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MECHANISMS OF COMPENSATION IN AGENESIS OF THE CORPUS CALLOSUM

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A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Psychology University of Auckland, 2003
This thesis examines the compensatory mechanisms that allow information to be available to both cerebral hemispheres in individuals with agenesis of the corpus callosum.

The first set of experiments, detailed in Chapter Three, were designed to determine what types of visual information can be integrated interhemispherically in these subjects. Two acallosals, J.P. and M.M., and ten control subjects were tested. Results showed that M.M., whose anterior commissure was within normal limits, was much worse at matching colours and letters between visual fields than within visual fields, while J.P., whose anterior commissure was greatly enlarged, showed no evidence of interhemispheric disconnection on these tasks. This suggests that in some cases of callosal agenesis an enlarged anterior commissure may compensate for the lack of a corpus callosum. Neither acallosal subject showed disconnection on tasks requiring integration of location and orientation, however, suggesting that the anterior commissure plays no role in such tasks, although both subjects performed poorly relative to controls. These tasks may depend on subcortical commissures, such as the intertectal commissure.

The two experiments in Chapter Four tested J.P. and M.M. tested on a simple reaction-time (RT) task, with visual stimuli presented either singly to one or the other visual field or in bilaterally presented pairs. Stimuli were either white against a black background, or grey against an equiluminant yellow background. RTs to bilateral pairs were decreased beyond predictions based on a simple race between independent unilateral processes, implying interhemispheric neural summation. This effect was enhanced under equiluminance in M.M., but not J.P., suggesting that the anterior commissure may act, relative to its size, to affect cortical activation to bilateral pairs, which then acts to decrease subcortical neural summation.

In Chapter Five, J.P., M.M. and A.L.M. (the daughter of M.M.), and twelve control subjects were tested on a simple RT task, with visual evoked potentials collected using a high-density 128-channel system. Independent-components analyses were performed to isolate the visual components of interest.
Contrary to previous research with acallosals, evidence of ipsilateral activation was present in all three acallosal subjects. While ipsilateral visual components were present in all four unilateral conditions in M.M. and A.L.M., in J.P. these were present only in the crossed visual field/hand conditions and not in the uncrossed conditions. It is suggested that individual differences and methodological limitations in the previous studies due to the small number of electrodes used are the most likely explanation for the difference in findings.

Finally, due to the clear individual differences in aetiology, neurophysiology and compensatory mechanisms utilized by the three acallosal subjects tested here, a case study approach was taken with each subject discussed separately.
ACKNOWLEDGMENTS

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Finally I want to thank J.P., M.M. and A.L.M. for their participation in this study.

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CHAPTER ONE

Introduction

This purpose of this thesis is to investigate how information becomes available to both cerebral hemispheres in people with a congenital absence of the corpus callosum. The corpus callosum is by far the largest commissure in the human brain and allows lateralized sensory information to be available to both cerebral hemispheres. In cases where the corpus callosum has been surgically severed for the relief of medically intractable epilepsy there is a striking disconnection between the hemispheres, such that most types of information do not transfer from one to the other. However, this clear disconnection is absent, or much reduced, in the congenitally acallosal brain and research in this area has attempted to elucidate how individuals with callosal agenesis have compensated for its absence.
The Corpus Callosum

The corpus callosum is the largest commissure in the human brain, containing over 200 million axons (Gordon, 1990). It forms a neural pathway between the two cerebral hemispheres, allowing information to transfer between them and unifying information that enters the central nervous system lateralized to either the left or right hemisphere. While most of the callosal fibres interconnect homotopic sites in the two hemispheres, some do project to heterotopic areas (Berlucchi, 1990). With some important exceptions, including primary visual cortex and the motor and sensory areas for the distal parts of the limbs, most areas of the two hemispheres contain callosal fibres, although the density of connections varies widely between areas (Pandya & Seltzer, 1986). The rostrum (anterior part of the corpus callosum) and the genu (‘knee’) contain fibres connecting the prefrontal cortex, the body of the corpus callosum connects the premotor, motor, somatosensory and posterior parietal areas, while the splenium (posterior corpus callosum) connects superior and inferior temporal cortices and visual cortex (Kolb & Whishaw, 1996).

Since its description by Galen in ancient Rome the corpus callosum has been a controversial piece of brain anatomy. Views on its function have ranged from the belief in the 1500s that it was merely a supporting structure in the brain to the view of Willis and others in the 1600s that it was probably the “seat of the soul”, a theory that came about because of its widespread and numerous connections with the cerebral cortices. As recently as 1954 Tomasch went so far as to state that the corpus callosum “is hardly connected with psychological functions at all” (p.119; also see Bogen, 1993 for a review of the history of studies on the corpus callosum). The corpus callosum has also played an important role in the mind-brain debate, with the obvious question being what happens to the mind when the corpus callosum and other commissures are cut. If the dualists are correct then the mind would remain unified even though the brain is split, whereas the monist view would suggest the mind is the brain and hence both would be split. The work of Liepmann and others around the turn of the twentieth century suggested that callosal lesions could result in symptoms of hemispheric disconnection (Liepmann & Maas, 1908), providing evidence for the monist view. However, subsequent research with animals, and by Akelaitis in the 1940s with the first surgically split-brain humans, had predominantly negative results (see Sauerwein & Lassonde, 1996 for a review of Akelaitis’ research and the reasons for the negative results), with the consequence that interest in the role of the corpus callosum in interhemispheric integration waned considerably. It wasn’t until the influential work of Sperry in the 1960s and 1970s with split-brain patients that current views of callosal function came about. Sperry’s research, for which he shared the Nobel Prize in Physiology and Medicine in 1981, showed convincing evidence of deficits in interhemispheric transfer after callosal section and also provided clear proof of hemispheric specialization, specifically the lateralization of speech to the left hemisphere in his right-handed subjects. While not all researchers would go as far, Sperry himself concluded that the two hemispheres performed as if they had “two separate conscious entities or minds running in parallel in the same cranium” (Sperry, 1966-67).

Agenesis of the Corpus Callosum

Agenesis of the corpus callosum was first described at autopsy by Reil in 1812 (Wisniewski & Jeret, 1994) and has been described as “a natural model of the split brain” (Lassonde & Jeeves, 1994, p. v). In cases of agenesis of the corpus callosum, also called callosal agenesis, the corpus callosum is congenitally absent. The development of the corpus callosum begins with the
first axonal fibres crossing the midline between the hemispheres late in the first trimester, with complete formation by the twentieth week of gestation (Rakic & Yakovlev, 1968; Rauch & Jinkins, 1994). Whether there is complete or partial agenesis depends on the developmental stage of the foetus when insult occurs. Formation begins with the genu and develops caudally, with the rostrum being the last to form (Rauch & Jinkins, 1994). An insult may halt this development at any stage, resulting in partial formation. Probst’s bundles are another common morphological feature of callosal agenesis. These bundles, made of some of the fibres that would normally have made up the corpus callosum, run rostro-caudally in the median walls of the hemispheres (Jeeves, 1990).

It has proven difficult to estimate the incidence of callosal agenesis as some cases are clinically asymptomatic and therefore may not be diagnosed, while others can co-occur with other neurological syndromes (Wisniewski & Jeret, 1994). Estimates have ranged from 0.00005% based on post-mortem findings (Grogono, 1968) to 2% of an intellectually disabled population presenting for neurological assessment (Jeret, Serur, Wisniewski & Lubin, 1987). Another study of ultrasound scans from 1,359 infants found an incidence of 0.81% (Cioni, Bartalena, Biagioni & Boldrini, 1994), although this rate may be inflated as the infants were all either premature or considered at risk of a central nervous system condition.

While callosal agenesis can occur as an isolated abnormality, it is more often found in association with other developmental abnormalities, the most common of which are the Aicardi, Andermann, Shapiro, Acrocallosal and Menkes Syndromes (Geoffroy, 1994). However, cases without associated difficulties do exist, as seen in a review by Sauerwein, Nolin and Lassonde (1994), in which they discuss a list of at least 40 cases with IQs in the range of 71 to 115. They conclude that while people with callosal agenesis can have normal cognitive abilities, they are usually at the lower end of the normal range, and that this is especially likely when the condition occurs in association with other abnormalities.

Until recently most cases of callosal agenesis were discovered accidentally at post-mortem, but as less invasive techniques of scanning the brain have been devised an increasing number of cases are being diagnosed during the lifetime of the individual. However, identified cases are still biased towards a neurological population, as asymptomatic cases are more likely to go undiagnosed.
The Disconnection Syndrome in the Split Brain

*The Surgically-Split Brain*

The first split-brain, or callosotomy, operations were carried out in the 1940s by Van Wagenen and Herren (Sauerwein & Lassonde, 1996). This procedure involved surgically severing all or part of the patient’s corpus callosum and was designed to restrict seizures to one hemisphere of the brain in patients with medically intractable epilepsy. In the 1960s another series of operations was performed in California by Joseph Bogen and Philip Vogel (Bogen & Vogel 1962, 1975). These “west coast” patients not only had their corpus callosum severed but also all other forebrain commissures and were therefore labelled “commissurotomized”. A further series of callosotomy operations were carried out on the east coast of the United States in the 1970s (Wilson, Reeves, Gazzaniga & Culver, 1977). While these operations continue today, the “west coast” and “east coast” patients are the subjects for most of the classic research on the split-brain.

The daily lives of those with surgically split brains appear unaffected by the severing of the corpus callosum, presumably since unrestricted scanning of the environment allows bilateral representation of sensory experience. However, specific testing has revealed deficits in interhemispheric communication. Research into this ‘disconnection syndrome’ was begun by Ronald Myers and Roger Sperry in the late 1950s with animals and continued with the split-brain patients in the 1960s.

