motion in the surround. The illusion could be seen even if the surrounding figures were several degrees (say 3°) away from the central one. It was as though the particular hypothesis the brain had selected to resolve ambiguity in the centre was being automatically applied throughout the visual field. And in the absence of sufficient evidence the brain resorts to simply postulating the required dots behind the occluders.

An informal observation along these lines was made recently by Shepard[11]. Shepard's stimulus was a vertical bar rapidly alternating with a horizontal bar and one could see motion in either one of two different quadrants. Sometimes voluntary effort was ineffective in switching perceived motion from one quadrant to the other and so he had to occlude suitable portions of the display in order to encourage motion to be seen in the other (non-occluded) quadrant. He reports that on doing this he sometimes continued to see motion behind the occluder for a while but does not state how long this tendency persisted. Our effect (occult apparent motion) may, in a sense be regarded as the spatial equivalent of this persistence effect noted by Shepard.

We find that occult apparent motion is visible only if the SOA is sufficiently long. This may reflect the minimum time required by the brain to invoke the occlusion hypothesis. If the SOA is made smaller than 645 ms (mean for four subjects = 645 ms: s.d. = 84), the effect vanishes and the dots in the surround oscillate horizontally even when the dots in the central ambiguous figure are making vertical excursions. Oddly enough the presence of the masking tape, though helpful, is not essential. If the room lights are switched off, so that the tape is no longer visible, one can still see occult apparent motion. This suggests that under appropriate circumstances one can see apparent motion towards an invisible light spot hidden by an invisible occluder! Subjects reported that a faint subjective outline of the tape was visible corresponding to where it should have been physically present.

One does not have to use ambiguous displays to produce occult motion. The effect can also be seen, though less vividly, in displays such as Fig. 5*a* in which two light spots in the first frame (A) are alternated with a single light spot in the second frame (B). If the cardboard occluder is not shown then observers always see both spots moving towards the single one and fusing with it as expected. But if the occluder is added, the bottom spot appears to move horizontally to hide behind the occluder although there is no stimulus corresponding to it in frame B. The effect is even more striking if a long thin line is used instead of two separate spots (Fig. 5*b*). We have shown these displays to six naive subjects and all of them confirmed that they could see the illusion. As in the case of Fig. 3, the percept of the spot sliding behind the occluder was more striking at long SOAs (>500 ms).

The effects reported here, synchronized motion (Fig. 3) and occult apparent motion (Figs 4,5) suggest that spatial induction effects can be very compelling and may play an important role in perception. Whenever the brain applies a rule to resolve ambiguities in a given local region, there is a strong tendency to apply the same rule throughout the visual field and the system will go to tremendous lengths to achieve this.

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Specificity of cortico-cortical connections in monkey visual system

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When the primate primary visual cortex, area 17, is stained for the mitochondrial enzyme cytochrome oxidase[1], it shows a striking polka-dot pattern (cytochrome oxidase blobs). Area 18, the second visual area, shows a cytochrome-oxidase pattern of coarse alternating thick and thin stripes running perpendicular to the 17–18 border and separated by lighter (interstripe) regions. Here we show that the thin cytochrome oxidase stripes, and possibly also the thick stripes, in area 18 receive projections specifically from the blobs in area 17, and that the interstripe regions of 18 receive projections from the interblob matrix of area 17. This indicates a specificity of cortico-cortical connections far exceeding the demands of topographical mapping. Together with our physiological results, it suggests that within the pathway from area 17 to area 18 different kinds of information may be handled separately and in parallel.

