

It should be pointed out that it is conceivable that there could have been some functional compensation mediated by the crossed corticotectal pathway which we did not uncover in our experiments. Even if this is the case, we are still faced with the question of why there was no evidence for any sort of recovery in the ability of collicular neurones to code the direction of stimulus movement. The most straightforward explanation may be that the anatomical reorganization we observed was simply an inadequate response to the disruption of normal brain function. It may take more than the establishment of a projection from one structure to another, in this case from the visual cortex to the contralateral superior colliculus, to compensate functionally for what would normally be present if brain damage had not occurred.

While the mechanism for generating directional selectivity is unknown, the results of some of our experiments<sup>6,7</sup> indicate that this response characteristic is not simply relayed from the cortex to the colliculus. Most probably, the elaboration of

directionally selective responses involves an interaction between retinal and cortical afferents to the colliculus with a particular spatio-temporal sequence of postsynaptic activity derived from these inputs. Thus the aberrant projection may lack the necessary precision for generating this response property. (It is also possible, but perhaps more speculative, that postsynaptic elements may be actively suppressing the activity provided by the aberrant crossed projection.)

Regardless of which explanation is ultimately supported by future research, the results of the experiments summarized above underscore the importance of examining the functional concomitants of any reorganization which is uncovered by anatomical methods.

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## Subcortical vision in man

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*With improvements in recent years of psychological testing techniques, the existence of two levels of visual processing has become apparent. One system, the geniculostriate pathway to the visual cortex, has been appreciated for many years. The new techniques have brought to light a subcortical system involving retinotectal pathways - it is this latter system which is discussed in this article.*

Motor and sensory cerebral functions are usually emphasized as becoming increasingly controlled by cortical structures in the more advanced species on the phylogenetic scale. Accordingly, in primates and especially in man, corticization of function is thought to be almost complete, leaving only simple reflex or vegetative operations to be subserved by subcortical levels.

This view is particularly exemplified in the field of vision. Pathological destruction of the visual cortex in man is classically known to produce total blindness, except for the pupilar reflex response to light (cortical blindness). Persistence of crude visual perception (limited to sudden changes in illumination or to movement within the visual field) in a few reported cases has usually been attributed to the incompleteness of the lesion<sup>1,2</sup>.

In recent years, however, ideas about residual visual functions following lesions

of the visual cortex have undergone rapid changes. In fact, experimental studies in animals, and particularly in monkeys, seem to have largely contributed to this evolution by bringing out new data on anatomical and physiological properties of central visual pathways, and by renewing the methodology for testing the behavioural effects of lesions.

#### Multiple channels in central visual pathways

The wide distribution of optic nerve terminals throughout the central nervous system is now well-recognized. Several distinct pathways convey retinal information to a number of central areas, both cortical and subcortical, differing from each other by such characteristics as the diameter of the impinging fibres, or the arrangement of the receptive fields. The visual system can thus be viewed as an ensemble of parallel

channels, specialized for the processing of specific aspects of the visual environment.

According to the 'two visual systems' hypothesis<sup>11,13</sup>, two main channels can be clearly identified both anatomically and functionally: the retinotectal system, which is known to send further projections to the secondary visual cortical areas (mostly the prestriate cortex); and the retinogeniculostriate system, which only projects to the primary (striate) visual cortex.

The main central visual relays are organized retinotopically, i.e. they form a number of 'maps' of visual space, with a mutual correspondence (in the same way as in modern atlases the same country is outlined on several maps, each one exemplifying a given feature for that country). However, the projection of the central part of the retina, a high-resolution area, does not have the same magnification factor for maps of different channels. Although in the geniculostriate system, and especially in the primary visual cortex, the central retina has a relatively larger representation, this is not so exaggerated in the retinotectal pathway, where the peripheral retina, which is actually much larger than the central retina, represents the major projection.

Testing the functional role of a given visual channel implies a strong inference about structure-to-function relationships.

