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A NEUROPSYCHOLOGICAL INVESTIGATION INTO NASOTEMPORAL OVERLAP IN THE
HUMAN RETINA

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Submitted in requirement for the degree of Master of Science at St. Andrews
University, February, 1984.



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ABSTRACT

When light flashes are presented laterally simple vocal and manual responses are faster to stimuli in the visual half-field having direct access to the responding hemisphere (an 'uncrossed' reaction) than stimuli which go initially to the non-responding hemisphere (a 'crossed' reaction). In the latter case an interhemispheric crossing is presumably necessary and so the crossed-minus-uncrossed difference (CUD) can be tentatively identified with interhemispheric transmission time. This paradigm was used to investigate the problem of whether or not there is an overlap of ipsi- and contralaterally projecting ganglion cells at the border between nasal and temporal areas of the human retina, resulting in dual representation of the midline in the brain. If such an overlap does exist then presenting stimuli on this region ought to result in an abolition of the CUD since information would be equally available to both hemispheres and there would be no need for any interhemispheric crossing. Four experiments failed to confirm this prediction in that a CUD was found to be present with stimuli presented down to an eccentricity of 1/2 deg in conditions of: vocal (Experiment 1) and manual (Experiment 2) responding in partially dark adapted subjects; manual finger release and thumb press responding in light adapted subjects (Experiment 3); manual responding in an acallosal subject (Experiment 4). The results are interpreted as arguing against the existence of overlap in man though some possible reasons why this conclusion may be premature are discussed.

ABBREVIATIONS

ANOVA	=	analysis of variance
CUD	=	crossed-minus-uncrossed difference
Deg	=	degree/s of visual angle
IHTT	=	interhemispheric transmission time
LGN	=	dorsal lateral geniculate nucleus
LH	=	left hemisphere
ms	=	millisecond/s
RH	=	right hemisphere
RT	=	reaction time
VHF	=	visual half-field

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CHAPTER 1

THE HUMAN VISUAL SYSTEM AND THE PROBLEM OF OVERLAP

The question which this thesis addresses is an apparently simple one - does the midline region of the human retina project to both cerebral hemispheres or not? Why a satisfactory answer has not yet been forthcoming and why anyone should be concerned in the first place I hope to make clear in the next two chapters. The first contains a brief description of the human visual system in order that the nature of the problem under discussion be fully understood while the second reviews the arguments which have been put forward, for and against such a projection.

1.1 OVERVIEW (Full details concerning the points raised in this chapter can be found in Glaser, 1978; Bailey, 1981; Kandel, 1981 and Kelly, 1981).

The primate retinae project directly to at least four sites in the brain. These are (Marg, 1973; Mansfield, 1982):-

1. The dorsal lateral geniculate nucleus (LGN). This in turn relays information to primary visual cortex (also known as area V1, area 17, striate cortex and calcarine cortex).

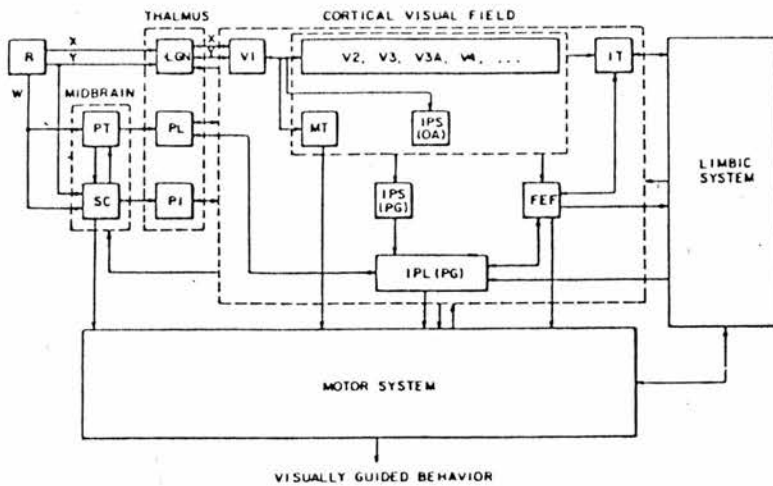
2. The superior colliculus.

3. The pretectum.

4. The accessory optic system - a blanket term comprising the target sites of all retinal axons which do not terminate in areas 1 - 3.

For this reason it may be more correct to speak of visual systems rather than a single system, even though interconnections between the various retinal termination sites are extensive (some of these are shown in

FIGURE 1. ANATOMICAL ORGANISATION OF THE PRIMATE VISUAL SYSTEM



R:	Retina
X, Y and W:	Ganglion cells
LGN:	Lateral geniculate nucleus
VI:	Striate cortex
V2 etc.:	Extrastriate visual areas
IT:	Inferotemporal cortex
MT:	Middle temporal area
IPS (OA):	Posterior intraparietal sulcus
IPS (PG):	Anterior intraparietal sulcus
FEF:	Frontal eye fields
IPL (PG):	Inferior parietal lobule
SC:	Superior colliculus
PT:	Pretectum
PL:	Lateral pulvinar
PI:	Inferior pulvinar

(Adapted from Mansfield, 1982)

This is an idealised diagram based on research from several species and omitting commissural connections.

Figure 1). That being said there is little doubt that the retino-geniculate pathway is by far the most important containing, as it does, at least 90% of all fibres leaving the retina and for this reason is often referred to as the visual system. The predominance of this pathway in primates is particularly striking when one considers that in another mammal, the rat, virtually all retinofugal fibres terminate in the optic tectum with only about 10% going, by means of bifurcating axons, also to the LGN. Interestingly, though, the total number of fibres in the extrageniculate projections remains the same in the two species ie: about 130,000 (Cowey, personal communication). The possible role of these pathways (in particular the one from the retina to the superior colliculus) in human vision should always be kept in mind.

1.2 THE RETINA

The human retina is shown diagrammatically in Figure 2 and consists of 3 main layers - the receptors (rods and cones), a layer of interneurons (amacrine, horizontal and bipolar cells) and the ganglion cells which project to the brain. These layers are arranged back to front so light has to pass through the ganglion cells and interneurons before it reaches the receptors, except at the very centre. Of particular interest here are the receptors and ganglion cells.

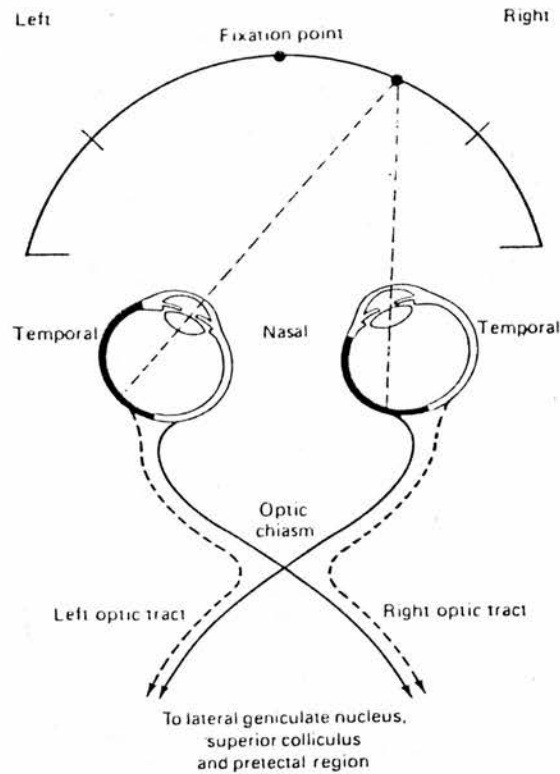
Receptors - the two receptor types are differentially distributed with a central area, the fovea, consisting entirely of cones, and rods predominating throughout the rest of the retina. Such an arrangement reflects the functional differences between the two types. Rods provide greater sensitivity and are utilised in scotopic vision while cones mediate colour vision under photopic conditions and also provide visual acuity for optimal pattern detection. This ability seems to reflect the fact that

cones, unlike rods, have an almost one to one pattern of convergence on retinal ganglion cells.

Ganglion cells - to some extent the distribution of ganglion cells reflects that of the receptor level with ganglion cell density being greatest in the area around the fovea. It is also the case that cells in this area have smaller dendritic fields compared to cells in the periphery, this density pattern ultimately influencing the topography of the visuotopic map in the brain. Following studies on cats and monkeys ganglion cells have recently been divided into 3 main types (Stone and Dreher, 1982). X-cells are particularly frequent at the fovea and are characterised by their small receptive fields and ability to resolve higher spatial frequencies. They project to the LGN and the pretectum. Y-cells project to both the LGN and superior colliculus, are found relatively frequently in the periphery and are responsive to fast moving stimuli. W-cells have large receptive fields, 'sluggish' firing patterns and project entirely to the superior colliculus. In cats X,Y and W cells constitute 55%, 5% and 40% respectively of the total ganglion cell population, with W-cells forming 90% of the collicular input. In monkeys the overall proportions remain uncertain though W-cells seem to be less commonly found than in the cat and may constitute only 10% of the total (Mansfield, 1982). However it is known that the central 1 deg of the fovea yields 90% X and 10% Y-cells, with W-cells lying outside the foveal region (Schiller and Malpeli, 1977; De Monasterio, 1978).

The central retina can be divided horizontally into three distinct regions which, for the purposes of this thesis, require precise definition (Bunt, Minckler and Johanson, 1977). The macula is a small yellow area approximately 3 x 5 mm in size within which lies the fovea. This has a diameter of approximately 1.5 mm and consists entirely of cones. Within

FIGURE 3. PROJECTION OF FIBRES FROM THE RETINA



Light from the right binocular field falls on the left temporal retina and the right nasal retina. Because fibers from the nasal retina of each eye cross to the opposite side at the optic chiasm, the left optic tract carries axons from the left temporal retina and the right nasal retina and therefore contains a complete representation of the right hemifield of vision.

(From Kelly, 1981)

the fovea is an area 500 um in diameter called the foveal pit which contains virtually no ganglion cells so that light has an uninterrupted path to the receptors at the region of greatest acuity.

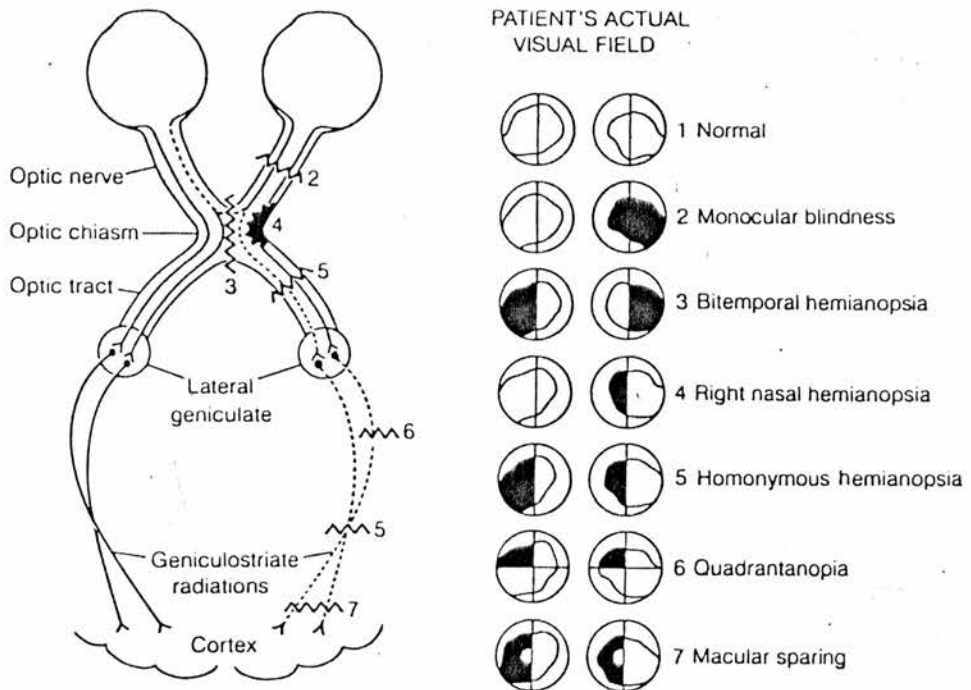
1.3 THE OPTIC NERVES, OPTIC CHIASM AND OPTIC TRACTS

Each retina can be further split into two distinct regions which are determined by the pattern of its fibre projections. The nasal hemiretinae constitute those areas medial to the fovea while the temporal hemiretinae lie lateral to it. Ganglion cell fibres leave the retinae via the optic discs in the nasal hemiretinae and from thereon go to the optic chiasm where, after partial decussation, they emerge into one of the optic tracts. It can be seen from Figure 3 that while fibres from temporal hemiretinae project ipsilaterally those from the nasal hemiretinae cross over and project to the contralateral hemisphere. Fibres then go to their respective target sites in the geniculate body, superior colliculus, pretectum or accessory optic system. This partial decussation has important consequences for how the visual field is represented in the visual system.

1.4 PROJECTION OF THE VISUAL FIELDS ON TO THE RETINA AND REPRESENTATION IN THE VISUAL SYSTEM

The effect of partial decussation can be seen in Figure 3. When a person is fixating it is possible to define a left and right visual half field (VHF). Under these conditions light from a stimulus in the right VHF will fall on the temporal hemiretina of the left eye and nasal hemiretina of the right eye. Fibres from the right nasal hemiretina cross at the chiasm and project to the left hemisphere (LH) while fibres from the temporal hemiretina of the left eye project ipsilaterally. Thus the right VHF projects to the LH and the left VHF to the right hemisphere (RH). This

FIGURE 4. VISUAL FIELD DEFECTS FOLLOWING DAMAGE AT DIFFERENT LEVELS OF THE VISUAL SYSTEM



Visual defects following damage at different levels of the visual system as denoted by numerals. A darkened region in the visual field denotes a blind area.

(From Kolb and Wishaw, 1980)

orderliness means that lesions at various stages of the pathway produce characteristic deficits (Figure 4). It is important to note that in descriptions of such defects the visual field is divided into nasal and temporal halves in the same way as the retina. However it should be borne in mind that the temporal VHF's project on to the nasal hemiretinae and the nasal VHF's on to the temporal hemiretinae. A midline lesion at the level of the optic chiasm, for example, will eliminate the crossed nasal projections and leave only the temporal hemiretinae functioning. When fixating a person suffering from this type of lesion will be able to see only in his nasal visual fields - hence the term bitemporal hemianopsia.

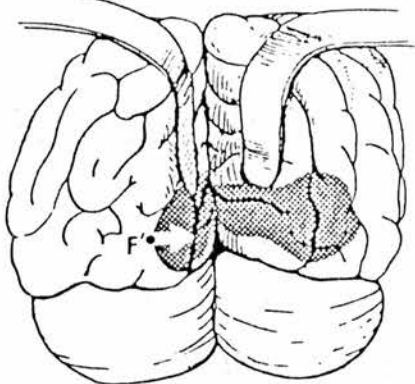
1.5 THE GENICULO-STRIATE SYSTEM

Fibres leave the LGN to form the optic radiations which terminate in the primary visual cortex, located mainly in the calcarine fissure of the occipital lobe (see Figure 5). The contralateral VHF is mapped on to the visual cortex in a very orderly fashion, about which a great deal is known. However for the purposes of this thesis only 3 particular points need mentioning:-

1. The representation of the macula occupies a disproportionately large area.
2. The central visual field is represented in the caudal cortex and around the occipital pole.
3. This area receives a triple blood supply from the calcarine, posterior temporal and middle cerebral arteries.

