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What does the brain see? How does it understand?

HORACE BARLOW

People interested in images, for whom this book is written, can be divided into two groups: those who are mainly concerned with images in the outside world before they are presented to the eye, and those, like myself, who investigate what happens to them after they have entered the eye. The first group includes artists who create all sorts of images, critics who examine them, historians who trace their origins, and a large group of people who use images for entertainment and utilitarian purposes – even commercial or political ones. The second group consists of those who try to find out how the images swallowed by the eye are digested to provide new insight and understanding in the hungry mind.

One reason for making this division is that the two groups use different languages, and it is sometimes hard for them to understand each other. The authors of this book are supposed to have presented their material in a non-technical way that is suitable for general readers, but we sometimes fail because it is so difficult to explain universally accepted preconceptions and to avoid buzzwords that one's colleagues understand perfectly well. What happens behind the eye is especially hard for in-front-of-the-eye experts to understand, and the first aim of this chapter is to give a brief account of the neural hardware that lies behind the eye and the way we think images are represented in it. Those who know all this should skip to Part 2 (p.20), where I attempt the more difficult task of defining what is meant by understanding an image, and indicate how I think the brain may start to do this.

Part 1 How the brain sees

There are philosophical difficulties in saying that the brain 'sees', and these are discussed further by Colin Blakemore (Chapter 17), Nelson Goodman (Chapter 22), and Roger Shepard (in his Postscript). Jonathan Miller (p.1)