Although the commissurotomized patients have had all their forebrain commissures severed, compared to just the corpus callosum in the callosotomized patients, there have been no obvious differences found between these two groups with respect to the extent of their disconnection. The deficits in interhemispheric communication have been clearly shown with experiments using visual input restricted to one or the other visual field. One of the most striking effects of corpus callosum section is that split-brained subjects are unable to name stimuli presented to the left visual field and hence right hemisphere (Gazzaniga, Bogen & Sperry, 1965; Sperry, 1966-67; Sperry, 1982). This confirmed earlier evidence based on unilateral brain injury that speech is located in the left hemisphere for most right-handed people, although the right hemisphere does have some language comprehension capabilities (Bogen, 1993). Another striking finding is that split-brained subjects are rarely able to perform at better than chance levels on tasks requiring them to determine whether stimuli presented to the two visual fields are the same or different. As this task requires the subject to compare information contained separately within different hemispheres it directly tests what information, if any, can be transferred interhemispherically. Numerous variations of this task have been reported in the literature, with mostly negative findings. This occurs whether the judgment needs to be made on the basis of colour, size, number or letter identity, or luminance (Brown, Jeeves, Dietrich & Burnison, 1999; Corballis, 1994; Corballis & Corballis, 2001; Corballis & Sergent, 1992; Gazzaniga et al., 1965; Johnson, 1984).

The disconnection syndrome can also be seen in other modalities. If objects are held out of sight split-brain subjects are usually unable to name or describe those that are manipulated by the left hand. However if the object is then placed in view along with a number of distractors the subject usually has no trouble in pointing out the correct object with their left hand; this is further evidence that the right hemisphere knows the correct answer but is hindered by a lack of speech. Split-brain subjects are also unable to make same-different judgments about objects held in different hands (Gazzaniga, Bogen & Sperry, 1962, 1963,
Neither are they able to indicate which finger has been touched by the experimenter (by touching together the finger with the thumb of the same hand) when they are required to respond with the hand opposite to that initially touched (Geffen, Nilsson, Quinn & Teng, 1985; Sperry, Gazzaniga & Bogen, 1969).

The Acallosal Brain

Individuals born without a corpus callosum have not shown the same conspicuous deficits as the surgically split-brains (Berlucchi, Aglioti, Marzi & Tassinari, 1995; Jeeves, 1990; Lassonde & Jeeves, 1994). Subjects without other associated abnormalities often present very normally, and it is only with specific testing that subtle deficits of interhemispheric transfer are found. Even then, these deficits are often revealed as reduced performance compared to that in neurologically normal control subjects, rather than as complete functional losses (Berlucchi et al., 1995).

Most acallosal subjects have little or no difficulty in reading words and naming colours, shapes, or objects that are flashed to the left visual field, and in most cases can visually match colour and form across the two visual fields (Chiarello, 1980; Corballis & Finlay, 2000; Ettlinger, Blakemore, Milner & Wilson, 1972, 1974; Lassonde & Jeeves, 1994; Sauerwein & Lassonde, 1983). While differences between acallosal and control subjects can arise when comparing speed of performance, this impairment occurs on intrahemispheric tasks as well as interhemispheric ones and cannot therefore be attributable to any limitations of the compensatory pathway being utilized (Lassonde, Sauerwein, McCabe, Laurencelle & Geoffroy, 1988). However, deficits due to slow compensatory mechanisms can be seen on simple reaction-time (RT) tasks (Jeeves, 1969, Milner, 1982). These are discussed in the section on techniques for measuring the interhemispheric transfer of information.

Unlike surgically split-brain subjects (Corballis & Trudel; 1993; Gazzaniga, Smylie, Baynes, Hirst & McCleary, 1984; Sperry et al., 1969), acallosal subjects show at least some continuity of form perception across the midline. Corballis and Finlay (2000) presented 6-letter words that were made up of pairs of three-letter words (e.g., carrot, father) to their three acallosal subjects. Even in the interhemispheric condition when the words straddled the midline the subjects always read them as whole words and never as separate three-letter words. The words were also correctly pronounced which they would not be if they were read as two three-letter words. However earlier evidence has suggested problems with integration of perceptual information over the vertical midline. Research carried out by Jeeves (1979) with chimeric faces found that acallosals were unaware that they were observing two half-faces that were joined at the midline and consistently pointed to one or the other of the complete faces when asked to identify what they had seen.

In the tactile modality most acallosals show little difficulty in naming objects manipulated out of sight by either hand (Sauerwein, Lassonde, Cardu & Geoffroy, 1981) or in matching objects by size, shape or texture both within and between hemispheres (Dennis, 1976; Jeeves & Rajalakshmi, 1964; Lassonde et al., 1988; Sauerwein et al., 1991). However, there are contradictory reports on their accuracy on tasks requiring inter-hemispheric transfer of localization of touch information, with some studies showing no disconnection (Lassonde, Sauerwein, Chicoine & Geoffroy, 1991; Sauerwein et al., 1991; Saul & Sperry, 1968), and others finding significant deficits (Dennis, 1976; Ettlinger et al., 1972; Reynolds & Jeeves, 1977), especially in more difficult versions of the task involving serial finger stimulation (Geffen, Nilsson, Simpson & Jeeves, 1994).
There are, however, areas in which acallosal subjects have consistently shown deficits. Acallosals are often observed to have deficits in motor operations, frequently appearing clumsy and slow in bimanual tasks (Dennis, 1976; Jeeves, 1969; Jeeves, Silver & Jacobson, 1988; Lassonde & Jeeves, 1994; Lassonde, Sauerwein & Leporé, 1995; Sauerwein et al., 1981; Silver & Jeeves, 1994). This can be seen in studies with acallosals using a task devised by Preilowski (Jeeves, 1986; Jeeves et al., 1988). Subjects are required to draw a line by turning two handles simultaneously, one of which controls the vertical movement and the other the horizontal. Even after extended practice, acallosal subjects are unable to achieve the speed or accuracy of controls, suggesting that the lack of anterior callosal fibres that allow integration of fine motor activity are not compensated for in callosal agenesis. Acallosal subjects are also deficient at producing normal prehension movements during a reaching and grasping task (Jeeves & Silver, 1988).

Other studies have found deficits in the interhemispheric transfer of learned unilateral visuomotor skills (Chicoine, Proteau & Lassonde, 2000), visuo-spatial or tactuo-spatial information (Jeeves & Silver, 1988; Lassonde, 1994; Martin, 1985, Meerwaldt, 1983) and binocular fusion and depth judgment (Jeeves, 1991; Lassonde, 1986).

Visual Pathways

As the research in this thesis focuses on the interhemispheric transfer of visual information in the acallosal brain, this section examines how visual information is relayed from the retina to the brain.

There are two main pathways from the retina to the brain. The principal route is the retino-geniculo-striate pathway, with information travelling via the dorsal lateral geniculate nucleus (dLGN) of the thalamus to the striate cortex (area V1) in the occipital lobe. The visual system is organized so that information from the left side of space, or left visual field, is projected to the right visual cortex and vice versa. The projections from the retinas are divided in two, with the information from the temporal hemiretinae of each eye projecting to the ipsilateral hemisphere while the information from the nasal hemiretinae projects to the contralateral hemisphere while the information from the nasal hemiretinae projects to the contralateral hemisphere, crossing via the optic chiasm.

From the occipital lobe the information branches off to the prestriate regions (areas V2, V3, V3A, V4 and V5) which each respond to specific features of visual information. While areas V3 and V5 receive only magnocellular information, areas V2 and V4 receive both parvocellular and magnocellular information. These two systems of information get their names from their origins in different layers of the dLGN. The parvocellular system is colour-selective and slow, with low contrast sensitivity but high spatial resolution. In contrast, the magnocellular system, thought to have evolved earlier, is colour-blind and fast, with high contrast sensitivity but low spatial resolution (Livingstone & Hubel, 1988).

The second pathway from the retina uses subcortical routes, and is considered more primitive than the retino-geniculo-striate pathway (Trevathan, 1990). This retinotectal pathway is thought to receive mostly magnocellular information, and terminates in the superior colliculi of the midbrain. Each superior colliculus receives information from the complete contralateral visual field (Sprague, Berlucchi & Rizzolatti, 1973) and from part of the ipsilateral field bordering the vertical meridian, with percentages ranging from 10% (Sprague et al., 1973) to 40% (Meredith & Stein, 1990). From the superior colliculi information is projected via the pulvinar nucleus of the thalamus to visual association cortex (Benevento & Standage, 1983; Bruce, Desimone & Gross, 1986), and the superior colliculi also receive descending projections from cortex (McHaffie, Norita, Dunning & Stein, 1993). While the
superior colliculus is known to play a role in control of eye movement, there has been little other conclusive evidence of its functions.

As the retinotectal pathway is thought to receive mostly magnocellular information, equiluminance should in theory largely restrict processing to the retino-geniculo-striate parvocellular system (Livingstone & Hubel, 1987). However, there is evidence from the squirrel monkey that a small percentage of cells in the superior colliculus respond differentially to colour stimuli (Kadoya, Wolin, & Massopust, 1969, 1971). In humans there is evidence from ‘blindsight’ patients, who have lesions of the optic radiations and visual cortex, that they can discriminate between narrow-band wavelengths in the ‘blind’ visual field (Stoerig & Cowey, 1992). These studies suggest that some collicular involvement in colour discrimination is possible.