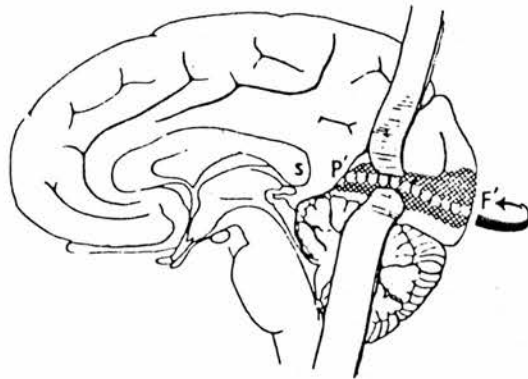
FIGURE 5. REPRESENTATION OF THE VISUAL FIELD ON PRIMARY VISUAL CORTEX

Posterior Aspect of Occipital Lobes

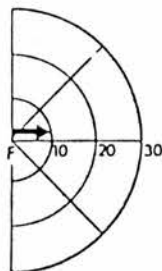


Fixation represented 1.5-20 cm from midline

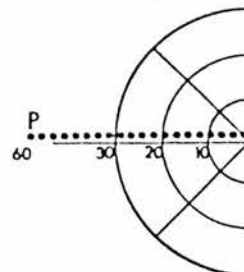
Medial Aspect of Right Visual Cortex



Horizontal meridian represented in depth of calcarine fissure



Right Hemi-field



Left Hemi-field

Location of visual cortex primarily in interhemispherical fissure. Lateral extension as illustrated is variable. Point F' corresponds to central fixation point F in contralateral field. Peripheral field point P is represented in rostral portion of cortex. P'. S, splenium of corpus callosum.

(From Glaser, 1978)

Beyond the primary visual cortex there are a number of secondary visual areas (also referred to as extrastriate and prestriate cortex) which, in humans, correspond to Brodmann's areas 18 and 19. In rhesus monkeys experimental studies have allowed the delineation of a number of sub-areas (see Figure 1) such as V2, V3, V3A and V4 of Zeki (1978) along with the visual parts of inferior temporal cortex (Gross, 1973; Gross and Mishkin, 1977) and the polysensory area of the superior temporal sulcus (Bruce, Desimone and Gross, 1981; Perrett, Rolls and Caan, 1982). Many of these areas contain their own representations of the visual field and seem to be concerned with analysing particular aspects of the visual world eg: colour (Zeki, 1977, 1980) and depth (Zeki, 1978) lending credence to the notion that the visual system is modular (Cowey, 1979, 1982; Van Essen and Maunsell, 1983). Occasional reports in the clinical literature of, for example, impaired colour (Meadows, 1974), motion (Zihl, Von Cramon and Mai, 1983) and face (Damasio, Damasio and Van Hoesen, 1982) perception following localised brain damage suggests that this picture may also be true for man.

A crucial point to note, as far as this thesis is concerned, is that the left and right hemispheres and hence the representations of the left and right VHF's are connected via fibres in the corpus callosum and partially the anterior commissure. Until recently it was thought that only those parts of visual cortex representing the midline region of the visual field (especially at the boundary between areas 17 and 18) were interconnected in monkeys (eg: Berlucchi, 1972). However it is now clear that as one moves into 'higher' visual areas increasingly large parts of the ipsilateral VHF are represented via these interhemispheric crossings (Desimone and Gross, 1979; Bruce Desimone and Gross, 1981). For example in inferior temporal cortex cells with receptive fields extending 30 deg into the ipsilateral VHF have been reported. Sectioning the corpus

callosum and anterior commissure entirely eliminates this ipsilateral response (Gross, Bender and Mishkin, 1977). A similar pattern probably exists in man.

1.6 THE RETINO-COLLICULAR SYSTEM

About 10% of fibres from the optic tract terminate in the superior colliculus. Like the visual cortex each colliculus contains a representation of the contralateral VHF. The two colliculi are connected via the collicular commissure which, in the cat, also forms a pathway to the opposite visual cortex. In addition ipsilateral corticotectal projections are known to exist (eg: Antonini, Berlucchi and Sprague, 1978). Following Schneider (1969) the retino-collicular pathway is thought to have a role in localising a stimulus. In humans unilateral occipital damage produces almost complete blindness in the contralateral VHF (see Figure 4) though the superior colliculus may be implicated in the phenomenon of 'blindsight' whereby these subjects can point accurately to a stimulus in their 'blind' field though they deny seeing it (Weiskrantz et al, 1974; Perenin and Jeannerod, 1979). However this interpretation has recently been questioned and the effect may be due to a combination of scattered light, spared cortex and near-threshold vision (Campion, Latto and Smith, 1983).

1.7 NASOTEMPORAL OVERLAP AND DUAL REPRESENTATION OF THE MIDLINE

The problem of nasotemporal overlap relates to what happens, functionally, at the border between nasal and temporal areas of the retina. If ipsi and contralaterally projecting ganglion cells intermingled at this junction then the part of the visual field projecting on to this area of overlap would go directly to both hemispheres (assuming the pattern was mirrored at the receptor level). Hence there would be a representation of

the midline region in both hemispheres. Of course such a dual representation also exists via interhemispheric pathways (see section 1.5) but this is an indirect route. The question as to the existence of an area of direct, functionally significant, overlap in humans is very much unresolved and of no little theoretical importance. Over the last 20 years many studies have employed divided visual field techniques to investigate hemispheric function in humans (see Beaumont, 1982 for a review). Since such studies assume the non-existence of overlap, at least beyond certain eccentricities (commonly 4 deg), a finding indicating a wider area would confound interpretation of much of the data. The arguments both for and against overlap will be considered next.

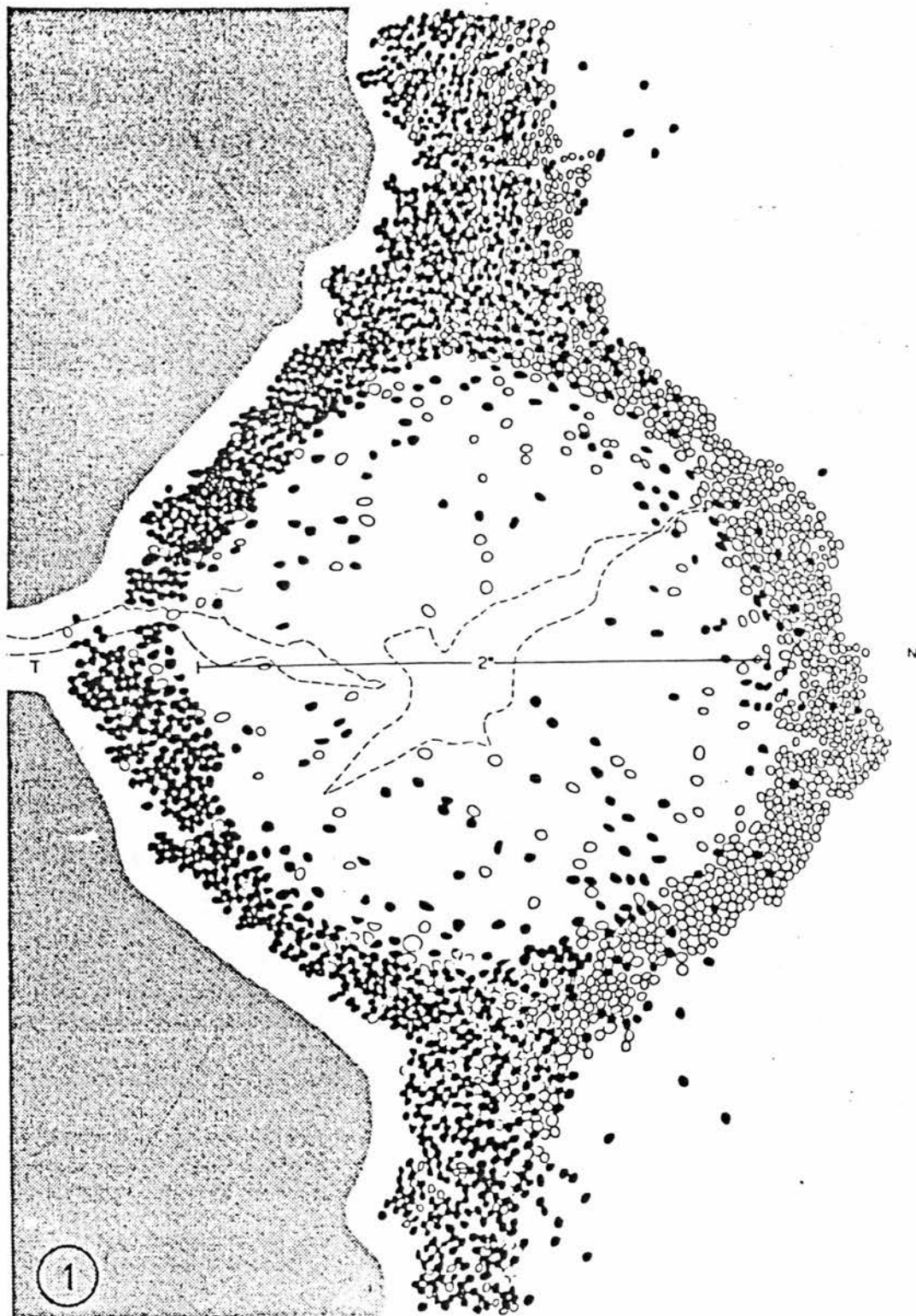
CHAPTER 2

ARGUMENTS FOR AND AGAINST OVERLAP

2.1 ANATOMICAL EVIDENCE

Undoubtedly the most persuasive reason for believing that there is a region of nasotemporal overlap in the human retina comes from anatomical studies involving cats and monkeys. The first study specifically designed to investigate this question was undertaken by Stone (1966) in cats and involved sectioning of one optic tract. Analysis of the pattern of retrograde degeneration in the ganglion cell layer revealed a strip 0.9 deg (0.2 mm) wide where cells projecting to both ipsi and contralateral tracts intermingled (with approximately 50% going to each tract). A follow-up study found that this pattern was particularly pronounced in the X-cells of the cat retina (Stone and Fukuda, 1974). A similar procedure has been adopted in monkeys and again a strip of overlap, approximately 1 deg wide, was found (Stone, Leicester and Sherman, 1973). There are, however, a number of problems with this technique (Bunt Minckler and Johanson, 1977). Firstly it is difficult to distinguish surviving ganglion cells from neuroglia and secondly it is possible that the remaining ganglion cells shift their positions following degeneration of neighbouring neurons. To circumvent these problems Bunt et al used the retrograde horseradish peroxidase tracing technique which does not, of course, stain glial cells and also allows the recognition of single labelled neurons. Unilateral injections of horseradish peroxidase were made into the LGN and optic tract and the pattern of retrograde labelling of ganglion cells examined. The results from the right retina of a monkey which received an injection into the right LGN are shown in Figure 6. In order to understand it properly 2 points should be appreciated:-

FIGURE 6. RETROGRADE HRP LABELING OF
GANGLION CELLS IN MONKEY RETINA



Camera lucida drawing of foveal ganglion cells from right retina of monkey 75228 which received an injection of horseradish peroxidase (HRP) into the right dLGN 24 hours prior to sacrifice. The original drawing was made with a $\times 63$ oil immersion lens and reduced photographically. Filled ovals are ganglion cells labeled with HRP, open ovals are unlabeled ganglion cells. Horizontal line indicates horizontal meridian, and cells have been traced away from the fovea superiorly and inferiorly along the vertical meridian. N, nasal; T, temporal. The dotted lines indicate cracks in the flat mount preparation. The grey shading indicates the region of temporal retina in which virtually every ganglion cell is labeled. Note labeling of most but not all ganglion cells lying within $1/2^\circ$ of the temporal rim of the foveola, and scattered labeled ganglion cells in a $1/2^\circ$ band around the nasal rim of the foveola. Scattered labeled and unlabeled ganglion cells lie across the floor of the foveola; within the 1° strip centered on the vertical meridian, approximately half of the ganglion cells are labeled and half are unlabeled.

(From Bunt, Minckler and Johanson, 1977.)

1. The retina is 'looking' at the reader so the nasal and temporal hemiretinae are on the right and left respectively.

2. The largely empty circle in the middle corresponds to the ganglion cell free foveal pit (see section 1.2).

Since fibres from ganglion cells in the temporal hemiretinae project to the ipsilateral LGN most of the labelled ganglion cells are on the temporal side. It is important to note, however, that not all of the ganglion cells on the temporal side are labelled - approximately 1 in 14 are not (Bunt and Minckler, 1977). Similarly in the otherwise unlabelled nasal hemiretina there are some labelled cells. The degree of intermingling seems greater above and below the foveal pit where the strip of overlap is approximately 1 deg wide. The distance between the 2 semicircles surrounding the foveal pit is about 2 deg.

Two important points should be made concerning this evidence for overlap in the primate retina. Firstly ganglion cells on the 'wrong' side of the midline are in a small minority. Secondly the finding does not tell us anything directly about overlap at the receptor level. Stone (1966) has pointed out that if ganglion cells were displaced in random directions by distances up to, say, 0.1 mm then a sharp division at the receptor level would be obscured at the ganglion cell layer. In order to determine the functional significance of the above-described overlap it would be necessary to cut the interhemispheric commissures and record from single units in the visual cortex. Assuming eye movements were excluded any remaining representation of the ipsilateral visual field would presumably reflect an overlap at the receptor level. Such an investigation has been undertaken in cats by Leicester (1968) who found that ipsilateral responses could still be recorded following section of the corpus callosum.

Unfortunately a similar study has not been undertaken in primates. However, as Cowey and Perry (1981) found no overlap in the ganglion cell projection to the monkey colliculus it would seem likely that the overlap described in the retino-geniculate pathway is not a consequence of displacement of the type described above. Nonetheless the functional significance of the monkey overlap remains undemonstrated.

A number of observations have been made of the distribution of ganglion cells in the human retina following chiasmal lesions (Kupfer, 1963; Von Buren, 1963). These studies found a sharp division between the degenerated nasal ganglion cell layer and the intact temporal ganglion cell layer. However as a similar pattern was revealed in monkeys (Von Buren, 1963) it is likely that the techniques used by these authors were not sufficiently sensitive to pick up the small overlap later demonstrated in monkeys by the more refined methods described above. There are therefore no grounds for believing that the human retina is substantially different from the monkey retina in this respect.

2.2 FOVEAL SPARING

The term foveal sparing is usually taken to refer to the sparing of a small island of centralmost vision which bulges into the 'blind' field (see figure 4) following suprageniculate damage (Walsh and Hoyt, 1969). However another type, where a strip running up the entire length of the vertical meridian is spared, has been described and is referred to as an overshoot field (Traquair, 1940). The term 'foveal' is used here to replace the historically more popular term 'macular' which refers to a larger area of sparing and may be a consequence of improperly controlled fixation (Bunt and Minckler, 1977). Modern studies typically find a sparing in the order of 1.5 deg (eg: Teuber, Battersby and Bender, 1960; Huber, 1962, 1970;

Koerner and Teuber, 1973) or less, though larger sparing is still reported (eg: Perenin and Vadot, 1981). The subject of sparing has been debated for most of this century (eg: Penfield, Evans and Macmillan, 1935; Halstead, Walker and Bucy, 1940; Walsh and Hoyt, 1969) and a number of possible explanations have been put forward. At present it is possible that the phenomenon could be due to:-

1. Poorly controlled fixation during perimetry.

2. Surviving primary visual cortex. Areas representing the fovea are more likely to survive because they are represented over a disproportionately large area of cortex and because the occipital pole where the fovea is represented receives a triple blood supply (see section 1.4) giving it added protection against damage due to ischaemic lesion.