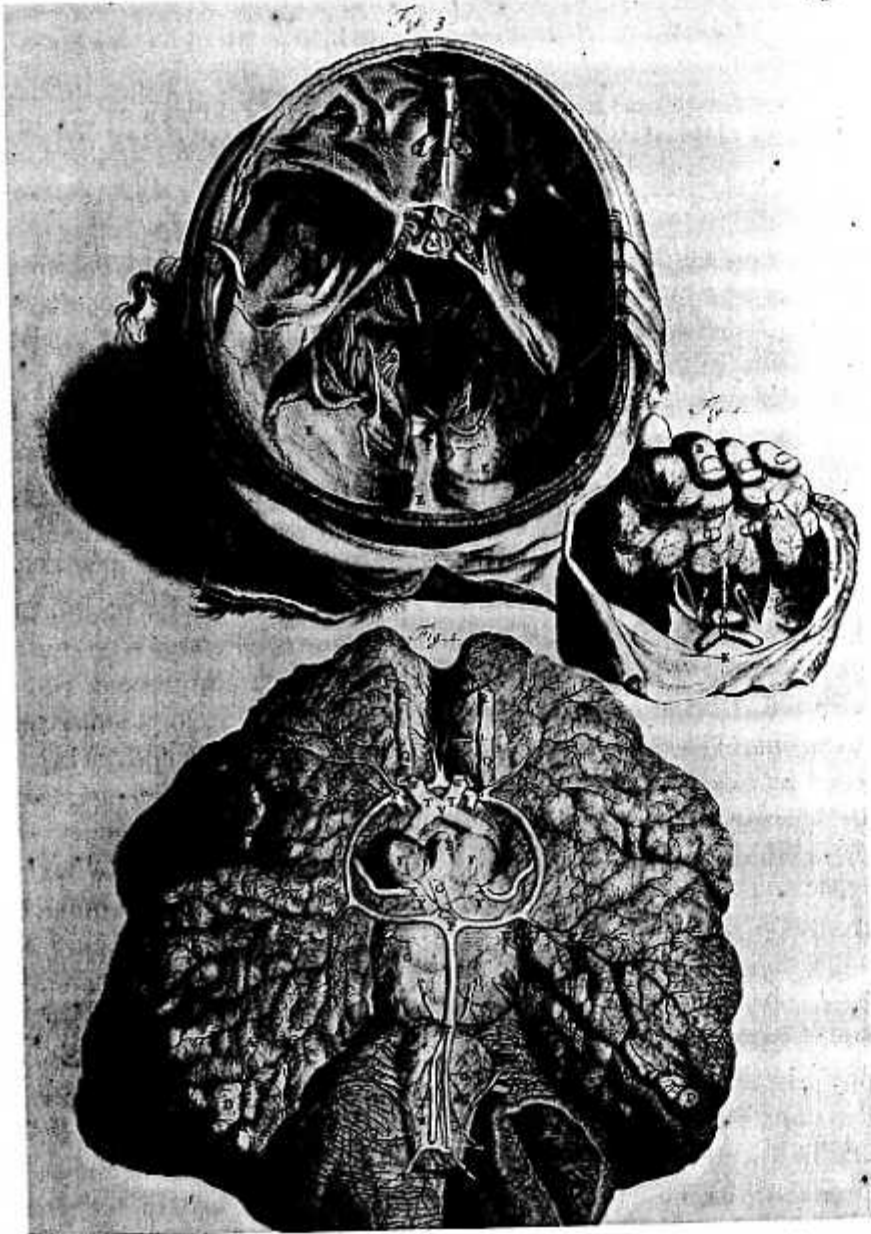


Fig. 1.1. This 18th century print shows an empty skull with the inverted brain beneath it. The optic nerves are marked W and T; the optic chiasma where some of the fibres cross is V. Laterally one sees the lower surfaces of the two crinkled and convoluted cerebral hemispheres with their rich vascular supply.

Notes

Notes to Chapter 1

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Barlow, H.B. (1985) Why have multiple cortical areas? *Vision Research*, 26, 81-90.

has already pointed out some of the ways images behind the eye differ from those in front of it, but anatomists and physiologists cheerfully ignore all these problems and talk about images in the brain in much the same way as they talk about a tasty meal that has just been consumed; this rapidly becomes something very different from the appetizing creation that tempted you to eat it, but we still refer to it as the *meal* because the chemical changes the food undergoes are the important matter, not the words used to describe them. It is these changes in the *image*, brought about by the mechanisms of the visual pathway and analysed by opening the skull, that I shall outline here. This knowledge should alter the way we think about 'seeing' in much the same way that astronomical observations changed our concepts of the universe, even though profound questions remain unanswered. Progress in understanding the brain has, however, been frustrating because one so rarely answers the question that prompted the search; but the answers that are obtained are the only ones available and we must be guided by them.

The cerebral cortex

The first figure shows what you see if you open the skull. The brain has been removed and its under-side is shown in the lower half of the figure. The prominent white X is the *optic chiasma* (marked V) where more than half of the fibres in the *optic nerves* cross over from one side of the brain to the other. The optic nerves have been severed at the top of the X and they plunge into the brain at the bottom of the X; in the brain they ultimately find their way, through a relay station called the *lateral geniculate nucleus*, to special regions of *cerebral cortex* at the back of the brain. These, it is generally agreed, are the structures that enable us to understand images.

The corrugated surfaces covered with blood vessels on either side of the optic chiasma are the under-sides of the cerebral hemispheres, and the *cortex* is the surface layer about one-tenth of an inch thick containing most of the cells. Since the total area on each side in humans is about one square foot it has to be crinkled to fit into the available space. Like everything else in this picture, what you can see is only a tiny fraction of what is there; in fact after the first moment of awe at seeing a human brain one cannot help being disappointed, for there is very little in its appearance to suggest what it does or how it works.

The cerebral cortex is surprisingly uniform in general appearance and microscopic structure, so if this is what enables one to understand images you will ask what ideas are held about its general function. Table 1.1 lists three suggestions. The first is from Judson Herrick, the great American comparative anatomist of the 1920s and 1930s of this century; he said the cortex is

Table 1.1. THREE IDEAS ABOUT THE CEREBRAL CORTEX**STORES KNOWLEDGE ACQUIRED ABOUT THE ENVIRONMENT**

C.J. HERRICK, 1928

CONSTRUCTS WORKING MODEL OF THE ENVIRONMENT

K.J.W. CRAIK, 1943

REVERSE OPTICS - RECONSTRUCTING OBJECTS FROM THEIR IMAGEST. POGGIO *et al.*, 1985

like the bank of filing cabinets in a government office, where all the records are kept¹. This was based on rather superficial observations of what animals with large cortices can do, and ones without them cannot, but it must be admitted that more detailed experimentation and observation has not added very much. On this view the main job of the cortex is to *store* knowledge of the environment.

Next consider the idea advanced by Kenneth Craik, a Cambridge psychologist who died tragically in 1944. He proposed that it makes a *working model* of the environment that an animal lives in². This is different from Herrick's view because it requires a component often missing in a government office, namely intelligent interpretation of the files. Anybody can jam things into a filing cabinet, but it is another matter to write a minute on each file that gives an account of the situation with the predictive power of a working model.