The prestriate cortex projects information onto two regions of visual association cortex: the inferior temporal cortex and the parietal lobe. These two pathways have been characterized as the “what” and “where” pathways respectively, with identity information being processed in the inferior temporal lobe and locational information being processed in the parietal lobe (Ungerleider & Mishkin, 1982).

The visual system is commonly tested in both the surgical split-brain and acallosal research because it is strictly lateralized in its pathways from the retina to the brain (Milner, 1994). Each cerebral hemisphere only receives information from the contralateral visual field, thereby allowing experimenters to restrict information to a single hemisphere by limiting the presentation of information to either the left or right visual field. While there is a small area of nasotemporal overlap where the information is sent to both hemispheres, it is thought to extend less than 1° either side of the vertical meridian (Fendrich & Gazzaniga, 1989; Sugishita, Hamilton, Sakuma & Hemmi, 1994), or at most 2° either side if more visually identifiable stimuli are used and presentation is for longer durations (Fendrich, Wessinger & Gazzaniga, 1996). The corpus callosum is the major commissure connecting the two hemispheres and is therefore important in allowing transfer, and consequently integration, of information from both sides of visual space (Berlucchi & Antonini, 1990).

Possible Compensatory Mechanisms in Callosal Agenesis

While people born without a corpus callosum do not show the prominent deficits seen in the split-brain patients, this is precisely why they are of so much interest. Why are they so different from the surgical cases? How do they compensate for the absence of the main connecting structure between the two hemispheres?

The reduction of disconnection deficits in acallosals has often been attributed to the fact that the conditions that result in callosal agenesis occur early in development, maximizing the opportunities for neural compensation due to enhanced neural plasticity during growth. That the age at which the subject is deprived of callosal connections is of vital importance is shown by a number of experiments by Lassonde and colleagues (Lassonde et al., 1991; Lassonde et al., 1988). They tested a number of different groups of subjects: split-brain subjects who had been operated on at a young age (less than 8 years old) and as adults (the youngest subject was 15 years old at the time of surgery), acallosal subjects and a sample of normal controls assigned to groups on the basis of age. They found that the performance of the normal sample on tasks involving hemispheric integration improved with increasing age coinciding with the phases of callosal maturation. They also found that while the split-brain subjects who had undergone surgery in childhood performed as well as their age-matched
control subjects, the others who had undergone surgery later in adolescence or in adulthood showed the classic disconnection syndrome discussed above. In some cases the acallosal subjects performed even better than their age-matched controls. Three possible neural mechanisms of compensation have been suggested to explain how interhemispheric transfer may occur in the absence of the principle commissure, although the fact remains that no compensatory mechanism or mechanisms has been shown to fully make up for the absence of the corpus callosum.

_Bilateral Representation of Function_

The first possibility is that some cognitive functions may be represented bilaterally. For example, bilateral representation of language would explain the ability of most individuals with callosal agenesis to name stimuli presented to either visual field (Sperry, 1966-67). However, a review by Sauerwein et al. (1994) suggests that most cases of callosal agenesis show normal hemispheric specialization, with most (41/45) showing a clear hand preference and six out of the eight acallosals tested with the Wada method showing normal left-hemisphere lateralization of speech (the other two were left-handed), although Jeeves (1994) suggests that further investigation is needed to assess whether there is the same degree of specialization as in controls. Furthermore, while bilateral representation of speech could explain why acallosals can name stimuli in either visual field, it cannot explain the matching of stimuli between visual fields.

_Enhanced Ipsilateral Sensory and Motor Pathways_

The second hypothesis is that people with callosal agenesis may develop enhanced ipsilateral sensory and motor pathways. In neurologically normal individuals the visual system is sharply divided with information from the left visual field sent to the right hemisphere and information from the right visual field sent to the left hemisphere, as explained earlier. In the motor system, while the trunk and proximal limb muscles are innervated by axons that descend both ipsilaterally and bilaterally from the primary motor cortex through the two divisions of the ventromedial motor pathway, the distal limb muscles are only innervated by axons descending contralaterally through the two divisions of the dorsolateral motor pathway (Pinel, 1997).

Ipsilateral sensory pathways would allow information to be available in parallel to each hemisphere even when stimuli are lateralized, explaining the ability of acallosal people to make same-different discriminations, while enhanced ipsilateral motor pathways would allow each hemisphere of the brain to control the movements of the distal muscles of both sides of the body not just the contralateral ones. Milner (1994) argues against ipsilateral sensory pathways on the grounds that, if it were the case, the information should reach both sides of the brain virtually simultaneously, resulting in equal RTs for ipsilateral and contralateral responses, whereas the difference is in fact greater in acallosals than in neurologically normal individuals (Jeeves, 1969). However, ipsilateral somatosensory pathways have been shown to be less efficient than contralateral pathways (Dennis, 1976; Vanasse, Forest & Lassonde, 1994) and as discussed by Vanasse et al. (1994) slower RTs can be explained by the different axonal properties, and therefore nerve transmission times, of ipsilateral pathways. Also, behavioural measures such as manual RTs are affected by many different cognitive and physical processes and in order to provide
information on interhemispheric transfer of visual information in callosal agenesis a more direct measure of brain activity, such as electroencephalography (EEG), is necessary. Numerous studies have now recorded visual evoked potentials in response to lateralized stimulus presentations and it is well known that neurologically normal individuals show visual activation both in the hemisphere contralateral to the stimulus and also in the hemisphere ipsilateral, presumably facilitated by interhemispheric transfer via the corpus callosum (see Rugg, 1982 for a review of the early studies; also Rugg, Lines & Milner, 1984). In contrast, the three studies investigating visual evoked potentials in people lacking a corpus callosum have shown that, while callosotomized and acallosal subjects show normal visual evoked potentials contralateral to the stimulus, they show no ipsilateral activation (Brown, Bjerke & Galbraith, 1998; Brown et al., 1999; Mangun, Luck, Gazzaniga & Hillyard, 1991; Rugg, Milner & Lines, 1985). These studies have therefore concluded that in the split brain visual information is confined to the hemisphere contralateral to the stimulus presentation. However, as discussed in Chapter Five there are reasons to be cautious in accepting the conclusions drawn from these studies. Furthermore, the experiment described in Chapter Five suggests that, at least in the acallosal subjects tested in this thesis, ipsilateral activation can occur in the absence of the corpus callosum.

Dennis (1976) argues for enhanced ipsilateral motor pathways as a compensatory mechanism on the basis of the dissociation shown between tasks of tactile discrimination and those of tactile localization in the two acallosal subjects tested, and also on the basis of difficulties in performing independent finger movements. She suggests that while ipsilateral pathways are able to transmit some discriminative information they are unable to compensate for the fine sensation and movement information mediated by the contralateral pathways. It is also suggested that in normal development the corpus callosum inhibits the development of these uncrossed pathways allowing the crossed pathways to develop very fine motor control and that the loss of this inhibition and consequent hemispheric competition may explain the deficits of acallosals in these behaviours. This explanation would also explain the deficits in reaching and grasping behaviours and other tasks requiring bimanual coordination (discussed above). Support for this inhibitory theory also comes from a transcranial magnetic stimulation (TMS) study by Meyer, Röricht, Gräfin von Einsiedel, Kruggel and Weindl (1995), who found that unilateral motor cortex stimulation suppressed voluntary electromyographic activity in ipsilateral hand muscles only in subjects with an intact anterior half of the body of the corpus callosum.

Non-callosal Commissures

The third hypothesis is an increased use of commissures other than the corpus callosum. For example, Milner (1994) has suggested that the intertectal commissure, a subcortical pathway that connects the left and right hemisphere superior colliculi, may play a role in the transfer of visual information. Since there is often some degree of interhemispheric transfer even in those with full surgical section of the forebrain commissures, Milner argues that subcortical transfer must be at least possible. In his work on both acallosals and cases with surgical section of the forebrain commissures, Corballis (1995, 1998) also concludes that the intertectal commissure is the most likely route for the interhemispheric transfer of visual information in these individuals. He found that individuals with callosal agenesis were able to name stimuli in either visual field and integrate letters and words interhemispherically, but they were relatively poor at tasks involving transfer of colour information, consistent with evidence that the superior colliculi are insensitive to colour. However, the superior colliculi
are relatively primitive visual centres, and it unclear how they could process the relatively sophisticated shape information contained in words, or even letters. The transfer of shape information appears to be abolished following surgical section of the corpus callosum, and it would require a greatly expanded capacity of the superior colliculi and the tectal commissure if these were to process shape information in the acallosal brain.

A more likely candidate, perhaps, is the anterior commissure, which crosses the midsagittal plane ventral and caudal to the rostrum of the corpus callosum (Di Virgilio, Clarke, Pizzolato & Schaffner, 1999) and has been shown to be present in most individuals with callosal agenesis (Rauch & Jinkins, 1994). However, while the anterior commissure was once thought to be enlarged in acallosals, more recent evidence has not shown it to be systematically larger than it is in the normal brain; post-mortem and MRI data suggest that it is only enlarged in about 10% of cases and is small or absent in about 10% (Rauch & Jinkins, 1994). Moreover there is evidence the average area of the anterior commissure in humans is only 1 percent that of the corpus callosum, which must severely limit the amount of information it can carry (Foxman, Oppenheim, Petito & Gazzaniga, 1986).

Although the anterior commissure has been shown to transfer visual information interhemispherically in non-human primates (Black & Myers, 1964; Gross, Bender & Mishkin, 1977; Noble, 1968), there is little evidence that it does so in humans (Gazzaniga, 2000). Foxman et al. (1986) found that the anterior commissure in rhesus monkeys is proportionally larger than in humans, with a mean area approximately 5% of the size of the corpus callosum, although a post-mortem study by Di Virgilio et al. (1999) suggests that the human anterior commissure contains axons from more widespread areas than found in non-human primates. While most of the axons originated in the inferior temporal lobes, axons were also traced into the inferior occipital lobes, occipital convexity and possibly the central fissure and prefrontal convexity.