Many major cortical and subcortical areas of the brain are known to be subdivided into columns, stripes or lattices. Areas as diverse as visual, auditory and somatosensory cortices, caudate nucleus and superior colliculus exhibit such subdivisions by local heterogeneities in physiological responses, anatomical connections and staining characteristics[2–9]. M. Wong-Riley (personal communication), using a stain for cytochrome oxidase in area 17 of squirrel monkey, discovered a regular series of densely labelled patches in layers 2 and 3. It was subsequently shown that in sections cut parallel to the surface these patches form a quasiregular array of round or oval blob-like regions 0.2 mm in diameter and spaced 0.5 mm apart[10,11]. In macaque

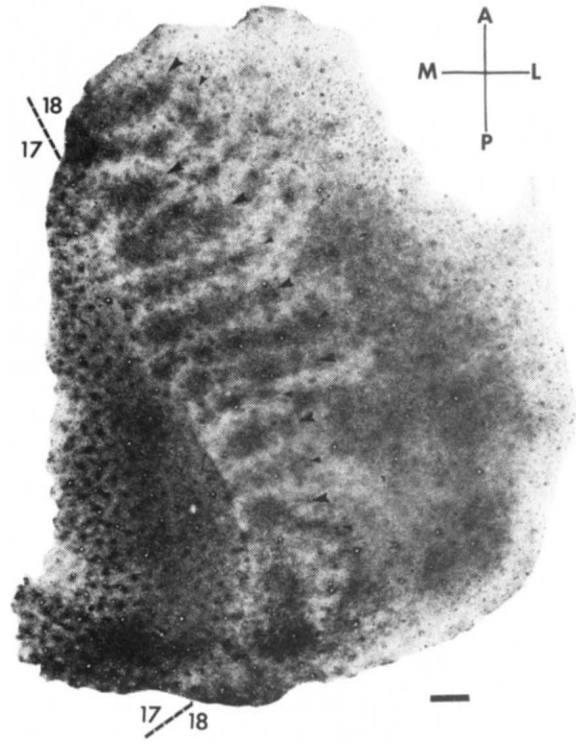

Fig. 1 Tangential section through a flattened squirrel monkey occipital lobe. Area 17 is on the left, and 18 on the right. The pattern in 18, although somewhat irregular, is roughly one of alternating thick and thin stripes, as indicated by large and small arrowheads. Scale bar, 1 mm.

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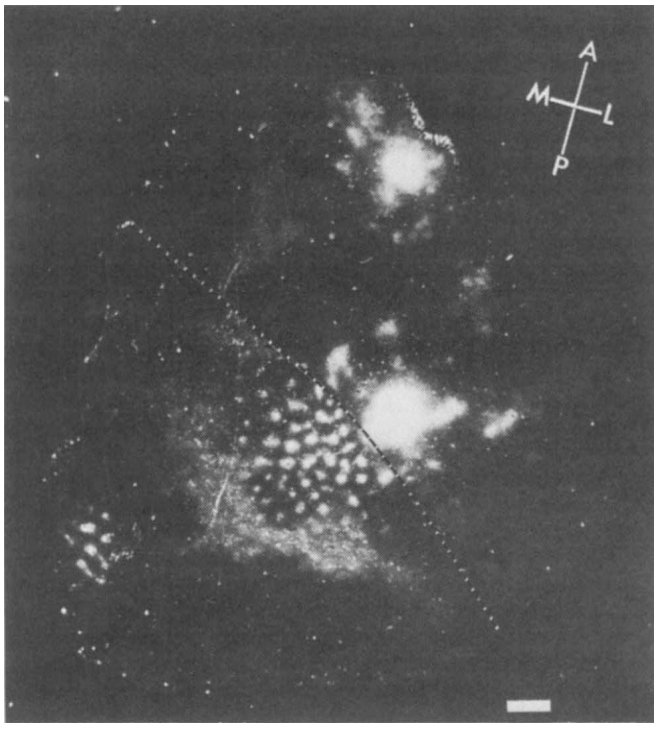

Fig. 2 Tangential section through layers 2–3 of squirrel monkey occipital lobe reacted with tetramethylbenzidine and showing two horseradish peroxidase injection sites in area 18. These are darkfield photographs, taken through crossed polarizers, and the label appears bright. The 17–18 border is indicated by the dotted line. The upper injection site was in an interstripe region in 18, and the lower was in a thin stripe in 18. The cores of the injection sites, not visible in this darkfield photograph, were less than 0.5 mm diameter. The left set of clumps of label in area 17 projected to the upper (interstripe) injection in area 18, and the right set of clumps in 17 projected to the lower (thin stripe) injection in 18. (The confluent grey area below and to the left of the right set of clumps in an artefact.) Scale bar, 1 mm. High-power views are shown in Fig. 3.