3. Surviving extrastriate visual cortex. It is now known that some extrastriate areas receive a direct input from the LGN even in monkeys (Benevento and Yoshida, 1981; Fries, 1981; Yukie and Iwai, 1981), in contrast to what was previously thought. This would, though, have to be selective for central visual field representation.

4. The existence of an interhemispheric link between the LGN of one hemisphere and visual cortex of the other.

5. The operation of sub-cortical visual pathways.

6. The existence of a region of nasotemporal overlap giving rise to a dual representation of the midline region, one in each hemisphere.

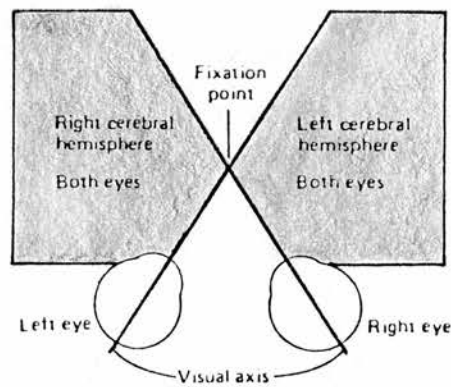
It should be noted at the outset that sparing almost certainly has different causes in different cases and hence no single explanation will be applicable to all instances. For example poorly controlled fixation may

have led to incorrect diagnoses of foveal sparing in some cases and contributed to the misnomer 'macular' sparing in others. However a number of studies have controlled fixation very carefully and still found the effect (eg: Halstead Walker and Bucy, 1940; Huber, 1962; Walsh and Hoyt, 1969). The possibility that all cases of sparing are attributable to poor fixation can therefore be ruled out. As far as the second possibility is concerned there is no doubt that foveal sparing can be attributed to surviving cortex in some cases (eg: McAuley and Ross Russell, 1979; Spector et al, 1981). The important point to consider here, therefore, is whether there exist any cases of sparing which can only be attributable to a region of overlap. The short answer is 'no', though a consideration of cases of sparing following hemispherectomy (Williams and Gassel, 1962; Perenin, 1978; Perenin and Jeannerod, 1978) helps rule out a number of possibilities. In particular one can eliminate the possibility that sparing could, in these patients, result from surviving primary or extrastriate visual cortex. Assuming that one rules out unstable fixation as a possibility only the final 3 explanations cited above are tenable. The suggestion of an interhemispheric link between the LGN of one side of the brain and visual cortex of the other was first made by Pfeifer (cited in Halstead, Walker and Bucy, 1940) following work on chimpanzees but rejected by Putnam (1926) who could find no evidence to support the claim in infants. Later Glickstein, Miller and Smith (1964) claimed to have shown such a tract in cats by using degeneration techniques though this finding was challenged by Wilson and Cragg (1969) who suggested it was an artefact resulting from accidental damage to the corpus callosum. Furthermore Polyak (1957) observed that degeneration following unilateral occipital lobectomy in monkeys and man is confined to the LGN on the same side and Garey (cited in Perenin and Vadot, 1981) has failed to find any evidence for such a tract using the horseradish peroxidase tracing

technique. The existence of this pathway can therefore be virtually ruled out. In any case sparing is apparently still found after hemispherectomy along with sectioning of the splenium (Koerner and Teuber, 1973) and so could not be attributed to a callosal pathway from the LGN to the opposite cortex, even if such existed. One is thus left with only two possible explanations of sparing in hemidecorticates - that it is due to the operation of sub-cortical visual pathways or a region of overlap. The most likely sub-cortical pathway to be involved is one including the superior colliculus. Until recently it was not certain whether the fovea was directly represented in the primate colliculus or not. It has now been shown in monkeys that the fovea is not only directly represented but also that the projection is disproportionately large (Cowey and Perry, 1981). However it seems unlikely that the colliculus by itself can give rise to the conscious experience of seeing (see section 1.6) so information would presumably have to be relayed from the colliculus on the hemispherectomised side of the brain to the visual cortex on the intact side. Possibly the greater strength of the foveal projection might explain why only that region of the ipsilateral VHF is spared. To determine the validity of this interpretation it would be necessary to see if sparing is still observed in cases of hemispherectomy along with midbrain damage. Unfortunately I know of no such reports in the literature. Thus sparing in hemidecorticates could reflect the operation of sub-cortical visual pathways or be due to the presence of a region of overlap. It is impossible at present to determine which of these explanations is the most likely.

2.3 MIDLINE STEREOPSIS

FIGURE 7. PROJECTION TO THE BRAIN OF STIMULI PRESENTED BEHIND AND IN FRONT OF FIXATION



Unfilled areas are those in which corresponding retinal areas reach opposite hemispheres of the brain.

(From Gouras, 1981)

It has been suggested that the neurophysiological basis of stereopsis is the coming together of disparity information from the two eyes at a single locus in one hemisphere (Barlow, Blakemore and Pettigrew, 1967; Bishop, 1973). If this is the case then there is a problem concerning stereopsis in the midline region where it is most acute (Gouras, 1981). It can be seen from Figure 7 that information from the two eyes for a stimulus presented behind or in front of fixation (the unshaded areas) instead of projecting to the same hemisphere goes to opposite hemispheres. The problem is how this information is united, and there are two possible solutions. The first is that information is joined via a crossing in the corpus callosum. As mentioned previously the areas representing the midline regions in the two hemispheres are known to be connected (section 1.5). However Bishop (1973) has pointed out that most of the fibres recorded from in the corpus callosum of cats (Hubel and Wiesel, 1967; Berlucchi, 1972) are binocularly activated, whereas one might expect them to be monocularly activated if they subserved the process of stereopsis outlined above. The second possibility is that the process is mediated by a region of nasotemporal overlap which would result in information from the two eyes being available in each hemisphere thereby eliminating the need for any interhemispheric crossing. In support of this proposition is the finding of Leicester (1968) that responses to stimuli in the ipsilateral VHF can still be recorded from cat visual cortex following section of the corpus callosum. However, as previously mentioned, such a study has not been undertaken in primates, except in inferior temporal cortex (see section 1.5).

If a region of overlap were the basis of stereopsis in man, rather than a commissural crossing, then it follows that commissurotomed patients ought to have impaired midline stereopsis. Mitchell and Blakemore

(1970) tested this prediction by looking at stereopsis in the commissurotomed subject L.B. Using a retinal disparity of 2 deg they found peripheral stereopsis was normal whereas midline stereopsis was severely impaired. Such a finding weighs heavily against the notion that a region of overlap mediates midline stereopsis in man. However in reply to this argument Bishop and Henry (1971) have argued that two types of stereopsis should be distinguished. Coarse stereopsis is said to operate at higher disparities, to be associated with double images and to possibly depend on interhemispheric integration while fine stereopsis is argued to operate at lower disparities, to be associated with the experience of 'seeing solid' and is presumed to depend on overlap. If this distinction is justified then the fact that Mitchell and Blakemore used a disparity of 2 deg would mean that they were looking at the former process. Unfortunately, as Bishop (1973) points out, earlier demonstrations that split brain subjects possess stereopsis (Akelaitis, 1941; Gazzaniga, Bogen and Sperry, 1962) cannot resolve the issue since it is not known whether these patients used retinal disparities that may have involved overlap. The crucial experiment thus remains to be done.

2.4 COMMISSUROTOMY STUDIES

A quite different method to that described above has been designed by Sperry (1968) to test for overlap in commissurotomed subjects. In this paradigm the patient is monocularly presented with a number of dots extending across the midline into right and left VHF's within a 1 deg range. Subjects were then asked to report the number of dots present by holding up the appropriate number of fingers and, in the case of right VHF presentation, confirming this verbally. If a region of overlap were present then one might expect that this would enable the patient to 'see into' a small part of the other hemisphere's VHF and hence lead to an

overestimation of the actual number of dots present in any one VHF. However no such overcounts (or for that matter undercounts) were found. Similarly Gazzaniga, (1970) using only verbal responding, reported that "All patients proved able to report only the dots that fell to the right of the fixation point. A dot 1 mm or more to the left of fixation went unnoticed by the left hemisphere." Unfortunately both these reports are brief and one would like more information concerning, for instance, the size of dots used and in the case above the visual angle represented by 1 mm. However as the total range covered was reported to be only 2 deg these results furnish reasonably good evidence against an overlap of any functional significance existing in man.

2.5 CONCLUSIONS

From the preceding discussion it is clear that the question of nasotemporal overlap in man is far from resolved. The degree of overlap demonstrated in closely related primate species leaves open the question of its functional significance, if any. Degeneration studies in humans are technically flawed and it is difficult to draw any firm conclusions from them. Alternative explanations make it difficult to conclude that cases of sparing are due to the presence of a region of overlap and the neuropsychological basis of midline stereopsis remains uncertain. Finally the commissurotomy studies of Sperry and Gazzaniga argue against the existence of overlap though in the absence of full details it would be premature to attach too much significance to these reports. The experiments reported here therefore aimed to throw some light on the debate by employing a quite different experimental paradigm, that of simple reaction times to lateralized light flashes.

CHAPTER 3

EXPERIMENTS

3.1 INTRODUCTION

The experiments reported in this thesis all employ variations of the simple reaction time (RT) paradigm outlined by Poffenberger (1912), whereby a subject is required to make a simple finger movement in response to a lateralized light flash. This paradigm is frequently used to obtain estimates of interhemispheric transmission time (IHTT), the rationale being based on the observation that fine finger movements are mainly under control of the hemisphere contralateral to the responding hand (Brinkman and Kuypers, 1973). Thus when a subject's responding hand is on the same side as the flash (an 'uncrossed' reaction), the hemisphere which first receives the input also controls the response. However when the stimulated VHF is contralateral to the responding hand (a 'crossed' reaction) information must presumably be passed between the hemispheres before a response can be made. Consequently the crossed-minus-uncrossed difference (CUD) has been identified with IHTT. It is important to emphasise that this rationale only seems applicable to RT paradigms where the subject is required to make a simple invariant response to an unstructured stimulus (Bashore, 1981). When choice RT paradigms or more complex stimuli are used factors such as attentional bias (Swanson, Ledlow and Kinsbourne, 1978) and spatial compatibility (Craft and Simon, 1970; Wallace, 1971) may obscure the underlying anatomy. In the simple RT task stimulus response compatibility has been shown to have no effect (Anzola et al, 1977; Berlucchi et al, 1977; see Chapter 4 for a more detailed discussion). The results of simple manual RT experiments reveal a consistent CUD of about 2.5 ms (see Bashore, 1981; Milner and Lines, 1982; Tassinari, Morelli and

Berlucchi, 1983) and an anatomical interpretation of this is supported by the finding that in acallosal subjects the CUD rises dramatically (Jeeves, 1969; Milner, 1982; Milner et al, 1984) and is in the order of 20 ms.

The above rationale can also be extended to simple vocal responding (eg: saying the word 'YES' upon seeing a flash) in subjects showing LH speech dominance (Milner and Lines, 1982). Here the CUD is equated with a right VHF advantage since information in the left VHF has presumably to be relayed from the RH to LH before a response can be made. Vocal CUDs have been found to be larger than manual ones and their size is dependent on the intensity of the stimulus - the vocal CUD increases with decreasing stimulus brightness (Milner and Lines, 1982). Manual CUDs, on the other hand, are invariant with intensity changes. This observation has led to the suggestion that manual and vocal CUDs reflect two distinct types of interhemispheric relay (Milner and Lines, 1982). As the vocal CUD varies with intensity this may reflect a sensory relay between the visual cortices while the invariant manual CUD may reflect the crossing of some sort of motor program between the motor cortices (Berlucchi, 1978).

It follows from the preceding considerations that if a nasotemporal overlap exists in man then stimuli presented on this region ought to be equally available to both hemispheres and there should be no need for an interhemispheric crossing of any kind. Consequently the CUD should be eliminated. This technique thus provides a method for seeking functionally significant overlap in humans. Experiments designed to test this prediction using both manual (Harvey, 1978) and vocal (Haun, 1978) RTs have failed to find evidence for overlap. Unfortunately neither study employed a simple RT procedure. Harvey presented stimuli (a letter 'O') at eccentricities ranging from 1/4 to 4 deg and required subjects to respond by pressing one of two keys. This procedure resulted in an IHTT estimate

of 25 ms, a value well outside the range of estimates derived from simple RT experiments. Haun's subjects were required to name laterally presented letters. While this procedure produced IHTT estimates in accord with the simple vocal RT paradigm, the possibility of a right VHF attentional bias due to LH activation when processing verbal stimuli cannot be ruled out. The aim of the present experiments therefore was to employ simple vocal (Experiment 1) and manual (Experiment 2) responses to an unstructured light stimulus in an attempt to find evidence for overlap.

3.2 EXPERIMENT 1

3.2.1 METHODS

Subjects

Twenty four University students (seventeen females and seven males) were paid at the rate of £1 per session to take part in the experiment. Age range was 18 - 32 with a mean of 21 years. Since the rationale of the experiment required using subjects with LH speech dominance only right-handed people were tested. Furthermore anyone who failed to show an overall right VHF RT advantage was excluded from the analysis. In practice this meant the exclusion of four subjects (two of each sex) out of 28 tested. Sixteen subjects had participated in previous RT experiments but were ignorant as to the purpose of both those and the present study.

Apparatus

Stimuli were presented on the CRT display screen of a DEC graphics computer (GT40). Extraneous visual stimulation was excluded by an opaque mask surrounding the screen which also provided a fixed viewing distance of 35 cms. A small (1/30 deg) fixation spot remained present in the centre of

the screen throughout each session. During test trials a 1000 Hz warning tone was followed by a delay varying pseudorandomly between 500 and 1500 ms after which a small (1/30 deg), green, dim stimulus light was flashed for 2 ms at an eccentricity of 1/2, 1, 2 or 4 deg of visual angle either to the left or right of fixation. The energy of the flashes, measured as a point source, was estimated at 9.4×10^{-5} microW/degree². The presentation and pseudorandomisation of the left - right trial sequence was controlled by computer and RTs outside the range 150 - 1500 ms were excluded and replaced automatically. Vocal responses were recorded by means of a standard tape recorder microphone, interfaced with the computer, whose sensitivity was adjusted to register subjects' reactions reliably. Irrespective of subjects RT the warning tone for the next trial came 1500 ms after stimulus onset in the preceding trial.