Studies of patients with surgical section of the corpus callosum have failed to reveal any transfer of visual information, even though the anterior commissure remains intact (Funnell, Corballis & Gazzaniga, 2000; Gazzaniga et al., 1965; Seymour, Reuter-Lorenz & Gazzaniga, 1994). There is some evidence, though, that the anterior commissure may at least sometimes mediate transfer in cases of callosal agenesis. In one man with callosal agenesis and a clearly enlarged anterior commissure, Martin (1985) found evidence for intact transfer of identification and shape information, but impaired transfer of locational information. He suggested that this could be explained in terms of the distinction between the ventral visual pathway, which processes identity information (the “what” system), and the dorsal pathway, which processes locational information (the “where” system) (Ungerleider & Mishkin, 1982). The anterior commissure connects areas of the inferior temporal lobes that are part of the ventral pathway, which may explain why it transfers “what” information but not “where” information. Further evidence for the involvement of the anterior commissure comes from a study by Fischer, Ryan and Dobyns (1992), who compared two acallosal boys on a number of tasks, one of which involved naming laterally-presented visual stimuli. While performance on the visual task was normal in the individual with an enlarged anterior commissure, it was impaired in the individual in whom the anterior commissure was absent (or at least very small).

There are a number of other routes that may be used in interhemispheric transfer, although as yet there is little evidence to support their involvement in the transfer of visual information. These include the cerebellar commissure (connecting the cerebellar hemispheres), the hippocampal commissure (connecting the crura of the fornix), the
habenular commissure (connecting the habenular nuclei) and the posterior commissure (connecting brain stem nuclei).

Techniques for Measuring the Interhemispheric Transfer of Information

The Crossed-Uncrossed Difference (CUD)

Experimental research into the interhemispheric transfer of information has used a number of different methods. A common technique is the use of simple RTs to measure manual responses to tachistoscopically-presented visual stimuli (Milner, 1994). In these experiments stimuli are presented to either the left visual field (LVF) or the right visual field (RVF) and the subject is asked to simply press a button as quickly as possible if either stimulus is seen. Responding hand changes between blocks of trials.

Using this methodology, Poffenberger (1912) showed that RTs to stimuli presented in one visual hemifield, and therefore projected to the contralateral hemisphere, are shorter when the responses are made with the hand ipsilateral to the stimulus (uncrossed responses) than when made with the hand contralateral (crossed responses). He hypothesized that this difference was due to the time taken for the information to cross over to the hemisphere controlling the motor response in the ‘crossed’ conditions. From these observations, Poffenberger then developed a measure of interhemispheric transmission time by subtracting the RTs for the two uncrossed conditions (LVF stimuli on left hand blocks and RVF stimuli on right hand blocks) from the RTs in the two crossed conditions (LVF stimuli/right hand blocks and RVF stimuli/left hand blocks), producing a crossed-uncrossed difference (CUD). In the case of simple RT paradigms it has been shown that the CUD is not affected by stimulus-response compatibility and that the responses in uncrossed conditions are faster regardless of the spatial relationship between the stimulus and the responding hand (Anzola, Bertoloni, Buchtel & Rizzolatti, 1977; Berlucchi, Crea, Di Stefano & Tassinari, 1977; Di Stefano, Sauerwein & Lassonde, 1992, Milner, Jeeves, Silver, Lines & Wilson, 1985). This suggests that the CUD is a measure of interhemispheric transfer time, and is not simply a consequence of stimulus-response compatibility.

It should be kept in mind that Poffenberger’s paradigm is the measurement of interhemispheric transfer time only for simple RT tasks. There is a wide range of different fibre densities in the corpus callosum, with theoretical calculations by Ringo, Doty, Demeter and Simard (1994) suggesting that callosal conduction times may range from less than 5 ms up to as much as 300 ms. The CUD calculated by the Poffenberger paradigm seems to reflect the fastest possible callosal transfer. When more complex tasks are used, such as go-no go tasks or two-choice tasks, different or multiple callosal pathways may be employed, with the result that the CUD is reflecting these pathways rather than that used in simple RT tasks. Poffenberger’s paradigm has now been applied in many different studies. In people with an intact corpus callosum, a CUD of between 2-6 ms is typically found (Bashore, 1981; Braun, 1992; Corballis, 2002, Marzi, Bisiacchi & Nicoletti, 1991), although the CUD has been found to vary considerably within subjects unless large numbers of trials (approximately 2000) are performed (Iacoboni & Zaidel, 2000). While this variability when using smaller numbers of trials can be offset by having a large sample size, for subjects treated individually, as the acallosal and split-brain subjects are, this variability needs to be taken into consideration.

Research has attempted to elucidate the nature of the information transferred in simple RT tasks by manipulating various properties of the stimulus or motor parameters and investigating the effect on the latency of the CUD. In neurologically normal individuals the
interhemispheric transfer underlying the CUD is probably of non-visual information (see Milner, 1994), as neither level of stimulus intensity (Clarke & Zaidel, 1989; Lines, Rugg & Milner, 1984; Milner & Lines, 1982) nor degree of stimulus eccentricity (Berlucchi et al., 1977; Berlucchi, Heron, Hyman, Rizzolatti & Umità, 1971; Clarke & Zaidel, 1989; Forster & Corballis, 1998; Lines & Milner, 1983; St.-John, Shields, Krahm & Timney, 1987) had any effect on the CUD, although a small positive correlation between eccentricity and CUD has been found in one meta-analysis (Braun, 1992).

Additional evidence that the CUD reflects the transfer of non-visual information comes from evoked potential studies that have found different estimates of interhemispheric transfer time (EP-IHTT) depending on the sites of the homologous electrode pairs that the estimate is based on. While the latency difference between the hemispheres at central sites was 3-4 ms, in line with the reaction-time data, the difference at occipital sites was much longer at 14-16 ms (Lines et al., 1984; Rugg, Lines & Milner, 1984). Further, while the occipital IHTT was affected by stimulus intensity, the central IHTT was not (Lines et al., 1984), adding to the evidence that the reaction-time CUD reflects the transfer of response-related information. An fMRI study using the same paradigm also suggested that interhemispheric transfer occurs at the premotor level, as it revealed significant activations in areas of frontal, parietal and temporal cortex and in the genu of the corpus callosum that were only present in the crossed conditions and therefore specifically related to interhemispheric transfer (Tettamanti et al., 2000). Further evidence that the CUD reflects interhemispheric transfer time comes from those without a functioning corpus callosum. In those with a surgically sectioned corpus callosum the CUD has been found to vary between about 50-80 ms, while individuals with callosal agenesis usually have a shorter CUD, lying somewhere between those of neurologically normal and split-brain people, in agreement with the contention that the greater the disconnection between the hemispheres the longer the time to transfer information between them (Aglioti, Berlucchi, Pallini, Rossi & Tassinari, 1993; Barr & Corballis, 2003; Berlucchi et al., 1995; Cailié et al., 1999; Clarke & Zaidel, 1989; Corballis, 1998; Di Stefano & Salvadori, 1998; Forster & Corballis, 1998, 2000; Jeeves, 1969; Iacoboni & Zaidel, 1995; Marzi et al., 1999; Milner, 1982; Roser & Corballis, 2002).

The evidence from studies with acallosal and split-brain people on the type of information that is transferred in simple RT studies has not been as clear as in the normal subjects. While some studies with acallosals have reported significant effects on the CUD of manipulations of stimulus luminance (Milner, 1982; Milner et al., 1985) and stimulus eccentricity (Lines, 1984), others have not (Clarke & Zaidel, 1989; Forster & Corballis, 1998). It may be that in some acallosal people the anterior or intertectal commissure mediates the transfer of visual information, hence the effects of manipulating stimulus parameters. However in other people the transfer of nonvisual information may be occurring or slower ipsilateral motor pathways may control the response.

In surgically split-brain individuals the picture is also mixed. While there is little evidence for any effects of stimulus luminance on the CUD, stimulus eccentricity does seem to affect the CUD of some split-brain subjects (Clarke & Zaidel, 1989; Forster & Corballis, 1998, Sergent & Myers, 1985). As all of the subjects tested in these studies had full forebrain commissurotomies the transfer of information must be occurring subcortically through visual pathways that are more sensitive to stimulus eccentricity than luminance. The superior colliculi are known to be retinotopically organized (McIlwain, 1973) and are connected via the intertectal commissure. It maybe that these split-brain subjects are using
this pathway to transfer visual information although, as with the acallosal subjects, there
maybe individual differences.

The Redundancy Gain

A well-established finding is that simple RTs are shorter when there are two stimuli than
when there is only one, a phenomenon known as redundancy gain. There are essentially two
possible explanations for this phenomenon. The first is based on the assumption that the
two processes are independent from one another and that the redundancy gain is simply the
result of probability summation (Miller, 1982; Raab, 1962). That is, if two stimuli activate
independent processes that are ‘racing’ to be the first to respond, then on average, RT will be
faster than when only one process is activated. The second explanation is that of neural
summation or the coactivation of the two processes (Miller, 1982). Neural summation is
implied if redundancy gain is greater than that predicted by the race model.