monkeys the blobs lie in rows centred on ocular dominance columns[12,13]. Cytochrome oxidase blobs are absent from layer 4C, which stains densely and evenly, but can be seen faintly in layers 4B, 5 and 6; they stain for a variety of other enzymes[13,14]; they are found in all primates so far examined and in no non-primates[12]; they can be seen in fetal brain[14]; they receive direct projections from the lateral geniculate body[15], probably specifically from intercalated layers[16]; and they are labelled with 2-deoxyglucose after any of a variety of visual stimuli, including, in squirrel monkeys, diffuse light[12,17]. Physiologically, the cells within blobs show no orientation selectivity; many cells show opponent colour responses, and of these the commonest are double-opponent cells, a type that has never been seen in the lateral geniculate body. Cells between blobs, in contrast, are orientation selective, and only a minority are colour coded[18,19].

Area 18 (visual area II) borders area 17, receives from it a systematic topographical projection mirror symmetric across the 17–18 border, and sends a reciprocal projection back to 17[20–23]. When area 18 is stained for cytochrome oxidase it shows a coarse pattern of parallel stripes running perpendicular to the 17–18 border. These stripes are coincident with the stripes of label produced by 2-deoxyglucose after stimulation with diffuse light[15,24], and also coincident with stripes formed by the projection from the pulvinar to area 18[15,25,26]. The stripes have a tendency to be alternately wide and narrow, more marked in the deeper layers than in the superficial, and more obvious in some individual animals than in others; the narrow stripes are 0.5–0.7 mm across and come right up to the 17–18 border, where they are most dense, whereas the wide ones are 0.8–1.2 mm across and usually stop 0.5 mm from the 17–18 border (Fig. 1)[15,27]. The total periodicity (for example, thin stripe to thin stripe) is 2.2–2.7 mm. Both types of stripes, especially the thin, tend to be subdivided by paler transverse stripes with a periodicity of 0.75 mm.

That cells in area 17 projecting to a small region in area 18 can be distributed in small patches has been shown by making small horseradish peroxidase injections into area 18[28,29,34], but this heterogeneous origin has not been correlated with cytochrome oxidase staining. Three similarities between blobs in area 17 and stripes in area 18 suggested to us that blobs in 17 might selectively project to stripes in 18: first, by definition, both stain for cytochrome oxidase; second, blobs in 17 and stripes in 18 are probably metabolically more active than intervening regions, as indicated by the 2-deoxyglucose results and indeed suggested by the elevated cytochrome oxidase levels; and, finally, both probably receive direct thalamic inputs, from the geniculate to the blobs in area 17 and from the pulvinar to the stripes in 18.

To test the idea that 17 to 18 connections are blob to stripe and interblob to interstripe, we made small iontophoretic injections of wheat-germ agglutinin conjugated to horseradish peroxidase into area 18 of one macaque (5 injections) and seven squirrel monkeys (35 injections). The injections were made blindly, and the locations, whether in a stripe or non-stripe, were determined afterwards histologically. The lectin–horseradish-peroxidase conjugate is transported in both retrograde and anterograde directions[30]. Current (2 μA for 5 min, electrode positive) was passed through pipettes with 10–20-μm tips filled with 5% lectin–horseradish peroxidase (Sigma) in Tris buffer (0.2 M *p*H 8.6). Survival time was 48 h. Brains were perfused with mixed aldehydes[31], flattened and frozen, and alternate tangential sections were reacted for cytochrome oxidase[1] or for horseradish peroxidase[30]. We could align neighbouring sections by overlapping the blood vessels, which run in a precisely radial fashion. Four of the macaque injections and 16 of the squirrel monkey injections were successful in that the central core was localized to either a stripe or an interstripe and produced retrograde filling of cells in area 17. Although we made two to three injections in each hemisphere, the injections were sufficiently widely spaced for the correspondence across the 17–18 border always to be clear from the known topography. The injections were all within 6 mm of the 17–18 border. In seven injections the central core of the injection was confined to a thin stripe, and one injection was in a thick stripe. Each thin stripe injection resulted in a discrete set of labelled patches in area 17; each patch coincided with a cytochrome oxidase blob and consisted of a cluster of densely labelled cells. The one thick stripe injection that produced label in area 17 gave no clear pattern in 17, although there was a tendency for the blob cells to be selectively, but very faintly, labelled. (One other thick stripe injection produced no label in 17, a result that we cannot interpret.) In contrast, all 12 injections whose cores were confined to interstripes produced in area 17 selective labelling of cells outside the blobs. We have assumed that the central core of the injection site, and not the surrounding halo, is the primary source of the transported label, largely because of the cleanness of our results. Injections in which the core straddled a stripe and a non-stripe resulted in confluent label in area 17.