In fact, functional specialization, which might already be inferred from anatomical and physiological properties of the distinct pathways, seems to be confirmed by the effects of localized lesions. In monkeys, total ablation of the striate cortex primarily impairs the ability to recognize complex visual patterns, and to perform a discrimination between visual items based on such parameters as shape or orientation. In contrast, these destriated animals are still able to generate motor responses directed at unspecified objects appearing in, or moving across, their visual field. Hence, the retinotectal pathway, largely innervated by the peripheral retina, would appear to be more apt in detecting dynamic properties of stimuli, and spatial relationships<sup>5,15</sup>.

#### New methodological approach in man - 'seeing' and 'guessing'

In man, visual functions are commonly assessed by asking the subject whether or not he can 'see' a visual stimulus. This way of testing has been standardized in the technique of clinical perimetry, a technique designed to map the visual field: subjects are required to indicate (verbally or by pressing a key) the occurrence of luminous targets projected systematically at different locations. Patients suffering from a unilateral lesion of the visual cortex will not report seeing targets presented within the contralateral half of their visual field (the commonly observed disorder of lateral homonymous hemianopia).

In fact, the response of the visual system may depend on the requirements of the task. For instance, in monkeys (whose perceptual experiences are not accessible to the experimenter), visual abilities can only be tested through behavioural responses. Animals can be trained to reach for targets at different locations, or to indicate manually which of two patterns they have selected. Poeppel and colleagues<sup>10</sup> were the first to suspect that such behavioural responses could also be useful for testing visual capacities in man. Indeed, they asked their cortically lesioned subjects not to try to 'see', but rather to try to 'reach' with their eyes for, i.e. turn their eyes towards, targets presented within the blind area. They recorded eye movements, the direction and amplitude of which were weakly but definitely correlated with target position. (The occurrence of the stimulus was signalled to the subjects by an acoustic warning.) In other studies, also dealing with adults suffering from partial destruction of the visual cortex, similar results were reported: subjects were able to reach

out manually to targets which they could not see<sup>8,16</sup>.

Demonstration of 'blindsight' (a term introduced by Weiskrantz and his colleagues<sup>16</sup>) in hemianopic patients thus resulted from a methodological improvement, requiring subjects to abandon their usual, perceptual, mode of visual detection, and to use a visuomotor mode based on a forced response. Their subjective experience was that of 'guessing' instead of 'seeing'.

In their patient with a lesion mostly restricted to the primary visual cortex, Weiskrantz' group had found<sup>16</sup>, in addition to residual spatial abilities, a remarkable capacity to discriminate simple patterns (subtending a large angle) within the hemianopic field. In these experiments the

patient was forced to choose which of two alternative patterns (e.g. X v. O, or horizontal line v. vertical line) had been presented within his blind area.

Due to the limited character of the lesion of their patient, these authors hypothesized that his residual vision could be mediated by other, intact, parts of the posterior cortex (especially the prestriate areas, receiving indirect visual afferents through the retinotectal pathway), rather than merely by subcortical structures.

#### Residual vision in hemidecorticated subjects

Residual vision can be studied better in patients with larger and longer-term cortical lesions. In this respect, patients with a complete ablation of the cerebral cortex of