In neurologically intact people, at least in the case of visual stimuli, the redundancy gain is
usually less than that predicted by a simple race model (Corballis, 1998, 2002; Murray, Foxe,
Higgins, Javitt & Schroeder, 2001; Reuter-Lorenz, Nozawa, Gazzaniga, & Hughes, 1995;
Roser & Corballis, 2002; one exception, however, is the study by Miniussi, Girelli, & Marzi,
1998). In most people lacking the corpus callosum, however, the redundancy gain exceeds
that predicted by the race model when the two stimuli are presented to opposite visual fields,
and thus to opposite hemispheres (Corballis, 1998; Corballis, Hamm, Barnett, & Corballis,
2002; Iacoboni, Ptito, Weekes, & Zaidel, 2000; Marzi et al., 1997; Reuter-Lorenz et al., 1995;
Roser & Corballis, 2002). This enhanced redundancy gain implies interhemispheric neural
interaction, which is somewhat paradoxical, given that the two hemispheres are disconnected
at the cortical level.

A number of models have been proposed to explain how this interaction occurs and why this
effect is not seen in normal subjects. One possibility, elaborated by Reuter-Lorenz et al.
(1995), is that even when there is a single stimulus, interhemispheric transfer in intact
individuals essentially creates redundancy gain, so that there is no added advantage to having
double stimuli. Regardless of whether stimuli presentation is single or double, response
readiness in both hemispheres activates a logical AND gate, which removes response
inhibition and allows the motor response to occur. However, absence of the corpus callosum
means that unilateral input remains lateralized, effectively removing this redundant effect and
failing to meet the requirements of the AND gate so that RTs to single stimuli are slowed
relative to RTs to double stimuli. A modified and somewhat simpler version of this theory
has been suggested by Roser and Corballis (2002). They concur with Reuter-Lorenz et al.
(1995) that interhemispheric transfer in the intact brain creates redundancy gain even when
input is unilateral, but they propose that activation following presentation of stimuli feeds
into a neural summation mechanism rather than a logical AND gate.

An alternative view is that the corpus callosum acts to inhibit cortical activation with double
stimulation in intact individuals, perhaps through the dilution of attention, so that
subcortical summation arising from corticofugal stimulation is reduced (Corballis, 1998).
Section of the corpus callosum removes this inhibition, resulting in increased redundancy
gain. In most intact people, the redundancy gain is typically considerably less than that
predicted by the race model, which supports the idea that an inhibitory process is involved.

The implied neural summation is presumably subcortical since the effect occurs even in
individuals with full section of all the forebrain commissures. Further, an enhanced
redundancy gain to bilateral stimuli has been found in hemispherectomized subjects, even
though they fail to respond at all to unilateral stimuli presentations in the hemianopic field (Tomaiuolo, Ptito, Marzi, Paus & Ptito, 1997). One possible site is the superior colliculus (Corballis, 1998), although the effect does not appear to depend on spatial or exact temporal correspondence (Corballis et al., 2002; Reuter-Lorenz et al., 1995; Roser & Corballis, 2002), suggesting that the reticular formation may be the more likely site (Corballis et al., 2002).
This Study

This thesis reports experiments designed to investigate the nature of interhemispheric transfer in people with congenital absence of the corpus callosum. Chapter Three describes a series of three experiments that address the question of which types of visual information can be integrated interhemispherically in these individuals. As the two acallosal subjects tested had large differences in the size of their anterior commissure, these tasks also test the hypothesis that the anterior commissure may be a compensatory mechanism in those with callosal agenesis.

Chapter Four describes a reaction-time study that seeks to extend the current research on the paradoxical redundancy gain found in both acallosal and surgically split-brain subjects. The redundancy gain was examined under conditions of both luminance contrast and equiluminance to ascertain whether these conditions had a differential effect and, if so, whether this was dependent on the size of the subject’s anterior commissure.

Chapter Five describes an event-related potential experiment using the same methodology as in Chapter Four (luminance contrast). A third acallosal subject was also tested. Only two previous studies have investigated early visual evoked potentials in acallosals and both had suggested that there was no evidence that the potentials are able to transfer interhemispherically as they do in neurologically normal individuals. However, these studies had methodological limitations that may have precluded them finding ipsilateral activation.

The experiment described in Chapter Five is an attempt to overcome some of these limitations through the use of a high-density 128-electrode EEG system, enabling a more extensive coverage of the scalp area than in previous studies.
CHAPTER TWO

General Method

Subjects

Three acallosal subjects were tested in the experiments described in this thesis. Two of these, J.P. and M.M., participated in all the experiments, while A.L.M. participated only in the ERP experiment described in Chapter 5. A number of control subjects were also tested but as these changed between experiments they will be described within the methods specific to each chapter.

J.P.

J.P. was aged 33 years at the time of the testing described in Chapters Three and Four, and 34 years by the time of the testing in Chapter Five. She was diagnosed by CT scan with agenesis of the corpus callosum in 1998 after presentation with major depression, recurrent migraines and some left-sided weakness. No other abnormalities were found on the CT scan and an EEG recording proved to be normal. A MRI scan (see Figure 2.1) taken a year later confirmed diagnosis, and also showed prominent Probst’s bundles and an anterior commissure with a cross-section estimated at 28 mm², more than three times the normal area as estimated from several sources (Allen & Gorski, 1991; Demeter, Ringo & Doty, 1988; Meyer, Röricht & Niehaus, 1998). J.P. is adopted and nothing is known of her biological family.

J.P.’s Wechsler Adult Intelligence Scale - Third Edition (WAIS-III; Wechsler, 1997) scores were in the borderline range/extremely low range with a Full Scale IQ of 66 (Verbal IQ 66, Performance IQ 74). However, she presented quite normally during experimental testing sessions and lives independently in the community with her husband of six years. It is possible that her depressed state during the neuropsychological testing (from which she had recovered by the time we tested her) had deflated some of the scores. In general she performed better with visual than with verbal information, and had particular difficulty dealing with large amounts of information at a time. Her laterality quotient on the Edinburgh Handedness Inventory is 77 (Oldfield, 1971), showing a dominance of the right hand.
Figure 2.1 Mid-sagittal MRI Scan of Acallosal Subject J.P. showing Complete Absence of the Corpus Callosum. Arrow indicates Anterior Commissure.
M.M. was 39 years old at the time of the testing described in Chapters Three and Four, and 41 years by the time of the testing in Chapter Five. MRI confirmed total callosal agenesis (see Figure 2.2) with prominent Probst’s bundles. There were no signs of any other cerebral abnormality and her anterior commissure was within normal size limits (7 mm\(^2\) in cross-section). There was no evidence of ventricular enlargement, although M.M. has a large head circumference (above the 98th percentile) and low prominent forehead—features sometimes found in cases of callosal agenesis. She was born after a normal pregnancy and delivery, but there were developmental delays throughout childhood. After the birth of her first child she developed epilepsy and has taken daily doses of 400 mg phenytoin since, including during her four subsequent pregnancies. She has not had a seizure for some years. She was investigated for agenesis of the corpus callosum only after the birth of her fifth child, A.L.M., who was diagnosed as acallosal soon after birth. Her oldest child was given up for adoption at birth, and nothing is known of his subsequent development, but the fourth child, a girl, is also acallosal. The second and third children, also girls, are not acallosal.

Neuropsychological assessment using the Wechsler Adult Intelligence Scale - Revised (WAIS-R; Wechsler, 1981) showed M.M. to be functioning in the borderline/low average range with a Full Scale IQ of 79 (Verbal IQ 71, Performance IQ 90). It was noted during testing that she had difficulties with attention and concentration. Her laterality quotient on the Edinburgh Handedness Inventory is 64 (Oldfield, 1971), indicating right-hand dominance. For further details of her history and neuropsychological status, see Finlay et al. (2000).
Figure 2.2  Mid-sagittal MRI Scan of Acallosal Subject M.M. showing Complete Absence of the corpus callosum. Arrow indicates Anterior Commissure.

A.L.M.

A.L.M. is the daughter of M.M. She was 13 years old at the time of the testing in Chapter Five. Complete callosal agenesis was diagnosed a few days after birth following an ultrasound and CT examination to investigate sucking difficulties and an unusually large head. While subsequent MRI scans found no evidence of any other cerebral abnormality, the anterior commissure has been estimated to be approximately twice normal cross-sectional area (actual figure not available). For MRI scan see Figure 2.3. A.L.M. was born after a normal pregnancy and delivery, but has been late for all developmental milestones and has had remedial teaching because of poor performance at school. Neuropsychological testing at the age of 6 years 10 months, using the WPPSI (Wechsler, 1967), showed A.L.M. to be functioning in the low average range (Full-Scale IQ 84, Verbal IQ 77, Performance IQ 95) (Finlay et al., 2000). While these scores suggest some impairment of her verbal abilities, A.L.M. presented as lively and interested and school reports show her to be motivated and attentive in class. On the Edinburgh Handedness Inventory (Oldfield, 1971), she was clearly right handed with a laterality quotient of 50%.
Abstract

Two cases of callosal agenesis (J.P. and M.M.) and 10 neurologically normal subjects were tested on tasks requiring interhemispheric visual integration. M.M., whose anterior commissure was within normal limits, was much worse at matching colours and letters between visual fields than within visual fields, while J.P., whose anterior commissure was greatly enlarged, showed no evidence of interhemispheric disconnection on these tasks. This suggests that in some cases of callosal agenesis, probably a minority, an enlarged anterior commissure may compensate for the lack of the corpus callosum. Neither acallosal subject showed interhemispheric disconnection on tasks requiring integration of location and orientation, however, suggesting that the anterior commissure plays no role in such tasks, although both subjects performed poorly relative to controls. These tasks may depend on subcortical commissures, such as the intertectal commissure.