Procedure

Subjects attended two test sessions which lasted about an hour each and were always on different days. Four positions of eccentricity were used - 1/2, 1, 2 and 4 deg. Each session consisted of five 60-trial blocks at one position of stimulus eccentricity followed by five blocks at a different position, with a coffee break in between. Order of presentation was counterbalanced with the constraint that presentations at 1/2 and 4 deg were always given at the same session as were presentations at 1 and 2 deg. A block consisted of 60 pseudorandomised left and right VHF presentations each preceded by a 50 ms warning signal. The length of time between the warning tone and stimulus appearance varied pseudorandomly between 500 and 1400 ms in 100 ms steps. Subjects were told to respond by saying 'YES' in a clear voice and as fast as possible upon seeing a flash. The importance of steady fixation was strongly emphasised and subjects were also told that warning period length would vary and that left and right VHF presentations

Table 1: Vocal reaction times to left and right stimulation
at four points of eccentricity

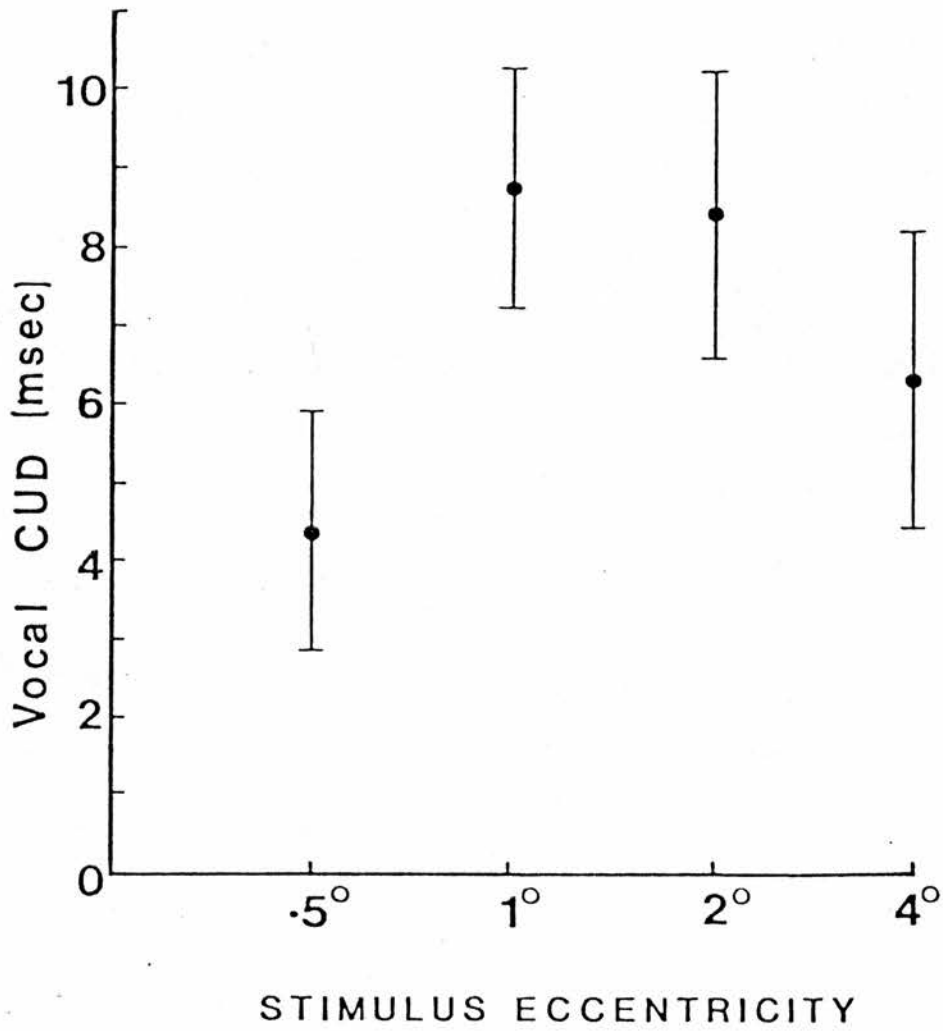
Subject	1/2°		1°		2°		4°	
	Left	Right	Left	Right	Left	Right	Left	Right
1	307.13	313.55	296.99	300.70	303.59	303.20	338.57	323.80
2	324.16	313.85	293.38	281.54	303.91	296.60	404.44	398.76
3	369.02	365.98	349.62	352.74	354.93	356.16	424.71	414.57
4	414.01	410.77	417.32	407.97	433.24	444.86	444.89	440.28
5	401.80	407.52	404.34	388.25	409.03	403.27	367.57	375.77
6	376.26	352.93	329.17	330.96	399.57	389.62	389.01	378.64
7	385.01	380.22	415.66	399.64	424.25	400.17	442.65	415.31
8	316.00	311.07	350.09	324.95	357.26	343.07	369.39	359.44
9	281.79	280.97	279.61	278.16	314.39	303.21	315.00	309.91
10	315.58	324.83	373.84	365.61	343.87	344.55	367.50	345.17
11	283.42	286.70	286.47	282.86	283.75	276.73	294.15	285.83
12	388.53	388.03	408.26	387.41	469.23	441.60	449.45	442.51
13	305.59	300.98	340.99	333.70	344.05	324.82	366.60	359.15
14	415.95	414.65	383.13	373.74	380.37	379.25	407.42	408.87
15	331.56	319.79	280.37	270.65	303.28	292.17	359.01	339.03
16	324.57	323.27	289.82	268.81	305.41	284.59	380.44	377.44
17	321.24	314.66	341.73	330.39	362.46	352.16	363.29	353.47
18	355.19	355.24	329.99	327.24	357.45	353.19	365.01	371.18
19	306.43	300.98	304.46	302.07	308.99	303.31	351.15	342.38
20	346.56	342.47	335.13	329.20	332.85	321.20	383.68	387.95
21	335.81	333.25	306.21	299.69	313.27	303.11	358.50	348.85
22	320.83	308.18	311.78	301.75	306.25	308.11	356.85	362.40
23	385.02	371.11	340.86	329.88	346.19	340.66	355.75	355.83
24	322.57	308.15	313.09	304.65	337.15	328.21	343.36	350.67
Mean	343.08	338.71	336.76	328.02	349.78	341.40	374.93	368.63

would be at random. A practice block was given at the beginning of the first session.

3.2.2 RESULTS

Mean RTs for the four stimulus positions are given in Table 1. A two-way repeated measures ANOVA (the two factors were eccentricity - 1/2, 1, 2 or 4 deg and VHF - left or right) revealed a significant main effect of VHF, $F(1,23) = 51.35$, $p < .0001$ which was unsurprising in view of the fact that only those subjects giving an overall right VHF advantage were used in the study. Also present was a significant main effect of eccentricity, $F(3,69) = 18.61$, $p < .0001$. Generally this reflects a trend for RT to increase with increasing eccentricity though it can be seen from Table 1 that RTs at 1/2 deg are actually slower than at 1 degree. Tukey tests, however, revealed no significant differences between mean RTs at these two positions. The fact that both left and right VHF RTs show the effect is presumably due to the fact that they originate from the same session. The most important finding from the point of view of the aim of the experiment was a clearly non-significant eccentricity x VHF interaction, $F(3,69) = 1.62$, $p > .1$ reflecting the fact that the CUD (right VHF advantage) was present at all four eccentricities. (Furthermore a one-way ANOVA performed on the CUDs rather than raw data (a procedure which removes the common variance associated with the overall effect of eccentricity on RT) also showed no significant effect of eccentricity). The mean value of the CUD was 6.94 ms with a range of 4.37 - 8.74 ms (Figure 8). Finally it is worth noting that although the smallest CUD was at 1/2 deg 19 of the 24 subjects did show positive CUDs at this position as compared with 21, 20 and 18 at 1, 2 and 4 deg respectively. The result was not, therefore, due to a few atypical subjects.

FIGURE 8. EXPERIMENT 1: VOCAL CUDs
AT FOUR ECCENTRICITIES



3.2.3 DISCUSSION

The finding that RT increases with increasing eccentricity (for the most part) is a common one in RT experiments and presumably reflects the changing receptor density of the retina (Berlucchi et al, 1971). As far as the aim of the present experiment is concerned the most interesting finding was that the CUD remained invariant over the four positions tested and was present even at 1/2 deg, thereby arguing against the existence of any overlap in the human retina. (Also, although no specific check on fixation was made the presence of such an effect indicates that subjects were fixating properly). However a possible criticism of this interpretation of the results is that the vocal CUD might actually reflect a right VHF attentional bias on the part of our selected subjects rather than being due to IHTT (Tassinari, Morelli and Berlucchi, 1983). Such a criticism would not be applicable to the simple manual RT paradigm since this does not require selection of subjects and the CUD is not equated with just one VHF advantage. For this reason the above experiment was repeated using manual instead of vocal responding. A similar finding to that reported above would be consistent with an anatomical interpretation of the vocal CUD whereas a finding supporting the existence of overlap (ie: abolition of the CUD at 1/2 and possibly 1 deg) would suggest the operation of an attentional bias.

3.3 EXPERIMENT 2

3.3.1 METHODS

Subjects

Sixteen University students (twelve females and four males) took part in the experiment and were paid at the rate of £1 per session. Eleven of

these had participated in previous RT experiments but were ignorant as to the purpose of both those and the present study.

Apparatus

The apparatus was the same as that used in Experiment 1 except that manual responses were recorded by means of micro-switches placed centrally on a table under the display screen.

Procedure

The same four positions of eccentricity as in Experiment 1 were used and with the same constraint, namely that presentations at 1/2 and 4 deg were always given during the same session as were presentations at 1 and 2 deg. In order that the design be properly counterbalanced four sessions were required and these were run in an ABBA order. A session consisted of five blocks of trials at one position of eccentricity followed by five blocks at another position, with a coffee break in between. Subjects used one hand for the first five blocks followed by the other hand for the remaining five. This order of hand use was retained for the second session and then reversed for the last two sessions. Half the subjects started off using the left hand and half the right. Each subject thus gave separate left and right hand responses for five blocks consisting of 60 trials each, at all four positions of eccentricity. Subjects were requested to hold down the micro-switch with the requisite index finger and to lift this as rapidly as possible upon seeing a flash. Practice blocks were given at the beginning of the two halves of the first session and at the beginning of the second session.

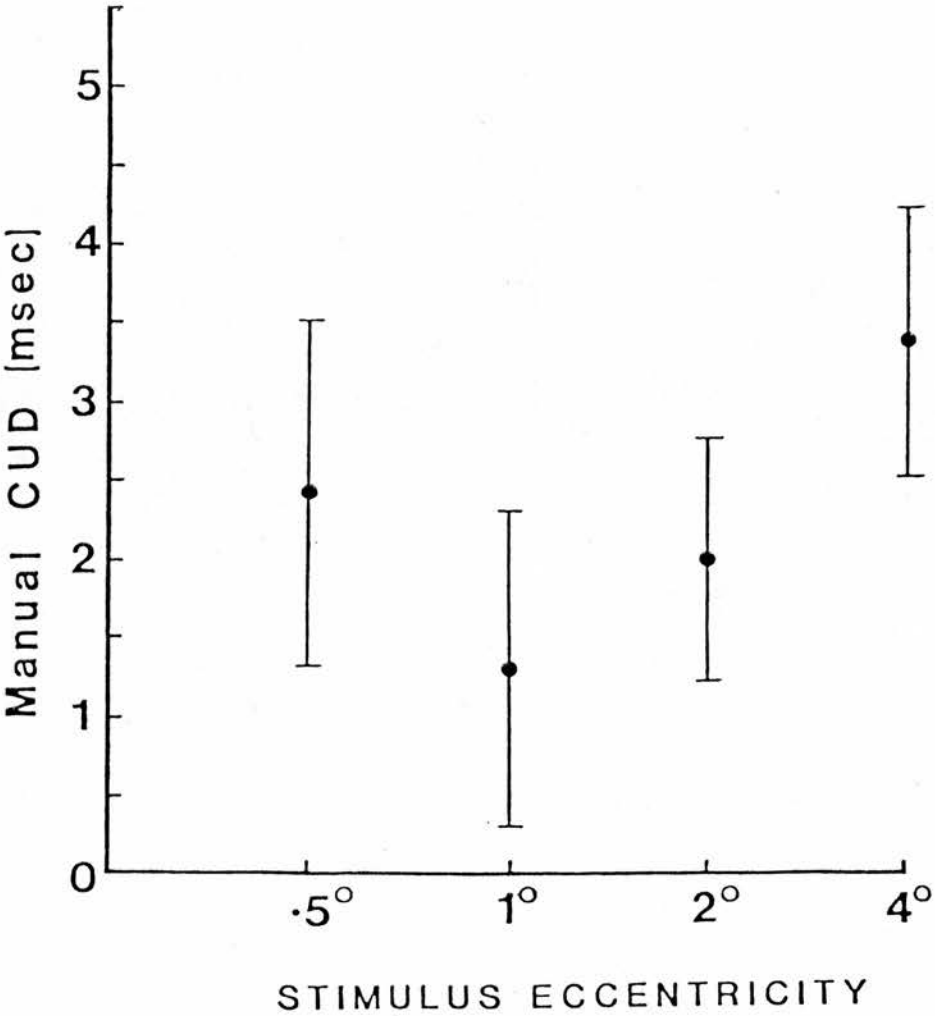
Table 2: Manual reaction times for crossed and uncrossed responding at four points of eccentricity

Subject	1/2°		1°		2°		4°	
	Crossed	Uncrossed	Crossed	Uncrossed	Crossed	Uncrossed	Crossed	Uncrossed
1	247.39	250.79	246.12	249.62	260.23	265.74	278.46	274.18
2	260.42	258.33	278.39	277.42	273.55	271.73	275.17	271.10
3	301.78	298.89	299.20	297.91	307.28	308.44	324.53	318.98
4	288.59	274.90	271.13	268.30	261.87	259.63	304.73	302.28
5	321.63	312.94	328.97	332.02	329.43	326.48	322.93	322.19
6	263.23	259.15	273.44	272.89	283.96	277.89	289.97	290.75
7	289.23	285.71	275.27	277.86	282.87	278.62	294.55	291.82
8	256.55	253.17	291.17	283.91	283.06	282.22	296.31	297.00
9	288.31	287.95	309.52	305.26	329.08	322.73	308.96	298.65
10	272.69	271.39	282.39	285.40	296.25	294.02	317.47	318.29
11	309.51	308.51	303.07	295.49	312.49	311.68	337.77	334.48
12	296.17	299.46	293.27	288.58	295.58	295.47	325.06	316.64
13	265.52	262.56	268.31	265.11	286.26	287.65	232.08	282.52
14	255.99	253.34	288.43	282.60	303.77	298.21	303.79	299.15
15	269.61	273.10	273.11	278.53	307.71	304.90	301.77	295.16
16	254.70	252.20	261.46	266.42	280.13	276.29	278.98	275.43
Mean	277.58	275.15	284.27	282.96	293.35	291.36	302.66	299.29

3.3.2 RESULTS

In order to facilitate comparison with Experiment 1 mean RT scores for crossed and uncrossed responses (rather than for separate hands and VHF) at each position of eccentricity are given in Table 2. A three-way repeated measures ANOVA (the three factors were eccentricity - 1/2, 1, 2 or 4 deg, hand - left or right, and VHF - left or right) revealed a highly significant main effect of eccentricity, $F(3,45) = 18.14$, $p < .0001$ which reflects the fact that RT increases with increasing eccentricity, as can be seen from Table 2. None of the other main effects reached significance level. The only significant interaction was that of hands x VHF, $F(1,15) = 22.94$, $p < .0005$ reflecting a clear CUD which was present at all four positions of eccentricity (Figure 9). The overall value of the CUD ranged from 1.31 - 3.37 ms with a mean of 2.27 ms, the CUD at 1/2 deg being the second highest (2.43 ms). Analysis of individual subject's data showed that 13 of the 16 gave an overall positive CUD at the 1/2 deg position and the fact that the eccentricity x hands x VHF interaction was non-significant ($F(3,45) = 0.97$, $p > .1$) indicates that the CUD was invariant as a function of eccentricity. (This interpretation is borne out by a two-way ANOVA on the CUDs rather than the raw data which, as in Experiment 1, revealed no significant effects). Finally it may be noted that a correlation analysis performed at individual eccentricities within each experiment to check intra-subject consistency failed to reveal any significantly positive correlations, presumably because the variability was too great. However mean CUDs in the two experiments were positively correlated over 6 subjects who took part in both ($r = 0.869$, $p < .05$), consistent with the interpretation that both were measuring the efficiency of commissural transmission.