Finally consider what Tommy Poggio and his colleagues in Artificial Intelligence at M.I.T. say about the visual parts of the cortex. This is the group that the late David Marr³ founded and did his best work with; they say it performs inverse optics – it *reconstructs* the objects that cause visual images from the images themselves³. At first this sounds radically different, but stored knowledge and models of the environment are what you need in order to make reconstruction possible, as is clearly brought out in Andrew Witkin's paper in this book (see Chapter 14). *Storage, modelling, reconstruction* are good ideas to have in mind as we proceed, but in the second part of this chapter (p.20) I shall amplify the view that *understanding* is the most fundamental cortical function, and that this depends upon detecting the relationships^{1, 3} between the parts of an image, and between the image and the environment.

Localisation of function

How can one give substance to these ideas? The methods for finding out what the brain does are very restricted, so progress has been slow and tedious. You can look at the anatomy in ever-greater detail, but very often this yields facts that cannot be interpreted, giving no clues about function. However by combining the anatomical study of diseased or damaged brains with careful observations of the behavioural and psychic defects of patients it has been shown over the last hundred years that different parts of the cortex handle different aspects of higher behaviour. In many cases this parcellation of function has been confirmed by experiments and observations on animals with carefully controlled lesions. Also one can stimulate electrically and observe reactions, or inquire about the subjective sensations experienced and introspections aroused. Finally one can record the activity of nerve cells through electrodes, as we shall see in a minute. But there is no magic microscope to show one what a piece of the brain does and how it does it: it is a matter of piecing together incomplete scraps of evidence from varied sources.

Figure 1.2 is a side view of the human left cerebral hemisphere with some prominent anatomical terms listed on the left, and a resumé of functional localisations derived from the effects of damage, stimulation and recording

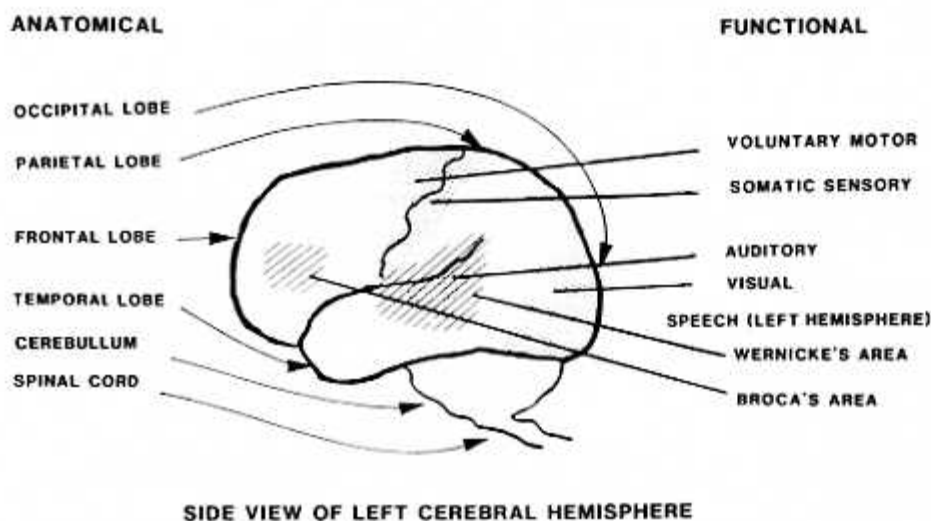


Fig. 1.2. Side view of the left cerebral hemisphere showing the anatomical terms and main functional areas. Evidence for the motor and sensory areas comes from knowledge of their anatomical connections and is amply confirmed by recording and by the effects of stimulation, damage, and disease. Knowledge of the speech areas comes mainly from clinical observation of patients with localised damage to the left hemisphere, often resulting from a stroke (cerebral thrombosis).

shown on the right. Stimulation of the three sensory areas in conscious humans causes sensations of sight, hearing, and touch, usually of a rather prosaic and uninteresting kind such as 'a luminous patch the size of a pea', or 'a faint buzzing sound', or 'light touch on the thumb'. Damage to one of these areas interferes with the corresponding sensation, and if one records electrically from these regions one detects signs of activity upon stimulation of the appropriate sense; I shall show some important results from the visual cortex in a moment.