1 This chapter is similar to a published journal article: Barr, M. S. & Corballis, M. C. (2002). The role of the anterior commissure in callosal agenesis. *Neuropsychology, 16*(4), 459-471.
Individuals born without a corpus callosum do not show the same degree of functional disconnection between the cerebral hemispheres as surgically split-brain people (Lassonde & Jeeves, 1994), leading to the proposal of a number of neural compensation mechanisms that may account for this difference. These are reviewed in detail in Chapter One and include ipsilateral sensory pathways, which would allow information lateralized to only one visual field to nevertheless be available to both cortical hemispheres, and various non-callosal commissures. Of these non-callosal commissures the two most likely candidates are the anterior commissure and the intertectal commissure in the midbrain.

The present study compares interhemispheric visual matching in two cases of callosal agenesis, one with an enlarged anterior commissure and one with an anterior commissure within normal size limits. While Fischer et al. (1992) simply compared left visual field (LVF) presentations with right visual field (RVF) presentations, in this study bilateral tasks were added, where information in one visual field had to be compared with that in the other, allowing a more direct measure of interhemispheric transfer. Experiment 1 investigates the subjects’ ability to integrate colour information interhemispherically, Experiment 2 the integration of letters, and Experiment 3 the integration of information about spatial location and alignment.

**Experiment 1 - Integration of Colour Information**

Although interhemispheric transfer of colour information is largely abolished after surgical section of the corpus callosum (Corballis, 1996; Corballis & Corballis, 2001; Funnell et al., 2000; Johnson, 1984; Reuter-Lorenz et al., 1995), congenital absence of the corpus callosum results in a more varied profile of disconnection. Sauerwein, Lassonde and colleagues (Lassonde et al., 1988; Sauerwein & Lassonde, 1983) tested six acallosal individuals, and found that they were above chance in making same-different judgments about both unilaterally and bilaterally presented pairs of colour stimuli, although they made significantly more errors in the bilateral condition than IQ-matched controls and were much slower at
performing the task. In contrast, an acallosal man tested by Karnath, Schumacher and Wallesch (1991) was unable to perform above chance on a similar task, although he could name colours presented unilaterally. Corballis and Finlay (2000) tested three cases of callosal agenesis from the same family, M.M. and A.L.M. (discussed in Chapter Two) and the other acallosal daughter A.M., and found that all three had greater difficulty performing same-different judgments to bilaterally presented colour stimuli than to unilateral stimuli, even though they were able name colours presented unilaterally. Only one of the subjects, A.L.M., scored above chance in all conditions.

Corballis and Finlay (2000) suggested that the lowered performance in the bilateral condition could be due to the colour information being transferred through pathways, such as the intertectal commissure or the anterior commissure, that can carry at best a degraded form of the information. However, verbal information must have been transferred from the right to the left hemisphere, since all three subjects could name colours presented to either visual field, and it is possible that they were making some use of this strategy in matching the colours. The subjects in this study may also have been aided by the use of only two colours in the stimulus set, so that all that is needed is the transfer of binary information. This might be accomplished by simple cross-cueing, such as raising the tongue to indicate one colour and lowering it to indicate the other (Corballis, 1995).

Experiment 1 extends Corballis and Finlay's (2000) experiment by including a third colour to rule out simple binary transfer. Both the naming of unilaterally presented colour stimuli and the intrahemispheric and interhemispheric matching of colour information are investigated in two acallosal subjects, one of whom is M.M. from the study by Corballis and Finlay (2000).

Method

Subjects

Two women with agenesis of the corpus callosum, J.P. and M.M., were tested in this and in the subsequent experiments in this chapter. The details of these subjects are given in Chapter Two. In this experiment, there were also ten neurologically normal subjects, who took part only in the same-different
task. All were right-handed and participated voluntarily. There were five men and five women, with ages ranging from 21 to 44 years and an average age of 30.8 years. In this and the following experiments, the aim was not to provide precise age- and gender-matched controls for the two callosal subjects, but instead to gain a general impression of how normal adults would perform.

Tests and Procedure

Colour-Naming Task

The stimuli were pairs of filled circular disks, 0.88° in diameter, centred 5.29° to the left and right of a central fixation cross. In this and the following experiments, the stimuli were viewed from a distance of 57 cm from the screen, so that 1 cm on the screen corresponded to 1° of visual angle, with a chin rest used to minimize head movements. Subjects were monitored by the experimenter to ensure eye fixation.

The stimuli were red, green or yellow, and appeared on a black background. The luminances of the three colours were adjusted to establish approximate equiluminance by setting the red stimulus to 63 on a scale that ran from 0 (black) to 63 (maximum brightness), and adjusting the luminance of the green and yellow until rapid alternation between both red and green and red and yellow produced no discernible flicker. The setting for green was thus set at 38 and the yellow was set at a combination of 63 red, 36 green. By approximating equiluminance, the possibility that the subject was using luminance rather than hue to complete the task was minimized.

The task comprised one practice block of 10 trials followed by two experimental blocks of 72 trials. A fixation cross was presented in the middle of the screen. The experimenter initiated each trial and 500 ms later the cross disappeared. The stimuli were then flashed up on the screen for 133 ms, after which they disappeared and the symbol < or > appeared in the middle of the screen indicating the stimuli the subject should respond to (i.e., left for <, right for >). Subjects had up to 5 s to verbally report the colour of the stimuli that the symbol pointed to. A correct response resulted in the reappearance of the fixation cross; an incorrect response led to a tone followed by the fixation cross.
On a given block of trials, there were 36 presentations where the symbol pointed to the stimulus in the left visual field (LVF) and 36 presentations pointing to the stimulus in the right visual field (RVF). Every possible combination of colours was presented four times, with the result that each colour was the correct response 12 times in each visual field. The different conditions were presented in random order within a block.

The control subjects did not perform this task. The acallosal subjects responded verbally, the experimenter then typing the response on a keyboard. In all experiments, stimuli were presented on a fast-fade videographics adapter (VGA) screen, and all were programmed with the software package Micro Experimental Laboratory (MEL) (Schneider, 1995).

**Colour-Matching Task**

The stimuli used were identical to those used in the colour-naming task. In this task, however, the distance between the centres of the two disks was 5.84° on the screen. The pairs were presented either unilaterally in which case the centre of the nearer disk was 2.92° from the centre of the screen, or bilaterally, in which case the disks were centred 2.92° on either side of the centre of the screen.

On a given block of trials there were 36 presentations in each of the three locations (LVF, bilateral and RVF). Within each location there were 18 trials in which the stimuli were the same colour and 18 trials in which they were different.

The task comprised of one experimental block of 108 trials for each hand. In this and all the following experiments where control subjects took part, half responded first with the left hand, while the other half responded first with the right hand. In this task, J.P. began with her left hand, M.M. with her right hand. All subjects were given 10 practice trials before each block.

Again, a fixation cross appeared in the middle of the screen at the beginning of each block. For the acallosal subjects the experimenter initiated each trial by pressing a key; 500 ms later the cross disappeared and the stimuli were presented for 150 ms. Control subjects initiated the trials themselves using their non-responding hand. The subjects were asked to decide whether the two stimuli were the same or different in colour. They responded by pressing the S key on the computer keyboard for same
and the D key for different, using the forefinger and middle finger of the same hand. The keyboard was positioned by the individual for the most comfortable responding. Subjects had up to 5 s to make a response. A correct response resulted in the reappearance of the fixation cross; an incorrect response led to a tone followed by the fixation cross.

Results

Colour-Naming Task

M.M. was close to ceiling in the naming task, making only one error, in the LVF, out of a total of 144 trials. While also well above chance in naming, J.P. made more errors, with significantly more errors in the LVF (16 out of 72 trials) than in the RVF (1 out of 72 trials), \( \chi^2(1, N = 144) = 15.01, p < .001 \). 15 out of the 16 errors made in the LVF were due to a failure to respond, not to incorrect responses.

Colour-Matching Task

The control subjects’ responses were close to ceiling in this task, with a mean accuracy of 97.9% (see Figure 3.1).

The acallosal subjects’ responses were analyzed using a multidimensional chi-square procedure (Winer, 1971). This was done separately for J.P. and M.M., with the classification variables being stimulus (same or different), response (same or different), visual field (LVF, bilateral, RVF), and responding hand (left or right).

When matching colours between and within visual fields, J.P. scored almost perfectly, with only 7 errors over the 216 trials (see Figure 3.1). There was a significant effect of stimulus on response selection, \( \chi^2(1, N = 216) = 188.92, p < .001 \), indicating excellent stimulus discrimination. There were no
other significant interactions, indicating that performance was consistently high over all combinations of hand and visual field. Her performance accuracy was statistically comparable to that of controls, $F(1, 9) = 0.55, ns$.

M.M.’s overall accuracy was significantly depressed compared to the neurologically normal subjects, $F(1, 9) = 71.84, p < .001$ (see Figure 3.1). Nevertheless, there was a highly significant effect of stimulus on response selection $\chi^2(1, N = 216) = 107.55, p < .001$, indicating that she was able to discriminate same from different pairs at considerably better than chance. While her errors were few in the two unilateral conditions, performance was poorer in the bilateral condition, as shown by a significant interaction between location (unilateral vs. bilateral) and stimulus on response selection, $\chi^2(1, N = 216) = 10.76, p < .001$. Although her performance was nevertheless significantly above chance in the bilateral condition when she responded with her right hand, it failed to reach significance with the left hand, $\chi^2(1, N = 36) = 3.01, ns$.