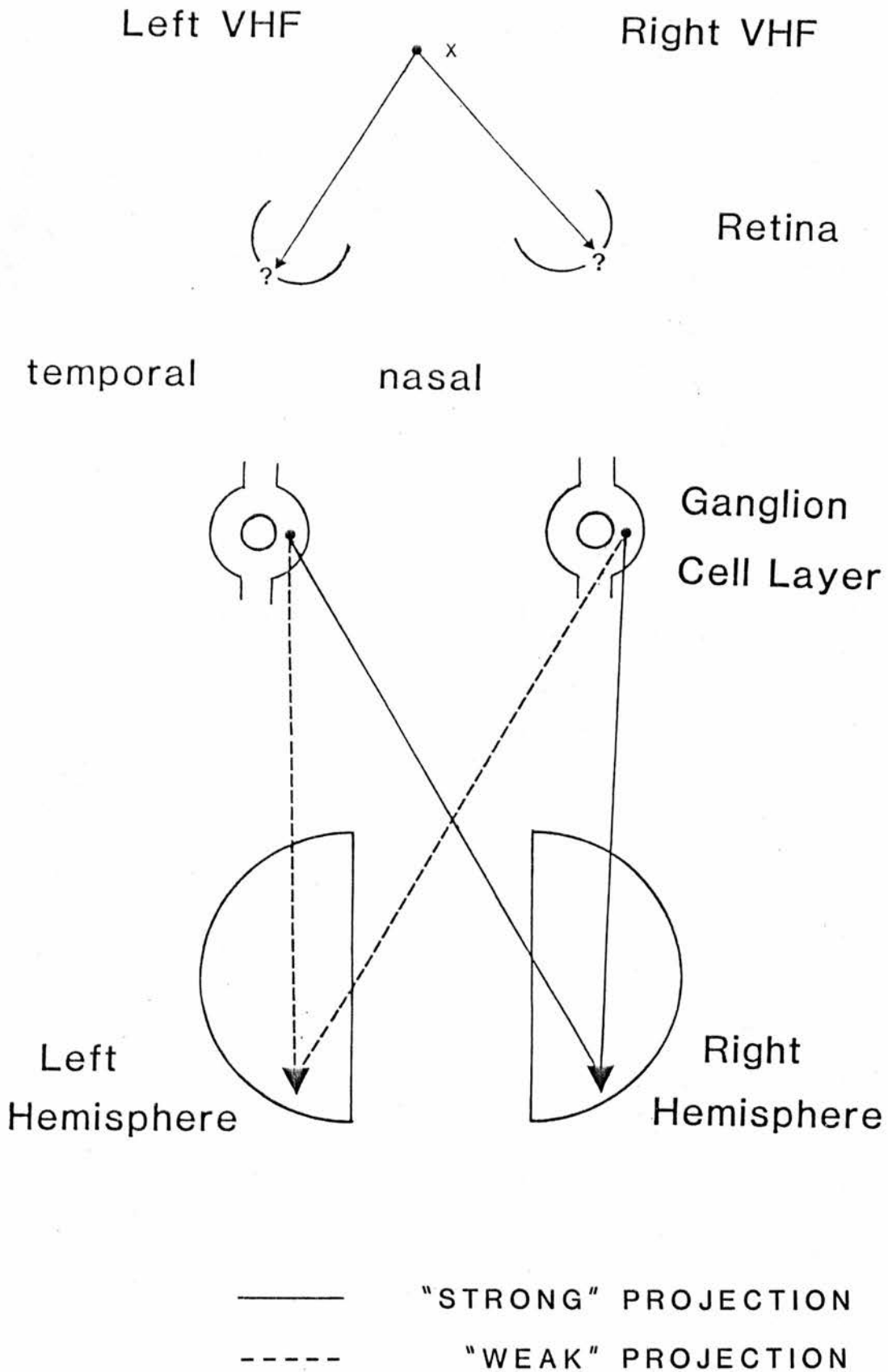
FIGURE 9. EXPERIMENT 2: MANUAL CUDs
AT FOUR ECCENTRICITIES



3.3.3 DISCUSSION

The results from the manual RT experiment are in agreement with those from the vocal RT experiment in finding a CUD even with stimuli presented very close to fixation. If the assumption is correct that the CUD in both cases reflects the time lost in interhemispheric transmission then the results argue against the existence of any functional overlap in man. This finding does not necessarily conflict with the demonstration of a small overlap in the monkey retina (section 2.1). As mentioned previously retinal ganglion cells on the 'wrong' side of the midline in the arcs of overlap around the foveal pit constitute only 1 in 14 of the total population (Bunt and Minckler, 1977). It may therefore be the case that these cells result in only a weak projection to the 'wrong' hemisphere (ie: the one ipsilateral to the stimulus) which is overshadowed by the much stronger projection to the hemisphere contralateral to the stimulus (see Figure 10). Given that dim stimuli were used in the present experiments it is possible that the weak input to the 'wrong' hemisphere was simply insufficiently strong to be separated from background noise or, as a result of the lower signal-to-noise ratio, in time to determine response. It may however be premature to conclude from the present results that no functional overlap exists in the human retina. In these experiments the subjects were partially dark adapted and the stimuli were dim, a consequence of which may have been that only rod receptors were being used. If ganglion cells in a strip of overlap received only foveal cone input then this might explain why no evidence of overlap was found. Such a proposition should be testable by measuring RTs to bright stimuli in light adapted subjects. Consequently Experiment 3 was designed to investigate whether any evidence for overlap would be found under these conditions.

FIGURE 10. SCHEMATIC DIAGRAM SHOWING POSSIBLE "WEAK" DUAL REPRESENTATION OF THE MIDLINE



3.4 EXPERIMENT 3

3.4.1 INTRODUCTION

This experiment sought to investigate the possibility that the failure of the previous two experiments to find any evidence of overlap was a result of the subjects being dark adapted and the stimuli dim, by measuring manual RTs to bright stimuli in light adapted subjects. An additional aim was to examine the effect of varying response type, since preliminary results from another laboratory had indicated an abolition of the CUD below 6 deg (Berlucchi and Marzi, personal communication) using a modified simple RT paradigm. Their procedure differed from the normal one in presenting stimuli at two eccentricities within any one run. One position was always 30 deg while the other varied between 1-10 deg over runs. Hence in any particular run a stimulus could appear at any one of 4 possible locations - in other simple RT experiments with randomised presentation the flash appears at 1 of only 2 possible locations. A thumb press response was also required and the response keys were placed 29 cm away from the midsagittal plane so they were nearer to the stimuli at 30 deg. The basis of this puzzling result remained uncertain though one difference between the two experiments lay in the type of response required. Previous studies requiring a thumb press have never looked at the effect of presenting stimuli below 5 deg. Although there is no known reason from an anatomical point of view to think this should have any effect on the CUD it was considered important to examine the effect of varying response type with stimuli presented close to fixation in the simple RT task. A finding that the CUD is abolished at small eccentricities using a thumb press response, but not a finger release one, might cast doubt on a simple anatomical interpretation of the manual CUD. For this reason half the subjects in the present experiment were tested using a thumb press, instead of a finger

release, response.

3.4.2 METHODS

Subjects

Sixteen University students and Research Assistants (5 females and 11 males) volunteered to take part in the experiment and were paid at the rate of £1 per hour. Age range was 18 - 38 years with a mean of 26 years and three subjects had participated in previous RT experiments. Although no selection criteria were employed all subjects claimed to be right-handed.

Apparatus

The stimuli consisted of two movable green LEDs which were mounted on a black aluminium perimeter curved such that stimuli at all eccentricities were equidistant from the subject's eyes. The fixation point was formed by a white plastic sphere covering an angle of 0.2 deg which was mounted at the centre of the perimeter, and a rubber mask fixed on a metal frame at eye level provided a fixed viewing distance of 57 cms. The stimuli, subtending an angle of 0.33 deg, were illuminated for 5 ms and had an intensity of 25 mcd at a wavelength of 565 nm. The experimental room was painted entirely black and illuminated by diffuse light from four 60 watt bulbs giving the background a luminance of 0.05 cd/m^2 as measured by an SEI Photometer. Presentation and pseudorandomisation of the left-right trial sequence was controlled by a Nova 1220 computer and trials in which an RT fell outside the range of 150-1000 ms were excluded and replaced automatically. Subjects responded by means of either micro-switches or a push button located at the top of a 28 cm high joystick. Both types of response apparatus were placed centrally on a table under the perimeter but different micro-switches were used for each hand whereas the same push

button switch was used for both hands.

Procedure

Subjects attended a single test session which lasted approximately an hour and 10 minutes, including a 5 minute coffee break. Each session consisted of 16 blocks of 60 trials with stimuli presented at two eccentricities - $1/2$ and 4 deg. These were run in an ABBA order with the sequence of responding hand being ABAB. Hence there were four blocks of trials at eccentricity A using hand A, followed by four blocks at eccentricity B using hand B. After the coffee break there were four blocks at eccentricity B using hand A and four at eccentricity A with hand B. Order of starting hand and eccentricity was counterbalanced across subjects. A block consisted of 60 randomised left and right VHF presentations each preceded by a 1000 Hz warning tone lasting 50 ms delivered through a pair of Sennheiser headphones. Thus each subject gave 120 responses for every VHF x hand x eccentricity combination. The length of time between the warning tone and stimulus onset varied pseudorandomly between 500 and 1400 ms in 100 ms steps. Half the subjects were requested to hold down the micro-switch with the requisite index finger and to lift this as rapidly as possible upon seeing a flash. The other half were told to grip the joystick with the appropriate hand and push the button down with their thumb upon stimulus appearance. In both cases subjects were told to fixate the central point on hearing the warning signal and the importance of this was strongly and repeatedly emphasised. Subjects were also informed that left and right VHF presentations would be at random and that warning period length would vary. A practice block was given at the beginning of the session. The LEDs were also interchanged after half the subjects in each group had been run in order to control for any unnoticed intensity differences.

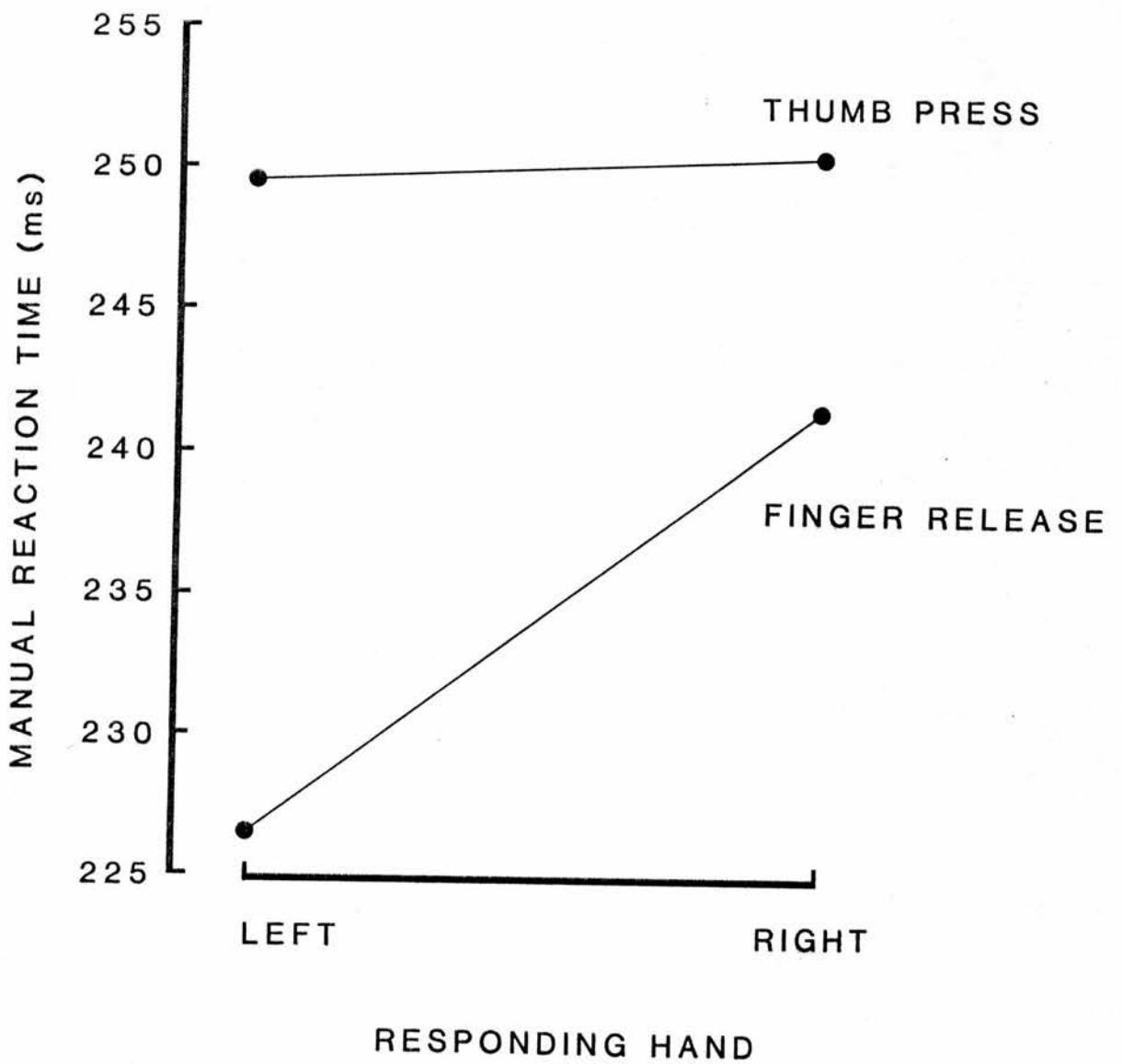
Table 3: Reaction times in ms for crossed and uncrossed responding at two eccentricities and with two manual response types.