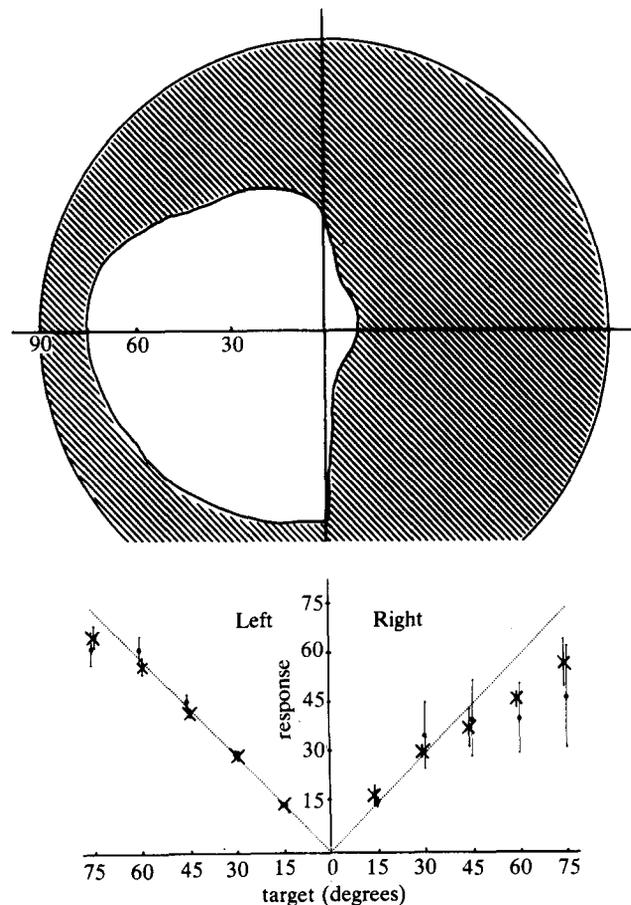


Fig. 1. Outline of the binocular visual field (above) and plot of average manual indications (means  $\pm$  S.D.) in the two hemifields (below) in a subject with a left-sided hemidecortication. The visual field has been mapped with the larger and brighter ( $116'$ ,  $320 \text{ Cd/m}^2$ ) spot of the Tübingen perimeter, by using a high mesopic background ( $3.2 \text{ Cd/m}^2$ ). The striped area represents the part of the visual field where the subject cannot 'see' the target. Manual indications were made in a forced-choice condition (the subject had to point whether he 'saw' the target or not) in response to a large ( $8^\circ$ ) grating as a target, with a 500 ms exposure time. Circles: stationary grating. Cross: moving ( $4^\circ \text{ s}^{-1}$ ) grating. The subject uses the left arm (ipsilateral to the lesion) for pointing in both hemifields. For this particular subject, movement within the stimulated area significantly improved the performance in the hemianopic field.

one hemisphere (for the purpose of curing otherwise intractable epilepsy) provide a unique opportunity for evaluating the functional role of subcortical structures in man. From reports in the literature, we know that such large cortical ablations result in an ipsilateral retrograde degeneration in the lateral geniculate body and the pulvinar, but other subcortical visual relays, such as in the superior colliculus, which do not send direct afferents to the cortex, are spared. Hence, if visual responses could be observed from the hemianopic side of the visual field in such patients, they should very likely be attributable to the retinotectal pathway, i.e. involving the superior colliculus and/or neighbouring visual relays belonging to the optic tectum.

All six such patients who were made available to us showed a dense hemianopia at the time of perimetric testing. By using the already-described forced choice procedure, they were all able to some extent to point by hand at bright targets presented for brief durations (100–500 ms) within their hemianopic field. However, the relationship of the pointing responses to the target's position was not the same as in the normal part of the field. As is shown in Fig. 1, the scatter of pointing responses at a given target presented several times in a randomized sequence was much larger in the blind area (the standard deviation around the mean was about five times greater than in the normal part of the field). This effect increased with the eccentricity of the targets. Furthermore, the gain of the pointing response at a given target (i.e. mean amplitude of a pointing response/target position) was not the same across the whole hemianopic field. Although for targets located within 30° to 45° from the midline, the gain was close to 1 (similar to that on the normal side); for targets located beyond 45°, it decreased below unity. Several attempts were made to improve the performances either by increasing the duration (from 100 to 500 ms) or the size (from 2° to 8°) of the targets, or by displacing a grating within the stimulated area. Either of these procedures was sometimes effective in reducing the scatter or increasing the gain of the responses, but only in a few sessions and not in all subjects<sup>9</sup>.