A low-power tangential section through the flattened cortex of a squirrel monkey is shown in darkfield illumination in Fig. 2. The upper injection site was in an interstripe region in area 18, the lower injection in a thin stripe in 18. Both injections produced a dozen or more clumps of labelled cells in the topographically corresponding region of 17, and also produced puffs of label around the injection site in 18. Figure 3*a*, *c* shows the clumps of retrogradely filled cells in area 17 at higher power and Fig. 3*b*, *d* the adjacent cytochrome-oxidase stained sections. Figure 3*a*, *b* shows the region of area 17 that projected to the thin-stripe injection. Almost all the labelled cells lie in

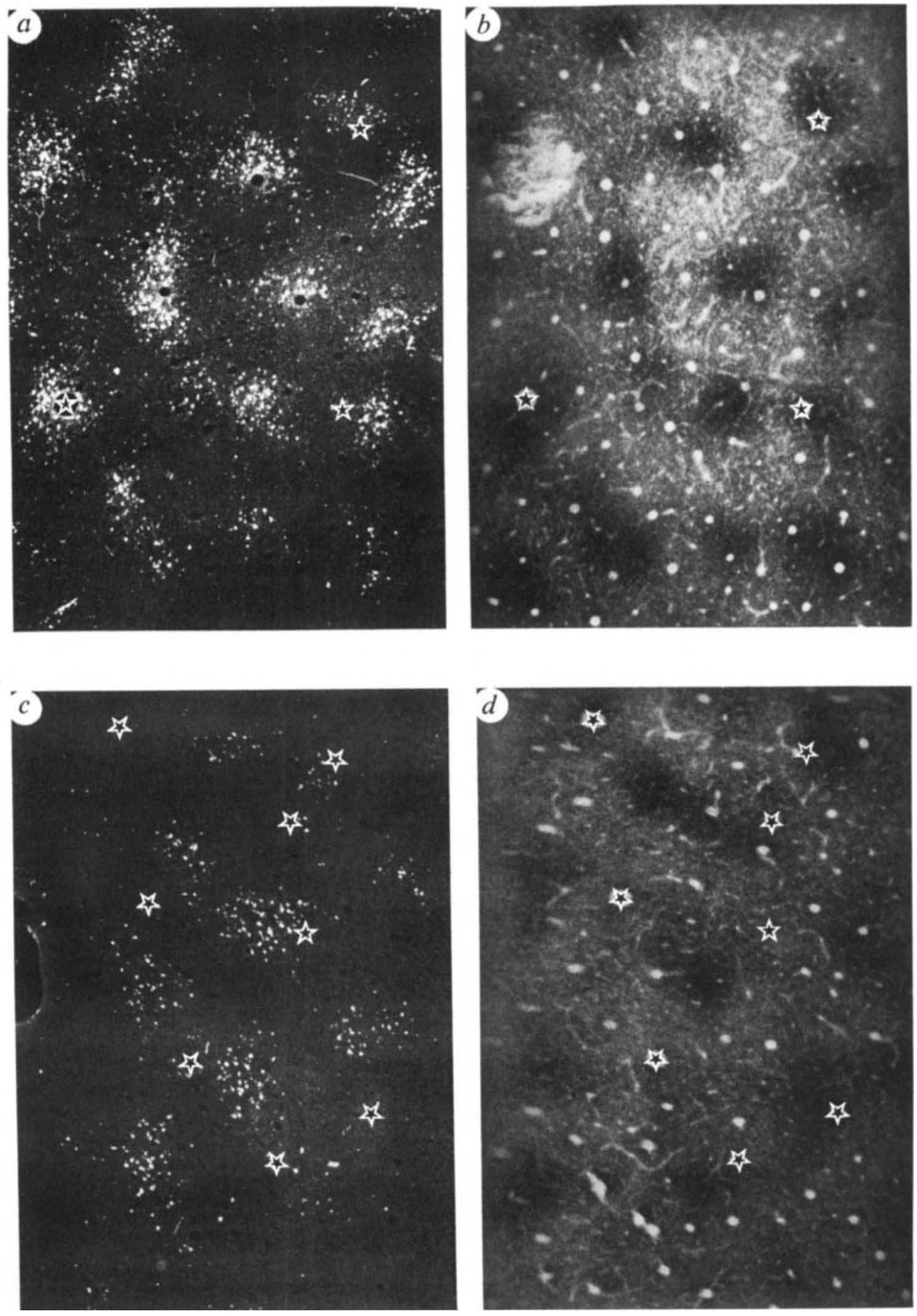

Fig. 3 Tetramethylbenzidine reacted section (*a*, *c*) and adjacent cytochrome oxidase stained section (*b*, *d*). *a* and *b* show the region in area 17 projecting to the thin stripe injection site in area 18, and *c* and *d* show the region in area 17 projecting to the interstripe injection site. In each pair of photographs the stars mark corresponding blood vessels. In *a* and *b*, labelled cell clusters and cytochrome oxidase blobs coincide, whereas in *c* and *d* the clusters fall in the spaces between blobs. The reader is encouraged to trace on a piece of clear plastic the blood vessel pattern and the labelled patches and then compare the tracing with the cytochrome oxidase pattern. (Because in sections stained for cytochrome oxidase we saw no preferential staining of the injection sites, we assume that horseradish peroxidase does not react in the cytochrome oxidase stain.) Scale bar, 0.5 mm.

blobs. Figure 3*c*, *d* shows the part of area 17 projecting to the interstripe injection site; here, in contrast, the labelled cells lie in interblob regions.

After injections into interstripe regions of area 18, there was variation in the distribution of interblob cells labelled in area 17: in some experiments, for instance that of Fig. 3, there were isolated non-blob clusters, but in others the labelled regions formed lines or zig-zags or even a lattice that nearly surrounded but always avoided the blobs.