More interesting, because more related to function, are the two cross-hatched areas. These are the approximate locations of two regions discovered more than 100 years ago, damage to which causes interference with speech – aphasia⁴. The surprising thing is that these areas are in the left hemisphere only; damage to corresponding areas in the right hemisphere leaves speech intact in the great majority of right-handed people. There are differences between the defects resulting from damage to the two regions, the anterior one – Broca's area – being more concerned with the production of speech, while the posterior region, named after Wernicke, has more to do with the conceptualisation of what is to be said. Marcus Raichle's chapter in this book (see p.284) tells us about some modern techniques that enable one to find which regions of the brain become active in normal humans performing various mental tasks, and this may open up a new subject – Psycho-Anatomy. But although this is a very exciting prospect, again one feels thwarted because it will only tell one *where* something is done, and will say little about *what* is done and *how*.

The visual pathways

In the hope of finding out more on the 'what' and 'how' the anatomy has been examined in greater detail, and Fig. 1.3 sketches some of these results in a diagram of the visual pathways seen from above. The eyes lie underneath the frontal lobes, and the optic nerves carry the image back from the eye to the brain.

Let me draw your attention to an interesting detail; light from objects in the right visual field is shown entering the eye as continuous lines, light from the left as dashed lines. These form images on the left and right halves of each retina respectively, because of inversion by the eyes' optics. As shown, at the chiasma only half the fibres cross: those from the right half of the visual field of *both eyes* go to the left half of the brain, while those from the left half-fields go to the right half of the brain. By this anatomical re-arrangement the images of the two half-fields seen through the two different eyes are brought together, and I think the brain's insistence that nervous activity which has the same

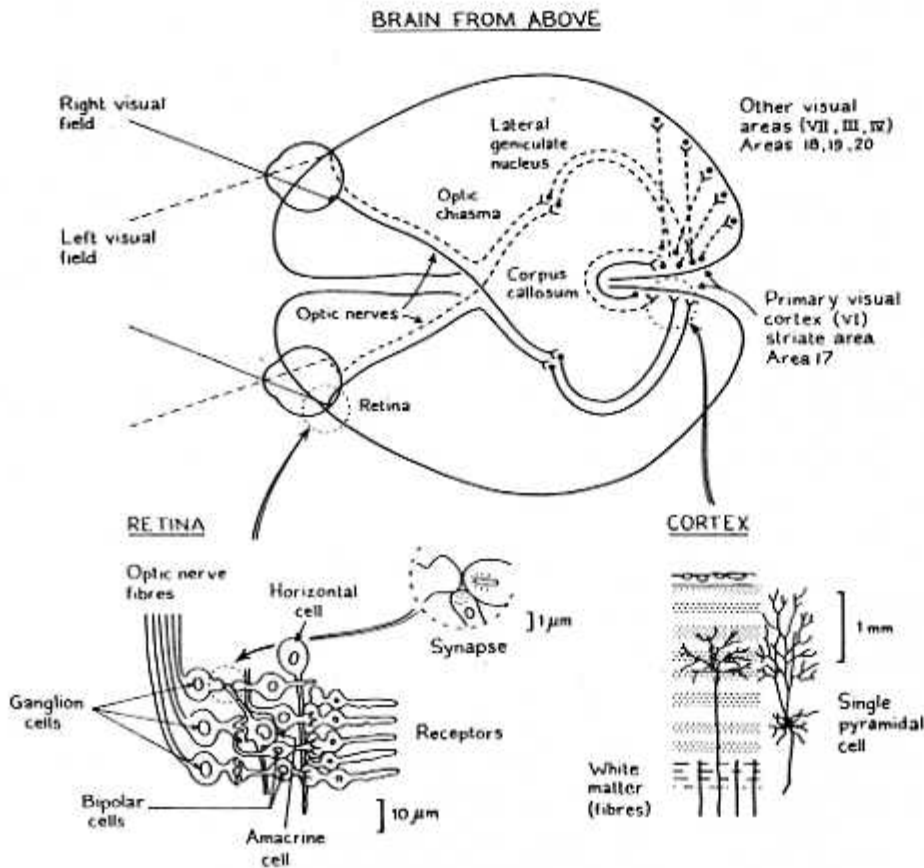


Fig. 1.3. Diagrammatic view of the human visual pathways seen from above. Note how the light rays (dashed) from the left visual field entering each eye excite ganglion cells whose axons (also dashed) synapse in the right lateral geniculate nucleus, whence the information is carried to the primary visual cortex (also called VI, area 17, or the striate area) in the posterior pole of the right cerebral hemisphere. Similarly rays from the right visual field are reunited in the left hemisphere. This is achieved by the appropriate fibres crossing in the optic chiasma while the rest remain on the same side. A portion of the retina is magnified to show the retinal ganglion cells, of which there are 10^6 in each eye in the human. Their axons carry the image to the brain, and they pick up their messages from the receptors through other neurons in the retina. To the right a portion of visual cortex is magnified. There are at least 100 cells for each input fibre and more than 10^5 per sq.mm. The axons of the pyramidal cells carry information to other visual areas and more distant parts of the brain.

origin in the external world should be reunited at the same place in the brain has an important message for us; I shall return to it.