It is unlikely that the better performance of J.P. in the bilateral conditions was due to behavioural cross-cueing as the mean reaction times of both subjects were too fast for this to have occurred (J.P. 691 ms, M.M. 560 ms).
Discussion

Both M.M. and J.P. were well above chance in naming colours presented to either the left or right visual field, although J.P. made significantly more errors in the LVF than in the RVF, perhaps reflecting some impairment in the transfer of verbal information. On the same-different task, however, J.P. was highly accurate and statistically indistinguishable from the control sample, while M.M. showed a clear disconnection; her accuracy in the bilateral conditions was significantly lowered compared to unilateral conditions, and in the case of left-hand responding not significantly above chance. These results suggest that the enlarged anterior commissure in J.P. may have mediated the transfer of colour information.

In contrast, the normal-sized anterior commissure in M.M. may not carry colour information; the weak but above-chance transfer with right-hand responding may have been due to the transfer of verbal labels. Others have also reported poor or negligible interhemispheric matching of colours in cases of callosal agenesis; there was no indication that these cases had enlarged anterior commissures (Karnath et al., 1991; Lassonde et al., 1988). However MRI has revealed that A.L.M., the only subject in Corballis and Finlay's (2000) study to consistently respond at above chance in interhemispheric colour matching, does have an enlarged anterior commissure.

Experiment 2 - Integration of Letter Information

Shape information, like colour information, does not appear to transfer between the hemispheres after surgical callosotomy or commissurotomy (Corballis & Trudel, 1993; Eviatar & Zaidel, 1994; Fendrich & Gazzaniga, 1989; Funnell et al., 2000; Johnson, 1984), but the evidence is again more variable in acallosals. For example, Sauerwein and Lassonde (1983) tested two acallosal subjects and found that they were able to make same-different judgments about both unilaterally and bilaterally
presented familiar shapes, although as in the colour task, they made more errors than IQ-matched controls in the bilateral condition and had much slower reaction times. In contrast, the acallosal subject tested by Karnath et al. (1991) was unable to perform at above chance levels on a similar task.

It is possible that the transfer of shape depends on the nature of the information to be transferred. Eviatar and Zaidel (1994) tested three surgically commissurotomized subjects on two letter-matching tasks, one requiring comparison of the physical properties of the letters (“Do they have the same or different shapes?”) and the other requiring nominal comparison (“Do they have the same or different names?”). They found that none of the subjects was able to compare nominal identity interhemispherically, while only one was able to compare physical identity across the left and right visual fields. Caillé et al. (1999) found that a subject born without either a corpus callosum or an anterior commissure was able to match physical identity between fields, but not nominal identity. They suggested that subcortical commissures such as the superior colliculi or the posterior commissure may transfer the sensory information needed for physical comparison, but that cortical commissures are necessary for the transfer of nominal information.

Corballis and Finlay (2000) found that three subjects with agenesis of the corpus callosum, M.M., A.L.M. and A.M., were all able to perform same-different letter judgments at above chance levels in both within- and between-visual field conditions. Brown et al. (1999) tested four individuals with complete callosal agenesis, two with partial callosal agenesis and one who had undergone commissurotomy surgery, and found that while the commissurotomized subject was unable to compare the nominal identity of bilaterally presented letters, all the acallosal subjects performed at well above chance levels. Brown et al. suggested that the anterior commissure mediated the transfer of nominal information in these cases.

However, both Brown et al. (1999) and Corballis and Finlay (2000) used only two letters in their stimulus sets, so it is again possible that only binary information and not more specific physical or nominal information was being transferred. In Experiment 2 a third letter was included. Both uppercase and lowercase versions of each letter were also used, as in the work of Eviatar and Zaidel (1994) and
Caillé et al. (1999), in order to assess the transfer of both physical and nominal identity.

Method

Subjects

The acallosal subjects, J.P. and M.M., were as in Experiment 1. No control subjects were run for the naming task as it was expected that performance would be at ceiling, but ten control subjects were included for the two same-different tasks. They were right-handed and participated voluntarily. There were five men and five women, with ages ranging from 23 to 62 years and an average age of 34.4 years.

Tests and Procedure

Letter-Naming Task

The stimuli consisted of pairs of the letters A, a, G, g, R and r. The letters were 1.20° in width, 1.40° in height and appeared 7.00° to the left and right of a central fixation cross. The stimuli were white against a black background.

The procedure was the same as for the colour-naming task in Experiment 1, except that the stimuli were presented for 150 ms, slightly longer due to the increased complexity of the stimuli. Every possible combination of letters was presented with the result that each letter was the correct response 6 times in each visual field.

Shape-Matching Task

The stimuli were the same as in the naming task. However, there were three different conditions in which the stimuli were presented—two unilateral conditions, in which both letters were either in the LVF or RVF, and a bilateral condition in which one letter was presented in each visual field. In the unilateral conditions the letters were centred 5.70° apart with the nearer letter centred 2.85° from the central fixation cross, while in the bilateral condition both of the letters were centred 2.85° from the cross.
The task consisted of two blocks of 180 trials, with 10 practice trials before each block. Within each block there were 60 presentations in each of the three locations (LVF, bilateral and RVF); 30 trials in which the stimuli were of the same shape and 30 trials in which they were different.

Procedure and responding were as for the colour-matching task in Experiment 1, except the task here was to decide whether the two letters were the same or different in shape. Of the acallosal subjects, J.P. responded first with her right hand while M.M. responded first with her left hand.

Name-Matching Task

This series was similar to the shape-matching task, except that subjects were required to respond same or different depending on the name of the stimuli. In this case a lowercase and uppercase version of the same letter would require a “same” response.

On a given block of trials there were 48 presentations in each of the three locations. Within each location there were 24 trials in which the stimuli were the same and 24 trials in which they were different. The timing and presentation were the same as in the shape-matching task.

Results

Letter-Naming Task

M.M. was close to ceiling in the naming task, making no errors in the LVF and only three errors out of the 72 RVF trials. While also significantly above chance in responding, \( \chi^2(1, N = 144) = 116.28, p < .001 \), J.P. made 22 errors in the LVF and 13 in the RVF. Although J.P. performed more poorly in the LVF, the difference between fields did not reach significance, \( \chi^2(1, N = 144) = 3.06, \text{ ns} \). 27 out of the 33 errors made by J.P. were due to failure to respond, not to giving an incorrect response.

Shape-Matching Task

The control subjects showed a high level of accuracy across conditions on this task with a mean accuracy of 95.2% (see Figure 3.2). Percentages of correct trials were subjected to an analysis of variance (ANOVA) for the within-subjects factors of hand and visual field (LVF, bilateral, and RVF).
There was a significant effect of field, $F(2, 18) = 5.87, p = .019$, reflecting greater accuracy in the bilateral condition (97.4%) than in the two unilateral conditions (mean accuracy 94.1%), $F(1, 9) = 13.18, p = .005$.

The responses of each acallosal subject were analyzed using multidimensional chi-square, with the classification variables being stimulus (same or different), response (same or different), visual field (LVF, bilateral, RVF) and responding hand (left or right). While J.P.’s overall accuracy was significantly depressed compared to the controls, $F(1, 9) = 14.86, p = .004$ (see Figure 3.2), there was a highly significant effect of stimulus on response selection, $\chi^2(1, N = 360) = 169.28, p < .001$, indicating that she was nevertheless able to discriminate same from different pairs of letter shapes at a better than chance level. The effect of visual field on accuracy (interaction between stimulus, response and field) was not significant, $\chi^2(2, N = 360) = 2.48, ns$; if anything performance was slightly higher for bilateral than for unilateral presentations.

M.M.’s overall accuracy was also significantly lower than that of the control subjects, $F(1, 9) = 46.03, p < .001$ (see Figure 3.2), although she showed a highly significant effect of stimulus on response selection, $\chi^2(1, N = 360) = 99.88, p < .001$, indicating stimulus discrimination that was well above chance overall.

M.M. also showed a significant interaction between stimulus and visual field on response selection, $\chi^2(2, N = 360) = 11.85, p < .01$, indicating better discrimination with unilateral than with bilateral presentations, $\chi^2(1, N = 360) = 11.69, p < .001$. Although the combined interaction of stimulus, visual field and hand on response selection was non-significant, $\chi^2(2, N = 360) = 3.95, ns$, M.M.’s performance with her left hand in the bilateral condition failed to exceed chance levels, $\chi^2(1, N = \ldots$
Figure 3.2 Mean Accuracy of Responses made by Hand and Visual Field in Shape-Matching and Name-Matching Tasks of Experiment 2. Error Bars represent Standard Deviations of the Mean.

60) = 1.92, ns, although her right hand performance did, \( \chi^2(1, N = 60) = 9.32, p < .01 \). Again, the fast RTs in the bilateral conditions make it unlikely that the better performance of J.P. was due to behavioural cross-cueing (Mean RTs: J.P. 731 ms, M.M. 621 ms).

Name-Matching Task

Control subjects showed a high level of accuracy across conditions on this task with a mean accuracy of 94.3% (see Figure 3.2). Percentages correct were again subjected to ANOVA for the within-subjects factors of hand and stimuli location (LVF, bilateral and RVF). The control sample showed a significant effect of hand, \( F(1, 9) = 13.30, p = .005 \), with greater accuracy with the right hand.
(95.1%) than the left (93.4%). There was also a significant effect of field, \( F(2, 18) = 4.15, p = .034 \), with greater accuracy in the bilateral condition (95.9%) than the two unilateral conditions (mean accuracy 93.4%), \( F(1, 9) = 7.15, p = .025 \).