When examined for pattern discrimination, the same group of six patients gave less homogeneous responses. Simple patterns from pairs equated with respect to their total luminous flux (e.g. circle v. triangle, or horizontal line v. vertical line) were presented tachistoscopically at different retinal loci within the hemianopic field (e.g. near or far from the midline). The

cumulative score (across all sessions) was well above chance in two subjects only (72 and 57% of correct responses, respectively). In one of them, individual scores could reach values as high as 87% of correct responses for detection of line orientation, or 82% for a triangle v. circle discrimination. Increasing the stimulus strength (i.e. by increasing contrast, size, or duration of presentation), or decreasing its retinal eccentricity, resulted in an inconsistent improvement of performance<sup>7</sup>.

It should be noticed that the two subjects who were able to discriminate simple patterns within their hemianopic field also performed best in pointing at targets. The main factor which might have contributed to a better development of subcortical visual capacities in these two patients is their young age (7 years) at the time of operation. Indeed, the worse performances in both spatial localization and pattern discrimination tests, were obtained from the subject operated the latest (17 years). The relative precocity of the lesions in our hemidecorticated group might also account for the overall better residual vision that we observed in these patients, as compared with the group of patients lesioned as adults whom we had tested previously (and who in fact had smaller lesions)<sup>8</sup>.

#### **Possible functions of subcortical vision in man**

According to our previous suggestion, residual vision on one side after hemidecortication would be subserved by the retinotectal system. We can now speculate on whether the observed visual capacities can tell us something about the normal functions of the optic tectum in man. In fact, our arguments will remain indirect, and mostly drawn from lesion experiments in animals. We are also aware that the precocity and the completeness of cortical lesions in our patients may have helped them to develop vicarious subcortical visual function by using structures whose normal function is under cortical control. Corticotectal connections are well documented, and cortical lesions are known to disrupt a major facilitatory input to the superior colliculus. With time, collicular dysfacilitation may have been largely compensated in our subjects.

Collicular lesions in monkeys clearly impair orienting reactions and tracking eye-movements, although these effects usually recover within a few days. More subtle effects can persist over time, such as inaccurate or delayed visually elicited saccades, or inaccurate pointing at brief visual stimuli appearing in the far peripheral

field. A similar deficit has been reported in a case of surgical ablation of the superior colliculus in man<sup>4</sup>. In addition, recent work in the monkey by Mohler and Wurtz supports these findings. These authors have shown that animals with a partial lesion of the visual cortex on one side may recover the ability to direct their eyes at visual stimuli appearing within their hemianopic field. A subsequent ablation of the homologous part of the superior colliculus definitely abolishes this ability<sup>6</sup>.

Animal experiments have shown that tectal or pretectal lesions may impair learning of a pattern discrimination<sup>2,14</sup>. In this case, however, we have to keep in mind that such lesions interrupt the transfer of part of the retinal information to the posterior association cortex where further processing relevant to pattern discrimination is known to occur. In fact, by comparing our results with those of Weiskrantz' group<sup>6</sup>, it clearly appears that tectal vision (as in our patients) is less proficient for pattern detection than is extra-geniculostriate vision (as in the Weiskrantz patient). After total cortical ablation, subcortical relays may be able to extract from the stimuli simple attributes which could become relevant for crude pattern discrimination. This mechanism, based on such cues as differences in local luminous flux emitted by patterns of different shape, could account for the performance above chance level that we observed in two of our patients.

To our understanding, subcortical (tectal) vision in man as well as in monkeys is primarily organized for spatial detection and for the generation of visuomotor behaviour. This function would be achieved through the role of the superior colliculus in guiding visual attention to a given area of the visual field. Psychophysical observations by Singer and colleagues<sup>12</sup> have shown that the elevation in visual threshold produced within a limited area of the visual field by repeated visual stimulation (adaptation) can be abolished by stimulating, or directing a saccade to, a mirror symmetric point of the visual field. This mechanism is likely to occur at the subcortical level since it persists in hemianopic patients: in this case, adaptation produced locally within the normal field can be reset by a mirror symmetric stimulation within the hemianopic field.