Two regions of the pathway are shown in greater magnification in the lower part of Fig. 1.3. The important components are the *nerve cells* and *synapses*; thus it is the *ganglion cells* in the retina that pick up the messages from the *receptors* which have been stimulated by light in the image. They do this through junctions or synapses with intermediate cells called *bipolars*, and the complex synaptic connections between the various cell types in the retina do the computations that determine what property of the light, shade, and colour in the image excites a ganglion cell. These cells then transmit their messages to the brain as electrical impulses travelling along their long processes called *axons*, which constitute the fibres of the optic nerve. Note that what I told you about the optic chiasma proves that the long tails of these retinal ganglion cells, their axons, have an uncanny capacity to find their way to the right place in the brain: they seem to know exactly where to go.

After one more relay, or synapse, at the *Lateral Geniculate Nucleus* they proceed to the *Primary visual cortex* (V 1), also called *area 17*, or *striate cortex*. After further relays the information is disseminated to other visual cortical areas and other regions of the brain which have a multiplicity of not very illuminating names. On the right is shown an enlarged diagram of the cortex. Again the nerve cell is the important component, and I've shown a single example of one of the commonest types, the *pyramidal cell*. But there are in fact a bewildering variety of different types, some of them shown in Fig. 1.9, and also a bewildering number of actual cells. In the human retina there are about a million ganglion cells, and consequently about a million axons reach the brain on each side. But in the primary visual cortex alone there are at least 100 times as many cells as there are input fibres. Let us see how these cells are arranged.

The map of the visual field

Figure 1.4 shows a postero-lateral view of the left cerebral hemisphere of a monkey. In this species much of the primary visual cortex is visible from this aspect, unlike the case in humans where the primary cortex is tucked round the corner in the fissure between the two hemispheres, leaving only secondary areas visible from the side. The map of the central 8 degrees of the contralateral hemifield is shown; it was constructed by noting whereabouts in the visual field one must place a stimulus in order to excite the cells of that region⁵. Note that it is very distorted in the sense that *equal* areas of the visual field occupy very *unequal* areas of the cortical surface. The centre point of the visual field maps to the point where the lines marked horizontal and vertical