Finger Release	1/2°		4°	
	Crossed	Uncrossed	Crossed	Uncrossed
Subject				
1	215.54	214.01	234.65	226.90
2	236.67	230.03	242.89	236.17
3	241.29	233.48	254.03	255.85
4	246.26	242.93	251.69	251.12
5	224.34	222.20	229.73	226.09
6	206.99	206.38	229.64	230.61
7	266.41	262.08	287.83	280.95
8	199.05	202.82	201.79	202.87
Mean	229.57	226.74	241.53	238.82
Thumb Press				
9	243.45	246.13	262.47	267.66
10	252.29	246.32	270.37	267.70
11	238.24	234.68	248.22	241.36
12	213.96	213.14	220.58	215.80
13	249.91	249.62	258.57	253.83
14	256.63	252.86	262.07	260.69
15	260.81	264.23	269.15	276.79
16	246.91	238.17	260.47	258.22
Mean	245.27	243.14	256.49	255.26

3.4.3 RESULTS

Mean RT scores for crossed and uncrossed responses are given in Table 3. A four-way mixed measures ANOVA was carried out on the data (the independent variable was response type (finger release or thumb press) and the 3 repeated measures factors were eccentricity (1/2 or 4 deg), hand (left or right) and VHF (left or right)). This revealed two significant main effects. Firstly there was an effect of eccentricity due to the fact that, as in the previous experiments, RT increases with increasing eccentricity. Unlike the previous manual RT experiment there was a significant effect of hands $F(1,14) = 8.79, p < .05$ with left hand responses being 7.97 ms faster than those made with the right hand. The reason for this somewhat puzzling result is elucidated by the significant two-way interaction between response type and hands $F(1,14) = 6.83, p < .05$ shown in Figure 11. It can be clearly seen that there is no difference between the two hands for thumb pressing but a strong left hand advantage for finger releases. The most plausible explanation for this result is that the left hand micro switch was 'faster' than the right hand one for some reason (eg: the distance it had to be lifted before breaking contact may have been smaller). Counterbalancing of switches was considered unnecessary since no hands effects had been observed in previous manual RT experiments carried out in this laboratory. However the fact that the switches had recently been replaced was overlooked. The interpretation of the result as being due to a difference in the micro switches' performance is borne out by the fact that in the thumb press condition, where subjects used the same switch, no overall difference between the two hands was observed. The only other significant two-way interaction was that of hands x VHF $F(1,14) = 6.02, p < .05$ reflecting clear CUDs which were present at both eccentricities and for both types of responding (Figure 12) - a conclusion which can be

FIGURE 11. EXPERIMENT 3: MEAN RTs FOR LEFT AND RIGHT HAND FINGER RELEASE AND THUMB PRESS RESPONDING

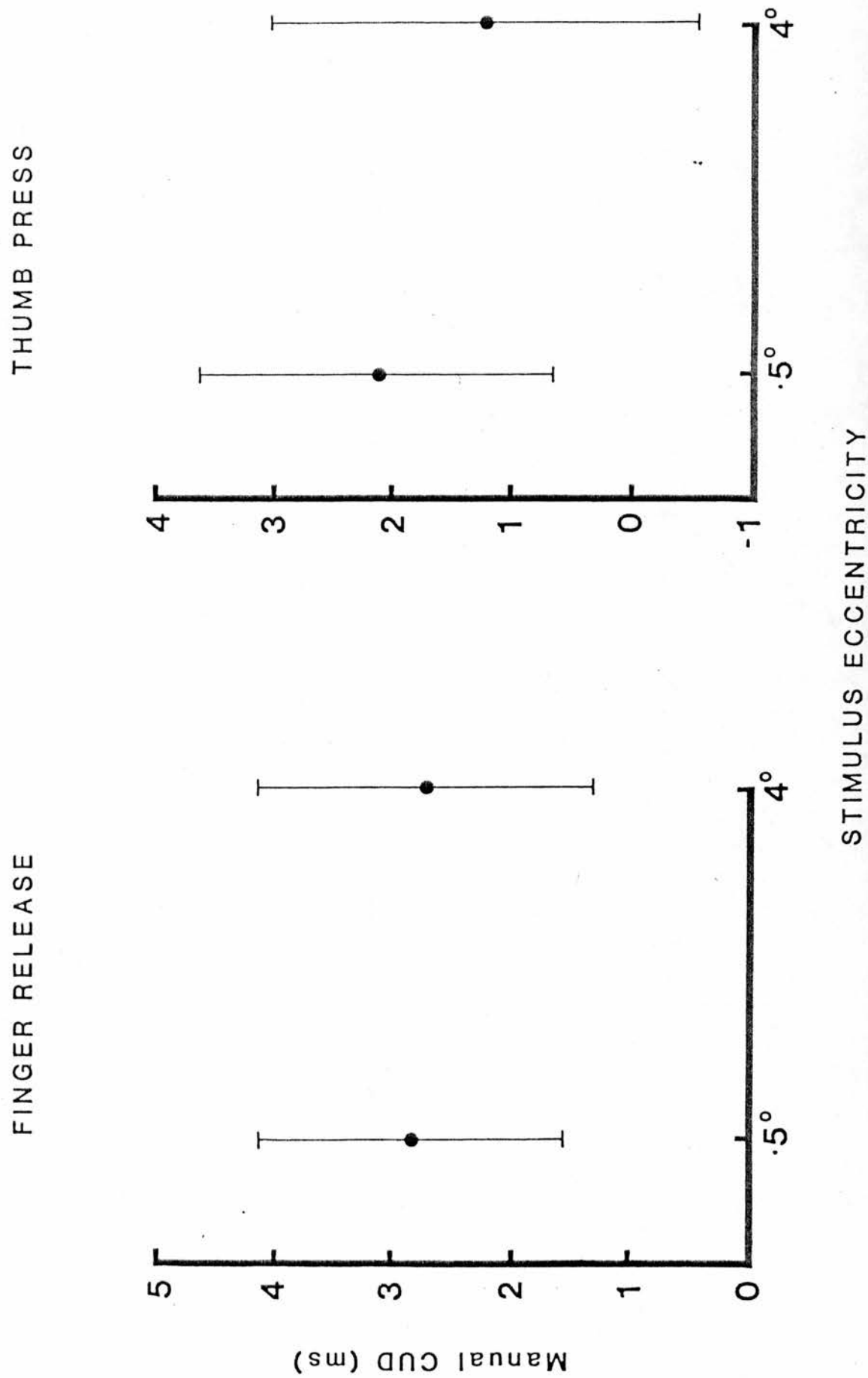


drawn from the fact that neither the three-way eccentricity x hands x VHF or four-way response type x eccentricity x hands x VHF interactions approached significance ($F(1,14) = 0.22, p > 0.1$ and $F(1,14) = 0.12, p > 0.1$ respectively). Furthermore a three-way ANOVA on the CUDs rather than raw data, as in the previous two experiments, revealed no significant effects. For finger release responding the CUDs at 1/2 and 4 deg were 2.83 and 2.69 ms while for thumb pressing they were 2.14 and 1.23 ms respectively. In both cases the larger CUD was at 1/2 deg - in the finger release group 7 of the 8 subjects gave an overall positive CUD at this eccentricity while in the thumb press group 6 out of the 8 did so. Although subject's mean standard deviations were slightly higher in the thumb press group (53.34 versus 43.34 ms) this difference was not statistically significant. Finally there was a 3 three-way interaction between response type, eccentricity and hands $F(1,14) = 4.63, p < .05$. This reflects the fact that the left hand in the finger release group, for reasons outlined above, is faster at both 1/2 and 4 deg (13.68 and 15.97 ms respectively). In the thumb press group, however, the left hand is 10.58 ms faster than the right at 1/2 deg but 8.97 ms slower at 4 deg. The reason for this result remains uncertain and in any case it is incidental to the theme of this thesis.

3.4.4 DISCUSSION

The present results agree with those from Experiment 2 in failing to find any abolition of the CUD with stimuli presented at 1/2 deg to the left and right of fixation. Furthermore the present Experiment shows that that finding was not a consequence of the subjects being dark adapted or the type of manual response required. In addition further studies using the modified simple RT procedure described in the Introduction (which initially found no CUD below 6 deg), have now shown that a CUD is present below 6 deg (Berlucchi, personal communication). There is, therefore, no discrepancy

FIGURE 12. EXPERIMENT 3: CUDs FOR FINGER RELEASE AND THUMB PRESS RESPONDING AT TWO ECCENTRICITIES



between the results from that study and those reported here. The experiments so far reported in this thesis thus all lead to the conclusion that there is no functional nasotemporal overlap in humans. Is it still possible that overlap might exist but not be evidenced by the methods described here?

A reason why this might indeed be the case has been suggested by Colenbrander (1975). According to this model the projection to the 'wrong' hemisphere is inhibited by the 'correct' hemisphere. For example, a stimulus presented in the left VHF on the area of overlap could go to both hemispheres but the RH, which receives a stronger input, is the 'correct' one and might inhibit the response of cortical cells in the LH. This scheme was originally proposed to explain the fact that while most cases of unilateral occipital lobectomy result in sparing a small minority result in splitting, ie: a complete hemianopia (Penfield, Evans and MacMillan, 1935; Halstead, Walker and Bucy, 1940; Walsh and Hoyt, 1969; Koerner and Teuber, 1973). According to Colenbrander sparing results from destruction of those areas where inhibition originates in one hemisphere, thereby releasing the region of overlap in the intact hemisphere and enabling it to become functional. Paradoxically splitting is argued to result from less severe damage which leaves the inhibitory influence intact. This assertion echoes the widely held belief that sparing is observed only following supragenulate damage (Kolb and Whishaw, 1980), a belief which has not gone entirely unchallenged (Liedenfelder, in discussion following Halstead, Walker and Bucy, 1940; Teuber, Battersby and Bender, 1960). Nevertheless the implications of such a hypothesis are rather far reaching as far as the present thesis is concerned since, if valid, it follows that evidence for overlap would never be found in normal subjects using purely behavioural techniques. On the other hand it might be possible to test the validity of

such a hypothesis using subjects suffering from agenesis of the corpus callosum. The reasons for this assertion are outlined in the next chapter.

3.5 EXPERIMENT 4

3.5.1 INTRODUCTION

Agenesis of the corpus callosum is an infrequently occurring condition also associated with absence of the hippocampal commissure, although as far as is known the other commissures are intact and normal (Milner, 1983). In acallosals, unlike split-brain subjects, there exists the possibility that some form of compensation may have occurred during development (Milner and Jeeves, 1979). For example enlargement of the most important remaining commissure, the anterior commissure, has occasionally been reported (Bossy, 1970; Geschwind, 1974; Stefanko and Schenck, 1979). At a behavioural level the simple RT paradigm has been used to investigate the functional significance of any remaining interhemispheric pathways. Information is apparently still relayed from one hemisphere to the other in acallosals but evidently via a less efficient route (most probably the anterior commissure) since the typical acallosal manual CUD is in the order of 20 ms (Jeeves, 1969; Milner, 1982). Furthermore it seems to be the case that even under conditions of manual responding the acallosal CUD reflects a sensory relay since it has been found to vary with intensity (Milner, 1982; Milner et al, 1984). In normal subjects the manual CUD is invariant with intensity (Milner and Lines, 1982) and may reflect a crossing between the motor cortices (see section 3.1).

As far as the present thesis is concerned the study of an acallosal subject might be interesting for two reasons. Firstly any decrease in the large acallosal CUD should be immediately apparent. Secondly if the model of inhibition described in the previous section (3.4.4) has any validity and the inhibition is callosally mediated, then it might be the case that the acallosal brain is released from this as a consequence of impaired

interhemispheric transmission. If so then one would expect an abolition or a greatly reduced CUD with stimuli presented close to fixation.

The previous literature relating to the question of overlap in acallosals has concentrated on the problem of midline stereopsis. If nasotemporal overlap exists and is responsible for midline stereopsis (see section 2.3) then one would expect this facet of acallosals' perception to be unimpaired. It is, however, still a matter of debate as to whether acallosals possess midline stereopsis or not. Jeeves (1965) and Ettliger et al (1974) have observed accurate depth judgements in their adult acallosal subjects using central presentation while Mackay (1977), Jeeves (1979) and McMahon (1979) employing conditions similar to those of Mitchell and Blakemore (see section 2.3) have found poorer central compared to peripheral performance. Milner and Jeeves (1979) have suggested that the discrepancy might be resolved in terms of the former studies involving 'fine' stereopsis (ie: one dependent on a region of overlap) and the latter involving the process of 'coarse' stereopsis (see section 2.3). However this hypothesis has yet to be explicitly tested. The possibility remains therefore that overlap, for which no evidence can be found in normal subjects, might become manifest in acallosals. Consequently simple RTs to lateralized light flashes were measured in an acallosal subject.

3.5.2 METHODS

Subject

The acallosal female KC, aged 20 - 22 years at the time of testing (1980/1982), was first diagnosed following air encephalography and angiography in July 1970. No other neurological abnormalities were evident until December 1979 when she suffered a grand mal convulsion and was admitted to Dundee Royal Infirmary where a dermoid cyst was removed from

the left ventro-medial frontal region. Her performance following this operation seemed unaffected and throughout the present experiment she remained a highly cooperative subject. Further details, including CT scans, are available elsewhere (Reynolds and Jeeves, 1979; Milner, 1982).

Apparatus

Stimuli were presented on the CRT display screen of a DEC graphics computer (GT40). Extraneous visual stimulation was excluded by an opaque mask surrounding the screen which also provided a fixed viewing distance of 35 cm. A small (1/30 deg) fixation spot remained present in the centre of the screen throughout each session. During test trials a 1000 Hz warning tone was followed by a delay varying pseudorandomly between 500 and 1500 ms after which a small (1/30 deg) stimulus light was flashed for 2 ms at an eccentricity of 1/2, 1, 2 or 4 deg of visual angle either to the left or right of fixation. The intensity of the flashes, measured as a point source, was estimated at 9.4×10^{-5} microW/deg². The presentation and pseudorandomisation of the left-right trial sequence was controlled by computer and RTs outside the range 150 - 1000 ms were excluded and replaced automatically. Manual responses were recorded by means of micro-switches placed centrally on a table under the display screen.

Procedure

KC attended three 1 hour and three 20 min test sessions which were spread over a period from 14/3/80 - 4/12/82. There was only ever 1 session per day and stimuli were presented at the same eccentricity throughout a session. For the three 1 hour sessions stimuli were presented at eccentricities of 1/2, 1 and 2 deg of visual angle. In these cases a session consisted of six 60-trial blocks using one hand, followed by six 60-trial blocks using the other hand with a coffee break in between. Hand

Table 4: Mean reaction times in msec made by KC at four points of stimulus eccentricity.