Following both types of injection, into thin stripe and interstripe regions, there was diffuse fine labelling interspersed between the cells but confined to the regions in which cells were labelled. This probably represents orthograde horseradish peroxidase transport from 18 to 17, and suggests that there are precise sets of reciprocal connections to and from blobs and to and from non-blob regions. It is possible that this fine diffuse label represents axon collaterals of the cells in area 17 labelled by retrograde transport from area 18, but given the known projection of 18 to 17, it is unlikely that such collaterals would be labelled and not the projections themselves. ^{3}H-proline injections into area 18 would probably settle the question as proline is transported only in an anterograde direction.

When the injection site was in a thin stripe, the patches of label in area 18 surrounding the injection also tended to be in stripes (both thick and thin), with the intervening interstripe regions unlabelled. In contrast, when the injection site was in an interstripe region, the patches in area 18 were predominantly in interstripe territory with the intervening stripes blank. Again, label was seen in cell bodies and in the regions between cells, suggesting that reciprocal connections exist between stripe regions and between interstripe regions in area 18. We saw projections between thick stripes, between thin, and between thick and thin. None of these segregations, however, were as complete as those of the 17 to 18 connections.

To summarize, blob cells in layers 2 and 3 of area 17 project to thin stripes in area 18, and probably receive reciprocal inputs

from them. We are not certain whether this is also true of thick stripes. Interstripe regions in area 17 clearly project to interstripe regions in area 18, and it is similarly likely that the reciprocal 18-to-17 projections are segregated.

