allowing that something with one advantage may serve a new quite different use. Who could have guessed that the jaw bone of ancient fish would become the human inner ear? Evolution of the eye and other senses may not be simple linear developments, with each step an improvement on the last for the same function, as new uses may appear. Thus a lens might start as a protective window, to become curved and focus light perhaps millions of years later.

How did eyes start? Almost every living thing is sensitive to light. Plants accept the energy of light, some moving to follow the Sun

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almost as though flowers were eyes to see it. The first eyes responded only to light and changing intensity of light, with no imaging. Perception of form and colour waited upon more complicated eyes capable of forming images, and brains sufficiently elaborate to interpret their neural signals in terms of objects.

The later, image-forming eyes, developed from light-sensitive spots on the surface of simpler animals. How this occurred is largely mysterious but we do know some of the characters in the story. Some can be seen as fossils; some are inferred from comparative studies of living species; some appear fleetingly during the development of embryo eyes.

Response to light is found even in single-celled organisms. In higher forms we find specially adapted cells to serve as receptors sensitive to movement. These cells may be scattered over the skin (as in the earthworm) or they may be arranged in groups, lining a depression or pit, which is the beginning of a true image-forming eye.

It seems likely that photoreceptors became recessed in pits because there they lay protected from the surrounding glare, which reduced their ability to detect moving shadows heralding approach of danger. The primitive eye pits were open to the risk of becoming blocked by foreign particles lodging within them, so shutting out the light. A transparent membrane developed over the eye pits, serving to protect them. When, by chance mutations, this membrane became thicker in its centre, it became a crude lens. The first lenses served merely to increase intensity: later they came to form useful images. An ancient pit type of eye is still to be seen in the limpet (Figure 3.1). One living creature—*Nautilus*—has an eye still more primitive, for there is no lens but just a pinhole to form the image. The inside of the eye of *Nautilus* is washed by the sea in which it lives; eyes such as ours are filled with a specially manufactured fluid (the aqueous humour) to replace the sea, and human tears are a salty re-creation of primordial oceans which bathed the first eyes.

Here we are concerned with human eyes and how we see the world. Ours are typical vertebrate eyes, and not among the most complex or highly developed, though the human brain is the most elaborate of all brains. Complicated eyes often go with simple brains: in pre-vertebrates we find eyes of incredible complexity serving tiny brains. The compound eyes of arthropods (including insects) consist not of a single lens with a retina of many thousands or millions of receptors; but rather it is many lenses with a small group of receptors, effectively a single receptor for each lens. The earliest known fossil eye belongs to the trilobites, which lived some 500 000 000 years ago.

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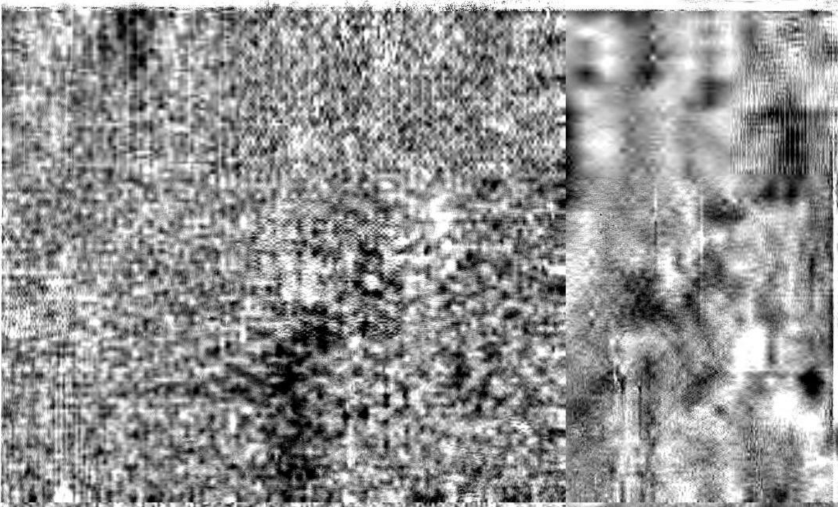

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