Block	Stimulus Eccentricity											
	1/2°		1°		2°		4°					
	Crossed	Uncrossed	Crossed	Uncrossed	Crossed	Uncrossed	Crossed	Uncrossed				
1	319.60	304.25	327.80	306.20	326.70	303.80	345.45	319.05				
2	300.15	296.60	311.45	297.40	320.00	297.15	341.25	320.10				
3	320.65	297.80	310.90	297.35	318.40	304.80	403.70	370.65				
4	334.75	313.00	335.65	304.75	351.95	323.85	348.60	312.30				
5	331.65	330.20	332.10	311.55	351.85	327.30	332.10	313.05				
6	320.60	309.55	336.00	313.45	355.40	323.00	342.35	320.25				
Mean	321.23	308.57	325.65	305.12	337.38	313.32	352.24	325.90				

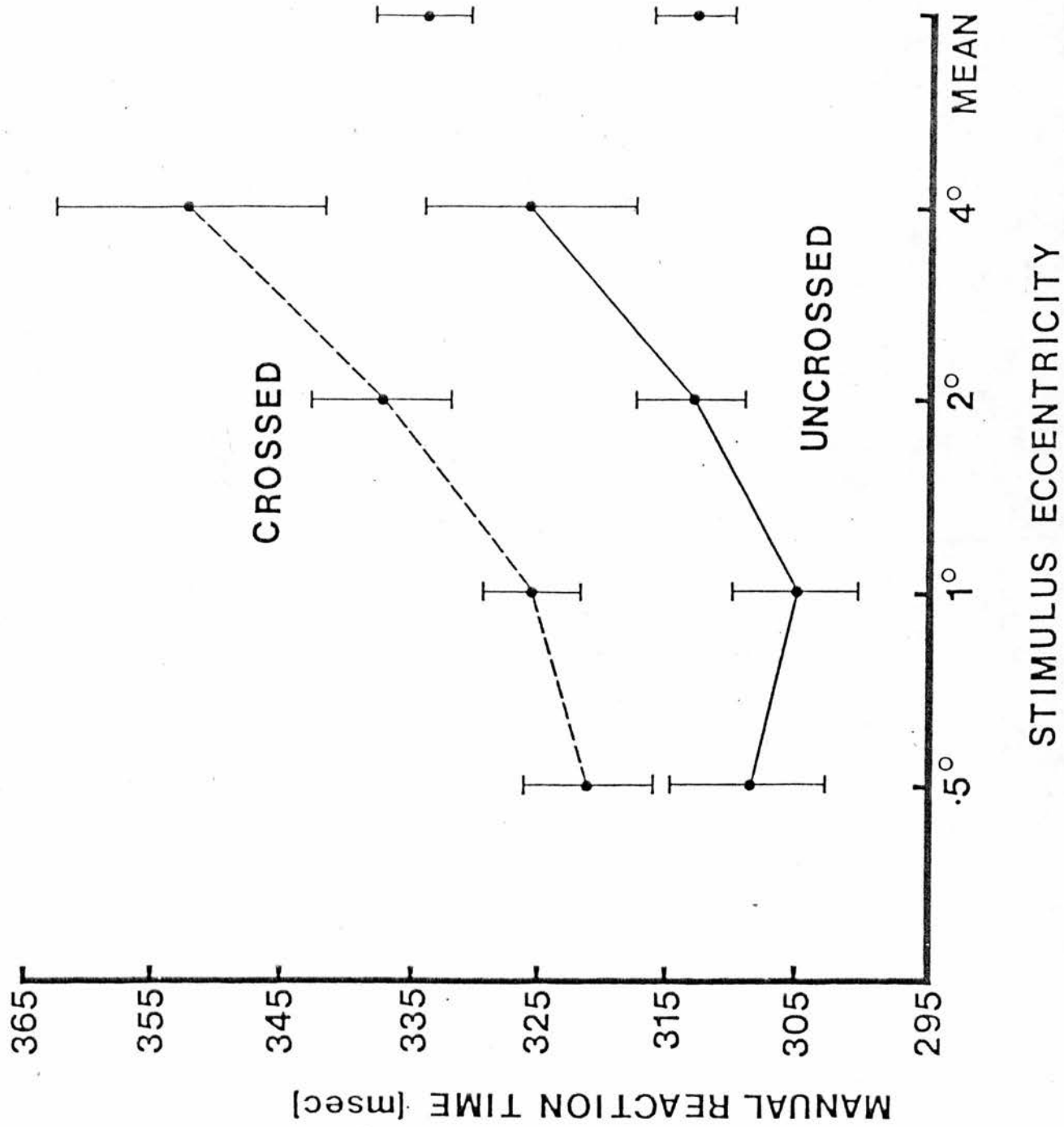
order was varied over sessions. Each 20 min session consisted consisted of four 60-trial blocks with the stimulus at an eccentricity of 4 deg using hand orders of ABBA ,BAAB and BABA respectively. Practice blocks were deemed unnecessary as KC was already highly experienced at this type of task. The subject was requested to hold down the micro-switch with the requisite index finger, fixate the central dot in response to the warning tone and raise the finger as rapidly as possible upon seeing the flash irrespective of its side of occurrence. The importance of steady fixation was repeatedly emphasised.

3.5.3 RESULTS

In line with previous work on this subject (Milner, 1982) a 3 standard deviation upper cut-off was applied to exclude abnormally high RTs. This procedure resulted in the exclusion of 41 responses from a total of 2880. The mean RTs for hands and VHF's at each position of eccentricity are given in Table 4. For the purposes of the analysis of variance blocks were treated as the random variable. Hence VHF (left or right) was the within blocks factor while hand (left or right) and stimulus eccentricity (1/2,1,2 or 4 deg) were between blocks. However since performing an analysis of variance on data of this type violates the independence assumption a more conservative F-test has been applied. Consequently the degrees of freedom of the denominator has been halved in all the values given below.

Following this procedure two of the main effects were found to be significant. Firstly there was an effect of stimulus eccentricity $F(3,20) = 3.85, p < .05$ which reflects a commonly found trend for RT to increase as the stimulus is presented further from fixation (see section 3.2.3). Also present was an effect of VHF $F(1,20) = 12.60, p < .01$ reflecting a right VHF advantage of 5.67 ms. While this is an opposite finding to the left VHF

FIGURE 13. EXPERIMENT 4: MEAN CROSSED AND UNCROSSED
MANUAL RTs IN KC AT FOUR ECCENTRICITIES



advantage occasionally reported in the simple RT literature on normals (Jeeves, 1969; Jeeves and Dixon, 1970) perhaps not too much importance should be attached to it in view of the fact that a previous study on this subject employing the same apparatus and similar task found no such effect (Milner, 1982). There were two significant two-way interactions. One was between eccentricity and VHF and seemed to be due to a large right VHF advantage at 1 deg (15.07 ms) but much smaller right VHF advantages at 1/2, 2 and 4 deg (0.20, 4.05 and 3.36 ms respectively). This impression was confirmed by separate analyses of variance at each position of eccentricity which showed a significant effect of VHF at 1 deg $F(1,5) = 55.54$, $p < .0001$ but non-significant effects at all other eccentricities. Of most interest from the point of view of the aim of the present study was the finding of a highly significant hands x VHF interaction $F(1,20) = 171.03$, $p < .0001$ (see Figure 13) reflecting a large CUD which was present at all four eccentricities (1/2 deg = 12.67, 1 deg = 20.53, 2 deg = 24.07 and 4 deg = 26.34 ms) with a mean value of 20.90 ms. Finally there was a significant eccentricity x hands x VHF interaction $F(3,20) = 3.52$, $p < .05$ due to a trend evident in Figure 13 for the CUD to decrease with decreasing eccentricity. It should be noted however that this effect was only marginally significant and separate analyses of variance at each point of eccentricity all showed significant hands x VHF interactions.

3.5.4 DISCUSSION

The first point to be made about the present results is that, as expected, KC showed a large CUD. The mean value of 20.9 ms agrees well with previously reported values (averaged across test conditions) for this subject of 20.3 ms using the same apparatus (Milner, 1982) and 18.74 ms using different apparatus (Reynolds and Jeeves, 1974). The interpretation of this finding given in the introduction is that the CUD reflects a

sensory relay via one of the remaining interhemispheric pathways. However an alternative hypothesis which argues that the acallosal CUD results from the use of an enhanced ipsilateral motor pathway has been put forward by Kinsbourne and Fisher (1971). Although Milner's (1982) finding that KC's CUD varies as a function of stimulus intensity does tend to support the former hypothesis from the point of view of the present experiment it does not actually matter which of these two interpretations is the correct one. A region of nasotemporal overlap should have led to the abolition of the CUD in both instances - in the first case because information would have been available in both hemispheres thereby alleviating the need for any interhemispheric crossing and in the second case because dual representation would mean that the (inferior) ipsilateral pathway would never have to be used for crossed responding. The present study thus concurs with the previous experiments on normal subjects (sections 3.2, 3.3 and 3.4) in finding a CUD even with stimuli presented very close to fixation.

An intriguing aspect of the present results, however, is that the CUD at 1/2 deg, while large, is significantly reduced. Although it is possible that this effect is due to slightly unsteady fixation around the centre an alternative interpretation could be that KC's overall CUD actually reflects the operation of two separate underlying processes. It was previously suggested (section 3.3.3) that the weak 'wrong' projections may be delayed in transmission and never arrive in time to determine responses in experiments involving RTs on normal subjects. It may be the case then that KC's CUD at 1/2 deg actually reflects this weak projection which, while slow, is still faster than the interhemispheric transmission underlying CUDs at the other eccentricities. (This suggestion receives some support from studies of KC's midline stereopsis (a series of student projects

supervised by B. Rogers at the University of St. Andrews). Initially these indicated results like those of Mitchell and Blakemore (Mackay, 1977; McMahon, 1979) but more recently no midline deficit has been found (Cooper, 1980). Since the latter two studies both employed disparities down to $1/4$ deg the reason for the discrepancy remains uncertain, though one possible explanation (Milner, personal communication) might be that KC has learned to use a weak overlap with experience.) Alternatively it could be argued that if KC's manual CUD does reflect a sensory relay (possibly via the anterior commissure), as proposed by Milner (1982), then a decrease in the CUD with decreasing stimulus eccentricity might be expected if more extensive interhemispheric connections existed for areas near to the midline. It is interesting to note that preliminary simple RT tests on another acausal, BF, using brighter stimuli presented at $1/4$ and 16 deg to the left and right of fixation do reveal a similar trend to that evident in KC - his CUDs averaged over 360 trials per eccentricity were 11.6 and 25.1 ms respectively. However until appropriate fixation checks have been made and the finding fully replicated it would be premature to attach too much significance to this aspect of the results. The implications of the present finding for Colenbrander's hypothesis and the question of overlap in general will be discussed in the following chapter.

CHAPTER 4GENERAL DISCUSSION AND CONCLUSIONS

The experiments reported here have all failed to find any evidence for a functional nasotemporal overlap, resulting in dual representation of the midline, in humans. This conclusion is drawn on the basis of findings that a CUD is present with stimuli presented at 1/2 deg to the left and right of fixation in conditions of vocal and manual responding in partially dark adapted subjects (Experiments 1 and 2); manual responding in light adapted subjects using bright stimuli (Experiment 3) and manual responding in an acallosal subject (Experiment 4). These findings are in agreement with previous studies on commissurotomed subjects and studies using choice RT measures (see sections 2.4 and 3.1). The most parsimonious explanation is that even if a small overlap similar to that demonstrated in monkeys (see section 2.1) exists in man then it has no functional significance. However there are a number of possible reasons why this conclusion may be unjustified, some of which have already been alluded to. These are:

1. The CUD derived from the simple vocal and manual RT task may not actually reflect an interhemispheric relay.
2. Nasotemporal overlap exists but is not revealed either because of some deficiency in the particular experimental conditions used here or because of a general insensitivity of the simple RT task in relation to the study of this phenomenon.
3. The simple RT CUD reflects a sub-cortical rather than interhemispheric relay.

4. There is inhibition of one hemisphere by the other.

The first possibility is potentially the most important since all the experiments reported here are based on the assumption that it is an interhemispheric transmission which is being indexed in the simple RT CUD. In discussing this question a distinction needs to be drawn between the simple vocal and manual RT paradigms and in the following sections each will be dealt with separately. Arguments that the simple manual CUD might actually reflect the operation of a stimulus-response compatibility effect (Wallace, 1972; Broadbent, 1974) or attentional bias (Swanson, Ledlow and Kinsbourne, 1978) were briefly dismissed in section 3.1. However in view of the recent criticisms of Peters (1983) these propositions should perhaps be dealt with in more detail. To take stimulus-response compatibility first it was previously mentioned that an 'anatomical' CUD is found even when subjects' hands are placed in a crossed position (Anzola et al, 1977; Berlucchi et al, 1977). Peters (1983) has argued that this is something of an oversimplification since the CUD, though present, is diminished in these studies. Nevertheless it should be pointed out that in no case has the CUD in normals been abolished by having the hands in a spatially incompatible condition. The possibility that the acallosal CUD may reflect a spatial compatibility effect has also been specifically tested in the acallosal BF by having his hands cross the midsagittal plane to as extreme an extent as possible (Milner et al, 1983). The results in no way support the idea that a compatibility effect might be operating since a positive CUD was found with the hands crossed over (16.6 ms) as well as in the normal position (15.2 ms). Therefore it seems reasonable to conclude that a compatibility effect if it occurs at all is slight and does not invalidate an anatomical interpretation of the CUD.

A further point made by Peters (1983) is that some authors (Broadbent, 1974; Swanson, Ledlow and Kinsbourne, 1978) " have interpreted negative findings in the literature as supporting the view that attentional factors (direction of attention) override structural factors. These authors stress the importance of the allocation of attention to left and right hemi-space and suggest that in simple RT paradigms potential IHTT values are obliterated by attentional strategies." This argument seems to deny that reliable CUDs can be observed at all. In fact as long as one is dealing solely with the simple visual manual RT paradigm, ie: an invariant response to an unstructured visual stimulus, only one study of the 12 reported (Poffenberger, 1912; Smith, 1938; Jeeves, 1969; Berlucchi et al, 1971; Anzola et al, 1977; Berlucchi et al, 1977; McKeever and Hoff, 1979; Di Stefano et al, 1980; Milner and Lines, 1982; Tassinari, Morelli and Berlucchi, 1983; also the present Experiments 2 and 3) has ever had a negative finding. This was the study reported by Smith (1938) and the failure may be attributable to the fact that too few responses were obtained from each subject (Berlucchi, 1978). The consistency of the mean population values of the CUD in the other studies is remarkable ranging, in the modern reports (ie: excluding Poffenberger, 1912), only from 1.0 (Anzola et al, 1977) to 3.3 ms (Berlucchi et al, 1977). Therefore it does not seem to be the case that the simple manual visual CUD is obliterated by attentional strategies or, for that matter, anything else. Peters' criticisms are based on his studies involving simple manual responding to tactile stimuli presented to a finger of one or the other hand which did fail to find CUDs. On this basis he concludes "if subjects can focus their attention on the hand which will receive the stimulus and on the hand which will respond no significant differences between RT to crossed and uncrossed stimulus presentations are observed." The visual analogue of this task, presumably, is that if subjects can focus their attention on the VHF in

which the stimulus will be presented and on the hand which will respond then no CUD should be observed. These conditions would seem to be met in studies where the stimuli are blocked and subjects respond with the same hand throughout a given block. Even though the subject is centrally fixating attention is presumably biased towards the VHF of stimulus presentation since this is entirely predictable. Such studies flatly contradict Peters assertion since reliable CUDs are still found (Poffenberger 1912; Berlucchi et al, 1971; Anzola et al, 1977; Berlucchi et al, 1977). It seems reasonable therefore to attribute the discrepancy in results to the differences in modality. One possibility acknowledged by Peters is that the simple tactile RT may be mediated by ipsilateral pathways. This possibility was tested by having subjects make a discriminative response on the assumption that ipsilateral latencies for this type of response are likely to be very long, if they can be made at all (Greenwood et al, 1980). Under these conditions again no CUD was found. The absence of a CUD in tactile studies is thus something of a puzzle though another possibility is that the interhemispheric distances involved, if the relay takes place at this level at all, are too small to yield any differences. In any case it remains true to say that CUDs are consistently found with simple manual responding in the visual modality and that there is no evidence that this does not reflect IHTT.