This mechanism might be triggered by elementary attributes of visual stimuli, such as brightness, or movement. Its consequence could be the generation of a motor output related to the spatial location of the stimulus, a process not requiring perceptual awareness from the subject.

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# Does the brain perform a Fourier analysis of the visual scene?

Norma Graham

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*The decomposition of a complex auditory sound into its constituent simple harmonic variations (pure tones) is an example of Fourier analysis. Does the brain do something like this to visual scenes, decomposing a visual pattern into some simpler representation to help ease the information-processing load? As Norma Graham explains below, the answer to this question is both yes and no. But, yes or no, the idea that the brain might do a Fourier analysis of the visual scene has been a powerful impetus to much exciting visual research in the last decade.*

## Fourier analysis

To discuss Fourier analysis as applied to visual patterns, I find it easiest to begin by considering one simple pattern, a *sinusoidal grating*. A sinusoidal grating is a pattern which looks like a set of blurry, alternating dark and light stripes (see Fig. 2a of the article by Murray Sherman<sup>3</sup>). The luminance in the direction perpendicular to the stripes varies sinusoidally, while the luminance in the direction parallel to the stripes is constant. The *spatial frequency* of a sinusoidal grating is the number of cycles of the sinusoid per unit distance, or, in other words, the number of dark-bar-light-bar pairs per unit distance. (The usual unit of distance is a degree of visual angle.) Spatial frequency and size of bar are inversely proportional to each other; a grating of high spatial frequency has narrow bars and a grating of low spatial frequency has wide bars.

The *mean luminance* of a grating is the average of the luminances at every point across the whole spatial extent of the grating. The *contrast* of a grating is a measure of the difference between the maximum

luminance and minimum luminance usually taken to be one-half that difference divided by the mean luminance. (One of the attractions of sinusoidal gratings is that the mean luminance of a grating can easily be held constant, keeping the observer in a relatively constant state of light adaptation, while the contrast and spatial frequency are varied.)

Now consider any visual stimulus, the luminance of which varies along only one dimension. As follows from a theorem due to the eighteenth-century mathematician Fourier, *any* such stimulus can be constructed by superimposing sinusoidal gratings of different spatial frequencies, contrasts, and phases (positions). Further, there is only *one* set of sinusoidal gratings which can be superimposed to form a particular stimulus. Thus, any one-dimensional visual stimulus can be described as containing certain spatial frequencies. The amount and phase of each spatial frequency contained in a stimulus (the contrast and phase of the component sinusoidal grating of that spatial frequency) are given by the *Fourier transform* of the stimulus.

Analysis into spatial frequencies is not restricted to one-dimensional visual stimuli. Consider an ordinary black-and-white photograph as an example of a two-dimensional visual stimulus. Any such stimulus can be constructed by adding up sinusoidal gratings which differ in orientation as well as in contrast and frequency and phase. A picture of fine-grained sandpaper, for example, could be formed by adding up sinusoidal gratings of high spatial frequencies and many orientations. A picture of coarse-grained sandpaper could be formed by adding up sinusoidal gratings of low spatial frequencies and many orientations. The amount and phase of each spatial frequency at each orientation is given by a *two-dimensional Fourier transform*. Fourier transforms can be computed in higher dimensions as well (allowing for depth, colour, and time, for example), but in this article I will talk, for simplicity's sake, as if all visual patterns were two-dimensional.

To do a Fourier analysis of a visual pattern is to compute the Fourier transform of that pattern, that is, to compute how much of each spatial-frequency/orientation combination is present in the pattern and at what phase it is present. In terms of the component sinusoidal gratings from which the pattern could be formed, to compute a Fourier transform is to compute the contrast and phase of each of these component gratings. There are well-established mathematical procedures for doing this computation.

## The brain does not perform a strict Fourier analysis of the visual scene

What would we mean if we said that the brain performed a Fourier analysis of the visual scene? We might mean, if we were speaking strictly, that there was a set of neurones that computed the Fourier transform of the visual pattern. The magnitude of the response of a particular neurone in