The present results show by direct anatomical methods that the already well-known orderly interconnections between two cortical areas are more specific than would be required by topographical correspondence alone. Taken together, the likelihood that area 17 forms the main visual input to 18 and the presence in both of orientation-specific cells grouped in columns[32] had already suggested that highly specific connections are likely to link columns of similar orientation selectivity in areas 17 and 18[33]. The interblob to interstripe connections may indeed be further segregated according to orientation preference. Here, however, we are apparently dealing not simply with one system in which the different values of a variable such as orientation are linked like-to-like between cortical areas, but with two distinct systems, one concerned with orientation and probably other variables, the other oblivious to orientation but concerned, at least to some extent, with colour.

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Processing of polarized light by squid photoreceptors

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Behavioural tests[1–4] have demonstrated that cephalopods can discriminate light polarized in different planes, and the receptors have been localized by electrophysiological studies of the eye[5–10]. Discrimination of the plane of polarization is a consequence of both the structure of the microvilli in the outer segments of the photoreceptors[11] and the orientation of the photosensitive chromophore on these membranes[2,12,13]. However, between the depolarizing receptor response resulting from photoreception and the behaviour of the animal, nothing is known about neuronal processing of polarized light by cephalopods. Here we show that some squid photoreceptors discriminate the plane of polarization within the spike train, and that any particular plane is seen as a variable intensity. Given the well known orthogonal orientation of microvilli in outer segments of adjacent photoreceptors and the physiological preference for one of two mutually perpendicular planes of polarization by single photoreceptors, we conclude that cephalopod vision is based on two complementary views of the world, each determined by the transformation of polarization-sensitive receptors into complementary intensity scales. A visual system based on this transformation would lead to enhanced contrast underwater and visualization of object details obscured by confounding highlights.

Individual and multi-unit spikes were recorded from photoreceptor axons in viable, isolated eye preparations[14] of the squid, *Loligo pealei*. A spike response of a squid photoreceptor to a step of increased illumination is a train of impulses in which the onset time and spike rate depend on the intensity of the incident illumination. The train reflects the generator potential, that is, the change in transmembrane potential resulting from photon capture by the chromophore, in that it consists of an initially fast spike rate (for <1 s) followed by a slower steady-state rate. The presence of the initial fast rate depends on exceeding a threshold, a phenomenon also seen for the early phase of the depolarizing generator potential[15]. The steady-state response encodes the plane of polarization of the stimulus as shown below. Thus, the two-phased behaviour of the generator potential[15] is reflected in the two-phased behaviour of the spike train.

We found that the initial presentation of a polarized light stimulus of any plane to a dark-adapted photoreceptor elicits a brisk response. Using spike rate (spikes per s) during the steady-state phase as a measure, one specific polarization plane was typically most effective (defined here as the 0° or 'preferred' plane). In the experiments reported, we observed only two preferred planes of polarization in a local patch of retina and they were orthogonal to each other. These preferences are probably defined by the orthogonal microvilli seen in adjacent photoreceptor outer segments[16–20] (Fig. 1*A*). Figure 1*B* illustrates the responses to a sequential presentation of light linearly polarized in the orthogonal and preferred planes. A photoreceptor's response to the preferred plane was more resistant to the effects of light adaptation than the response to a stimulus with another plane of polarization. The steady-state response to the preferred plane showed a small decrement due to the adaptive consequences of repetitive stimulation while the steady-state response to a stimulus having the orthogonal plane of polarization adapted to nearly no response. This response is just as would be predicted if the preferred orientation were seen as a brighter source.

Figure 2 illustrates how these photoreceptors discriminate the plane of polarization. Figure 2*A* shows responses to light polarized in the preferred plane (0°), polarized at 45° and at 90° to the preferred plane by the same photoreceptor, dark-adapted (left) and light-adapted (right). The total number of spikes between the second and eighth seconds of a 10-s light stimulus were compared with the number of spikes during the same interval elicited by light polarized in the preferred plane

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