If this can be said of the simple manual visual RT paradigm the interpretation of the simple vocal RT paradigm is more open to criticism. In Experiment 1 and the previous vocal RT study reported by Milner and Lines (1982) subjects were selected on the basis of showing an overall right VHF advantage (as evidence of LH speech lateralization). It might therefore be argued that the CUD in these studies reflects a right VHF attentional bias rather than the operation of a sensory interhemispheric

relay. How might such a bias work? Assuming that it takes time to 'direct' attention in a particular hemisphere, subjects with a right VHF bias may already be prepared to attend to stimuli arriving in the LH. When a stimulus arrives in the non-attended RH however it may take an additional time to bring attentional processes to bear before a 'message' is sent across to the responding hemisphere. In this case the vocal CUD would not reflect a sensory relay at all but a combination of the time taken to redirect attention and a non-sensory relay. However if this is the case it is difficult to see why the vocal CUD should vary with intensity unless it takes longer to process a weak stimulus. Estimates from the two simple vocal RT experiments vary from 6.3 (Experiment 1) to 12.24 ms (Milner and Lines, 1982) for stimuli presented at 4 deg and having the same intensity. This discrepancy presumably reflects the fact that laxer selection criteria were employed in the present study compared to that of Milner and Lines (1982). The former rejected only those subjects who failed to show an overall right VHF advantage while in the latter those subjects who failed to show an overall right VHF advantage in a significant ($p < .05$) majority of blocks, or an overall right VHF advantage in all 3 intensity conditions, were rejected. This resulted in rejection rates of, respectively, 14% (4 out of 28) and 50% (12 out of 24). Furthermore, a recent study by Tassinari, Morelli and Berlucchi (1983) using strongly right-handed subjects but no other selection criteria has failed to find any CUD with simple verbal responding. Possibly a selection taking into account familial sinistrality would have produced a clear asymmetry. However these results suggest at the very least that one should be cautious in interpreting the vocal CUD found in the present Experiment 1. For this reason the main conclusions of this thesis do not rest on results from Experiment 1 but on findings from the simple manual RT paradigm in which there is no evidence that the CUD is due to anything other than a crossing

between the two halves of the brain. Except where otherwise stated therefore the remainder of the discussion will concentrate on the simple manual RT paradigm.

The second possible reason for the failure to find evidence for overlap might be due to some insensitivity of the simple RT paradigm - either a general insensitivity which afflicts all such experiments or a particular weakness in the design of the present experiments. It may be the case, for instance, that simple RT tasks, depending as they do on small time differences, may not be suitable to detecting an area of overlap. If the weak 'wrong' projection representing the ipsilateral VHF were slowed down in its transmission then it might never arrive in time to determine response, the interhemispheric relay always arriving earlier. This might explain the diminution of KC's CUD at 1/2 deg (ie: at 1/2 deg the CUD could reflect this weak ipsilateral transmission). It might also explain sparing since this is not dependent on time factors and furthermore the operation of a weak pathway would correlate with the depressed functional capacity occasionally observed in the spared area (Koerner and Teuber, 1973). It is not clear however how one could account for splitting (see section 3.4.4) on such a model. One would have to resort to an explanation in terms of individual differences which assumes that while in most people there is some imprecision in the division of nasal and temporal fibres (a pattern which might be expected from an embryological point of view (Teuber, Battersby and Bender, 1960)) in some cases, presumably due to chance factors, the division is complete.

It is, however, possible that the present failure to observe overlap reflects not an inherent insensitivity but a more specific one arising out of some aspect of the particular procedure employed in the present experiments. One possibility might be that the stimuli were not presented

close enough to fixation to fall on an area of overlap. Wyatt (1978) has attempted to estimate how much of the visual field would be represented by the area of overlap described in monkeys by Bunt and Minckler (1977). He reasons that there may be as few as 0.9 ganglion cells per cone in this region (Missoten, 1974) which would give a total of 1940 cones in the circumfoveal strip, these occupying a disk 0.8 - 1.3 deg in diameter. Since 80% of the cells are midget ganglion cells having very small receptive fields and the remaining 20% are not likely to add more than 0.3 deg to the estimate (De Monasterio and Gouras, 1975), Wyatt calculates that the monkey overlap probably 'looks at' an area of the visual field only 1.1 - 1.6 deg wide. Since Experiment 3 used stimuli which were 0.3 deg wide and centred on 0.5 deg, their inner limit would have been at 0.35 deg to the left and right of fixation. Even under these conditions no abolition of the CUD was found. Furthermore the acallosal BF has been tested with stimuli down to 0.25 deg and a large CUD is still found. Therefore it seems doubtful, though not impossible, that the failure of the present experiments can be attributed to not using small enough stimulus eccentricities.

The third possibility raised at the beginning of this chapter was that while the CUD may definitely reflect a transmission of information between the two halves of the brain it is also true that the precise locus of this relay remains unknown. There are a number of potential sites which could be involved and would allow for a wide range of IHTTs. As Berlucchi (1978) has pointed out "it is possible that contralateral responses depend on callosal fibres which decussate from one cortex to contralateral basal ganglia or join the basal ganglia of the 2 sides. These fibres should be considerably shorter than cortico-cortical callosal fibres, thereby providing a shorter interhemispheric connection. This allows the

possibility for callosal fibres of a smaller diameter to participate in the transfer necessary for contralateral responses, or for such a pathway to contain more neurons and synapses than the pathway for ipsilateral responses." Indeed the relay need not even be interhemispheric at all in the strict sense of the term (technically a hemisphere consists of the cortex, white matter, basal ganglia, hippocampus, uncus and amygdala of one brain half) but could be extra-hemispherically mediated. It was mentioned in section 2.1 that Cowey and Perry (1981) found no evidence for an overlap in the ganglion cell projection to the monkey colliculus, unlike that to the LGN. Hence if a sensory relay at the level of the colliculus were responsible for the manual CUD estimate a crossing would be necessary even for stimuli presented very close to fixation. The simple manual RT task is so simple that it is not out of the question that it could be sub-cortically mediated. One would therefore not be looking at the operation of the retino-striate pathway in these circumstances and so it would not be surprising that no evidence for overlap is found. In this regard it is interesting to note that some studies which provide incidental evidence for overlap have used stimuli which are known to require cortical involvement. Holtzman et al (1981) state that their callosal sectioned subject JW "was unable to name any stimulus presented at least 1 degree of visual angle to the left of fixation" (my underlining) while Zihl and Von Cramon (1982) have reported that a colour anomia in their presumed splenial disconnection patient held only beyond 2 deg. However it seems fairly unlikely that the manual CUD could reflect a direct sensory relay between the two colliculi since the distances involved would probably be too small to be measurable by behavioural techniques. Furthermore it would be difficult to explain why the acallosal CUD should be so much larger if this route were implicated. It was mentioned in section 3.5.1 that while the hippocampal commissure as well as the corpus callosum is usually lacking in

acallosals the brainstem commissures are, as far as is known, intact (Milner, 1983). Hence if the relay were sub-cortical this pathway should also be intact in acallosals (though at present it is impossible to say whether this is the case in KC and BF) and one would expect to observe no difference between their CUDs and those of normals. The acallosal evidence is, in fact, the main reason for believing that the relay is callosally mediated. Nevertheless one could revise the model slightly so that the collicular path is still important in the simple RT paradigm but this relays information to, for example, the ipsilateral basal ganglia which in turn relay information to the opposite hemisphere via the corpus callosum. No nasotemporal overlap might then be implicated in the task. However such schema must, of course, remain entirely speculative at present.

The final possibility concerns Colenbrander's (1975) hypothesis that overlap might exist but be inhibited in normals (see section 3.4.4). Experiment 4 was an attempt to investigate the model by seeing if the CUD at 1/2 deg was eliminated in an acallosal subject and this was found not to be the case. On the basis of this finding along with those of Sperry and Gazzaniga on split brain subjects (see section 2.4) it seems clear that any such inhibition would have to be sub-cortically mediated. Colenbrander suggested that inhibitory fibres join the optic fibres in the course of the optic radiation and that these originate in the reticular substance, since stimulating this area is known to influence cortical responses in the visual cortex (Dumont and Dell, 1958). The nuclei of the midbrain reticular substance on the two sides are probably connected by the posterior commissure (Moyer, 1980) so this structure might be a possible mediator of the inhibition. Alternatively it could be the case that the reticular fibres do not inhibit but rather stimulate the 'strong' projection to higher levels of activity so the 'weak' projection is further

weakened. It is, however, difficult to derive any further predictions from this model, though one might expect that if it is valid splitting should never occur following hemispherectomy since there would be no chance of any inhibition remaining. As far as I know this is indeed the case so the model cannot be refuted on these grounds. However in the light of our present knowledge it is difficult to speculate further in this regard.

Given the preceding discussion of why overlap might exist but not be evidenced by the simple RT techniques employed in this thesis, how might one go about investigating the problem? There are in fact a few crucial experiments which could probably help resolve the issue one way or the other. Firstly a replication of Mitchell and Blakemore's commissurotomy study (see section 2.3) using disparities small enough to fall on any proposed area of overlap would be invaluable. If a similar deficit was found then one could virtually rule out the possibility that overlap has any functional significance in normals, though not that it may be responsible for sparing in brain damaged subjects. Secondly it would be very illuminating to put a split-brain subject through the simple manual RT task. If the CUD does reflect a non-sensory relay mediated via the corpus callosum then these subjects ought to be unable to perform crossed reactions. Eccentricity variations as in the present thesis should then provide clear evidence to resolve the issue. (Some partially-sectioned patients have been tested (Jeeves, unpublished data) but normal CUDs have been found in each case to date.) A third experiment of potential importance to the question of overlap would be to replicate the study of Leicester (see section 2.1) using monkeys instead of cats. If receptive fields extending into the ipsilateral VHF were still found following section of the forebrain commissures then one could, assuming eye movements were excluded, reasonably attribute this to a region of overlap. Finally a

possible way to investigate whether inhibition might be operating could be through the use of evoked potential techniques similar to those described by Rugg, Lines and Milner (1984). It would be interesting to see what effect, if any, presenting stimuli close to fixation has on the amplitude and latency of early components in the 'indirectly' stimulated hemisphere, which are normally delayed in latency and reduced in amplitude when compared to the same components in the 'directly' stimulated hemisphere.

In conclusion it can be said that the most parsimonious explanation of the present results is that no functional nasotemporal overlap exists in humans. However the possibility that the simple RT task might not be a sensitive enough tool with which to investigate the phenomenon remains and for this reason it is necessary to utilise other experimental approaches before a firm answer to the question asked at the beginning of this thesis can be given. Nevertheless it is justifiable to hope that such an answer should be forthcoming in the near future.

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ANOVA FOR EXPERIMENT 1

SOURCE	DF1	DF2	F	F VALUE	MEAN SQUARE	SUM OF SQ
dg	3	69	18.6106	0.0000	13839.2342	41517.7025
vf	1	23	51.3459	0.0000	2312.9022	2312.9022
dg vf	3	69	1.6253	0.1914	49.5758	148.7274
ss	23				11990.8986	275790.6680
ss dg	69				743.6200	51309.7798
ss vf	23				45.0455	1036.0474
ss dg.vf	69				30.5025	2104.6756

dg = stimulus eccentricity - 1/2, 1, 2 or 4 deg
 vf = visual half-field - left or right
 ss = subjects

ANOVA FOR EXPERIMENT 2

SOURCE	I	DF1	DF2	F	I	P VALUE	I	MEAN SQUARE	I	SUM OF SQ	I
I hs	I	1	15	0.2854	I	0.6010	I	80.9495	I	80.9495	I
I ds	I	3	45	18.1405	I	0.0000	I	7284.3093	I	21852.9279	I
I hs ds	I	3	45	0.1589	I	0.9234	I	115.9284	I	347.7851	I
I vf	I	1	15	0.3053	I	0.5887	I	31.4074	I	31.4074	I
I hs vf	I	1	15	22.9409	I	0.0002	I	328.0932	I	328.0932	I
I ds vf	I	3	45	2.0784	I	0.1164	I	52.3843	I	157.1539	I
I hs ds vf	I	3	45	0.9716	I	0.4145	I	13.2564	I	39.7691	I
I ss	I	15			I		I	5228.0351	I	78420.5264	I
I ss hs	I	15			I		I	283.6581	I	4254.8716	I
I ss ds	I	45			I		I	401.5486	I	18069.6950	I
I ss hs ds	I	45			I		I	729.6193	I	32832.0683	I
I ss vf	I	15			I		I	102.8759	I	1543.1379	I
I ss hs vf	I	15			I		I	14.3017	I	214.5250	I
I ss ds vf	I	45			I		I	25.2039	I	1134.1771	I
I ss hs ds vf	I	45			I		I	13.6436	I	613.9631	I

hs = responding hand - left or right
 dg = stimulus eccentricity - 1/2, 1, 2 or 4 deg
 vf = visual half-field - left or right
 ss = subjects

ANOVA FOR EXPERIMENT 3

I	SOURCE	I	DF1	DF2	I	F	I	P VALUE	I	MEAN SQUARE	I	SUM OF SQ
I	RE	I	1	14	I	2.7083	I	0.1221	I	8069.2632	I	8069.2632
I	DG	I	1	14	I	41.7002	I	0.0000	I	4484.5185	I	4484.5185
I	RE DG	I	1	14	I	0.0091	I	0.9254	I	0.9765	I	0.9765
I	HS	I	1	14	I	8.7883	I	0.0102	I	2031.5532	I	2031.5532
I	RE HS	I	1	14	I	6.8352	I	0.0204	I	1580.0631	I	1580.0631
I	DG HS	I	1	14	I	3.1188	I	0.0992	I	638.5845	I	638.5845
I	RE DG HS	I	1	14	I	4.6336	I	0.0493	I	948.7368	I	948.7368
I	VF	I	1	14	I	0.0469	I	0.8317	I	3.4322	I	3.4322
I	RE VF	I	1	14	I	0.2725	I	0.6098	I	19.9554	I	19.9554
I	DG VF	I	1	14	I	0.0447	I	0.8356	I	0.4513	I	0.4513
I	RE DG VF	I	1	14	I	1.4459	I	0.2491	I	14.5935	I	14.5935
I	HS VF	I	1	14	I	6.0212	I	0.0278	I	157.8420	I	157.8420
I	RE HS VF	I	1	14	I	0.3568	I	0.5598	I	9.3528	I	9.3528
I	DG HS VF	I	1	14	I	0.2170	I	0.6485	I	2.1684	I	2.1684
I	RE DG HS VF	I	1	14	I	0.1187	I	0.7356	I	1.1858	I	1.1858
I	RE SS	I	14		I		I		I	2979.4771	I	41712.6792
I	RE SS DG	I	14		I		I		I	107.5419	I	1505.5865
I	RE SS HS	I	14		I		I		I	231.1653	I	3236.3140
I	RE SS DG HS	I	14		I		I		I	204.7500	I	2866.5006
I	RE SS VF	I	14		I		I		I	73.2287	I	1025.2012
I	RE SS DG VF	I	14		I		I		I	10.0931	I	141.3034
I	RE SS HS VF	I	14		I		I		I	26.2146	I	367.0043
I	RE SS DG HS VF	I	14		I		I		I	9.9906	I	139.8690

RE = response type - finger release or thumb press
 DG = stimulus eccentricity - 1/2 or 4 deg
 HS = responding hand - left or right
 VF = visual half-field - left or right
 SS = subjects

ANOVA FOR EXPERIMENT 4

SOURCE	DF-1/	DF-2	F	P VALUE	MEAN SQUARE	SUM OF SQ
DG	3/	40	3.8501	0.0164	3085.0195	9295.0584
HS	1/	40	0.5490	0.4630	439.9308	439.9308
DG HS	3/	40	2.3654	0.0853	1895.3597	5686.0790
VF	1/	40	12.5962	0.0010	772.1258	772.1258
DG VF	3/	40	4.1105	0.0124	251.9662	755.8985
HS VF	1/	40	171.0328	0.0000	10483.9993	10483.9993
DG HS VF	3/	40	3.5184	0.0235	215.6689	647.0068
HS BL	40				801.2872	32051.4893
DG HS BL VF	40				61.2982	2451.9270

DG = stimulus eccentricity - 1/2, 1, 2 or 4 deg

HS = responding hand - left or right

VF = visual half-field - left or right

BL = blocks of trials