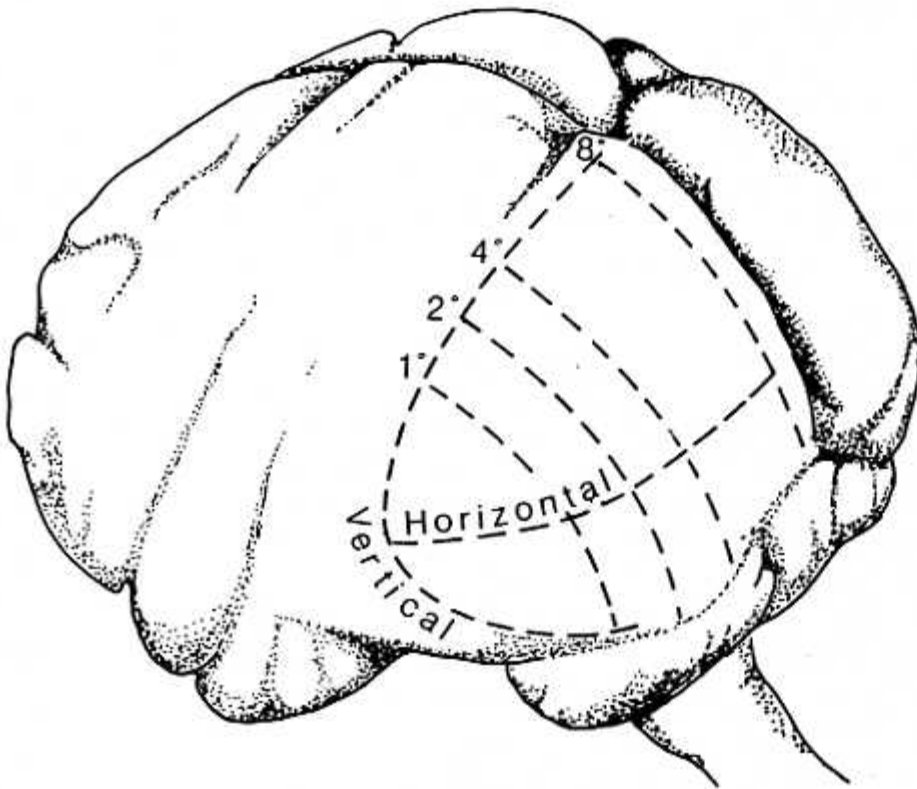


Fig. 1.4. Postero-lateral view of the left cerebral hemisphere of a *rhesus* monkey. In this animal (unlike *Homo sapiens*) the central 8° of the visual field is represented in a smooth, uncrinkled area visible from the side. The numbers give the degrees of eccentricity from the centre of the field, which corresponds to the left-most point on the map. The line marked horizontal shows where the horizontal meridian of the right visual field projects, and is itself roughly horizontal; the line marked vertical shows where the vertical meridian projects, and it is strongly curved as a result of the greatly expanded representation of the central parts of the visual field. The other half of the visual field is of course represented in the other hemisphere. Vertical positions (but not horizontal) are reversed, the upper part of the visual field projecting to the lower half of the map and vice versa. In spite of the distortions resulting from the expanded central representation the mapping is precise and accurate to about 1 mm.

intersect. Points along the vertical meridian in the visual field at various distances downwards plot along the upper part of the line marked vertical, while points along the horizontal meridian map along the line marked horizontal. Although distorted, the map is precise, so after a few points have been plotted one can predict where a new point will map on to the cortex with a precision of about a millimetre.

Maps within maps

That, however, is not the end of the story about the importance of position in the cortex. Hubel and Wiesel⁶ showed in 1962 that different cortical neurons respond to different orientations of a visual stimulus (see Fig. 1.8). They also found from painstaking anatomical reconstructions of electrode positions that cells with different orientation preferences were not scattered at random over a square millimetre of cortex, but were grouped in an orderly manner⁷. This has recently been demonstrated in remarkable experiments using voltage-sensitive dyes.

Figure 1.5 is a photograph of a small region about 4×5 mm on the surface of the primary visual cortex of a monkey; note the two blood vessels and their branches, which is all the detail you can see. When Gary Blasdel and Guy Salama, who did these experiments⁸, soaked the cortex with a voltage-sensitive dye and then stimulated it with gratings of differing orientations they generated the astonishing patterns shown in Fig. 1.6. Different parts of the cortex 'light up' when the eye is stimulated by stripes running in different directions, and the colour corresponding to each orientation is shown to the right of the figure. A good deal of wizardry is needed to do this, for the changes in luminance involved in generating this figure are of the order of a few hundredths of one per cent, but again we are seeing how modern techniques are opening a new vista on cortical function. Colin Blakemore (p.257) gives

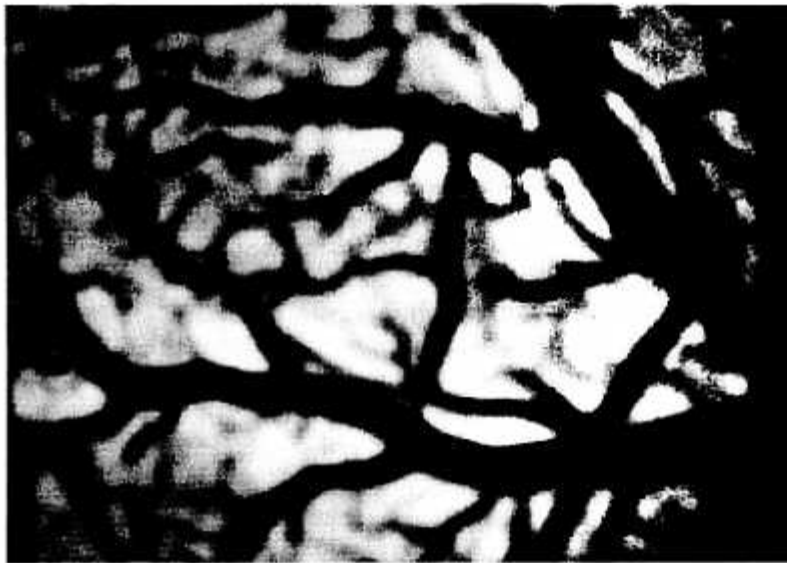


Fig. 1.5. View of a 4×5 mm patch of visual cortex showing only blood vessels.