J.P.’s overall accuracy was significantly depressed compared to the controls, \( F(1, 9) = 8.54, p = .017 \) (see Figure 3.2), although multi-dimensional chi-square analysis showed a highly significant effect of stimulus on response selection, \( \chi^2(1, N = 288) = 145.39, p < .001 \), indicating that she was above chance in discriminating same from different pairs of letter names.

M.M.’s overall accuracy was also significantly depressed compared to the control subjects, \( F(1, 9) = 25.26, p = .001 \) (see Figure 3.2), while she showed a highly significant effect of stimulus on response selection, \( \chi^2(1, N = 288) = 93.84, p < .001 \), indicating good stimulus discrimination overall. She also showed a significant interaction between stimulus and visual field on response selection, \( \chi^2(2, N = 288) = 7.56, p < .05 \). This was due to better discrimination with unilateral than with bilateral presentations, \( \chi^2(1, N = 288) = 5.47, p < .05 \), especially RVF versus bilateral presentations, \( \chi^2(1, N = 192) = 63.19, p < .01 \) (see Figure 3.2). Again, mean RTs were fast enough to rule out cross-cueing as an explanation for J.P.’s better performance in the bilateral conditions (J.P. 774 ms, M.M. 606 ms).

Discussion

The pattern of results was similar to that of the previous experiment. While both M.M. and J.P. were above chance in naming letters, J.P. made many more errors than M.M., especially in the LVF. In the two same-different tasks, both M.M. and J.P. performed at better than chance, but at a level that was significantly lower than that of the controls. On both tasks M.M.’s performance was significantly worse in the bilateral than in the unilateral conditions suggesting a degree of disconnection with respect to both shape and name information. This was particularly marked in the shape-matching task where her performance in the bilateral condition when using her left hand was no greater than chance. In contrast J.P., despite her relatively low performance overall, showed little evidence of disconnection,
and when responding with the right hand was actually better at matching between fields than at matching within them. These results again suggest an enlarged anterior commissure supported interhemispheric transfer in J.P., but that M.M., with her normal-sized commissure, had little ability to transfer either the shapes or names of letters.

Another sign of disconnection in M.M. is that she was worse in the two “crossed” conditions (LVF/right hand and RVF/left hand combinations) than in the uncrossed ones (LVF/left hand and RVF/right hand). In the name-matching task, she showed a RVF advantage regardless of the responding hand, perhaps reflecting the linguistic component. M.M.’s poor performance with bilateral matching contrasts with her good performance in the study by Corballis and Finlay (2000), where there was no evidence that she had any difficulty matching letters across visual fields. Her accurate bilateral matching in that study cannot be attributed to the transfer of nominal information, since in the present study she performed poorly with bilateral matching when the task specifically required her to match the letters by name rather than by shape. The more likely reason for her poor performance is simply that the pool of stimuli was increased by the addition of a third letter and of both upper- and lowercase versions. As explained earlier, this would have ruled out the effective use of any simple binary code.

Unlike M.M. and the control sample, J.P. showed an LVF advantage regardless of the hand or task—although the difference only reached significance in the name-matching task. This difference is difficult to explain. It is unlikely that it was due to right-hemispheric dominance for language, since she was more accurate in naming both letters and colours when they were presented in the RVF, implying left-hemispheric dominance.

Experiment 3 - Integration of Spatial Location and Alignment

Holtzman and colleagues (Holtzman, 1984; Holtzman, Sidtis, Volpe, Wilson & Gazzaniga, 1981) have reported that, in patients with surgical section of the corpus callosum, there is interhemispheric
access to crude locational information, which they suggest is mediated by the tectal commissure connecting the superior colliculi. However, on a task requiring finer degrees of spatial resolution the patients were significantly impaired, which Holtzman (1984) attributed to the limitations of collicular vision. Similar conclusions were reached by Corballis and Trudel (1993), who tested two subjects, one who had undergone full forebrain commissurotomy and one with section of the posterior corpus callosum, on tasks requiring judgment of whether pairs of sloping lines were aligned or not. The pairs were presented either wholly in the LVF or RVF, or bilaterally, with one member of each pair in the LVF and one in the RVF. As both subjects were able to perform at better than chance on the bilateral conditions, the authors suggest that information about alignment can be transferred subcortically, although performance was less accurate in the bilateral condition than in the unilateral ones, suggesting some loss of precision in subcortical transfer.

There have been few comparable studies on people with callosal agenesis. As noted in Chapter One, Martin (1985) has reported evidence that one acallosal man with an enlarged anterior commissure was able to transfer identity information between hemispheres, but had difficulty making locational judgments when the stimuli were in the RVF. On the assumption that accurate judgments of location depend on access to the right hemisphere, Martin suggested that the poor judgment of location in the RVF reflected a failure of interhemispheric transfer.

Experiment 3 extends location and alignment judgments to two further cases of callosal agenesis. The dot-location task was loosely modelled on the task used by Martin (1985); subjects were required to compare locational information in two displays, including a condition in which the displays were in opposite visual fields. This provided a more direct test of interhemispheric transfer than that used by Martin. The line-alignment task was closely modelled on the task used by Corballis and Trudel (1993).

Method

Subjects

The acallosal subjects were J.P. and M.M., as in Experiment 1 and 2. Ten control subjects
completed the dot-location task and ten others completed the line-alignment task. All participated voluntarily. For both series there were 5 men and 5 women. For the dot-location task the ages ranged from 21 to 55 years with a mean of 26.9 years, while for the line-alignment task the ages ranged from 22 to 62 years with a mean of 32.1 years.

Tests and Procedure

Dot-Location Task

The stimuli comprised filled circular disks, 0.44° in diameter. The stimuli were white and appeared on a black background. The stimuli were presented within pairs of squares measuring 4.38° by 4.38° that were also white. There were four possible locations for these squares, and nine possible locations for the dot within each square. In the unilateral conditions, where both squares were presented either to the left or right of the fixation cross, the edge of the nearer square was 1.10° from the centre of the screen, with the two squares being 1.10° apart. In the bilateral conditions the nearer edges of both squares were centred 1.10° from the centre of the screen, to the left and right.

On a given block of trials, there were 72 presentations in each of three locations of the squares (LVF, bilateral and RVF). Trials were divided equally between presentations where the dots were in the same position within their respective squares and presentations where they were in different positions. All of the possible same conditions, but only half of the possible different conditions, were presented. The different conditions chosen were those considered the most difficult in that they shared either the same vertical or the same horizontal plane as their paired stimuli.

The task comprised of two blocks of 216 trials, randomly ordered, with 10 practice trials before each block. J.P. responded first with her right hand while M.M. responded first with her left hand.

Presentation and responding were as for the colour-matching task, except that the stimuli appeared for 133 ms. In this experiment, the task was to decide whether the two stimuli had appeared in the same or in different locations within their respective squares (for example, see Figure 3.3). Subjects were given up to 10 s to make a response.
Figure 3.3 Trials in Dot-Location Task in Experiment 3 are responded to as “Same” or “Different” by Comparing the Relative Positions of the Dots within their Squares.

Line-Alignment Task

The stimuli consisted of 3.10° long lines drawn on an angle of 45°, so that they covered 2.19° of visual angle horizontally and 2.19° vertically. The stimuli were presented in pairs, side by side, such that there was a horizontal distance of 2.19° between their nearest points. The stimulus lines were either aligned, or they were misaligned by vertical displacements of 0.37°, 0.73°, or 1.10°, and were white against a black background.

Within a block of trials, the pairs of stimuli sloped upwards from left to right on half the trials, and downward on the other half. There were 32 trials in which the stimuli were presented wholly in the LVF, 32 trials in which they were wholly in the RVF, and 32 trials in which they were presented bilaterally. Figure 3.4 illustrates the possible locations for bilateral lines sloping up to the right in the aligned condition. For unilateral conditions, the displays were moved 4.40° to the left or right; left-right reversal
Figure 3.4  Location of Lines (not precisely to scale) used in Line-Alignment Task in Experiment 3 under the Bilateral Condition.

of the figure would show the possible locations of lines sloping up to the left.

The task comprised of one practice block of 12 trials and one experimental block of 96 trials for each responding hand. J.P. responded first with her left hand while M.M. responded first with her right hand. Presentation was as for the colour-matching task. In responding, the subjects were required to indicate whether the two lines were in alignment with each other, by pressing the B key on the computer keyboard for aligned and the N key for misaligned, using the forefinger and middle finger of the same hand. Subjects had 10 s seconds in which to make a response.

On all blocks of trials there were equal numbers of trials in which the lines were either aligned, 0.37° misaligned, 0.73° misaligned, or 1.10° misaligned. All possible locations of the aligned stimuli and the 0.73° misaligned stimuli were presented. However, in order to achieve equality in the number of trials across conditions, it was necessary to present all possible locations for the 1.10° misalignment twice, while only presenting two-thirds of the possible locations for the 0.37° misaligned stimuli. In this way there were 24 trials in each alignment condition in the experimental blocks. The 96 trials were
randomly ordered. On the practice block of trials, incorrect responses were followed by a tone to inform the subject when an error had been made. On the experimental block of trials no such feedback was given.

**Results**

*Dot-Location Task*

The control subjects were highly accurate across all conditions on this task, with a mean accuracy of 89.6% (see Figure 3.5). Percentages correct were subjected to ANOVA for the within-subjects factors of hand and stimuli location (LVF, bilateral and RVF). There was a highly significant effect of field, $F(2, 18) = 10.72, p = .001$, reflecting greater accuracy in the bilateral condition (92.2%) than the two unilateral conditions (mean accuracy 88.2%), $F(1, 9) = 16.71, p = .003$. There were no other significant effects.

The responses of J.P. and M.M. were analyzed using multidimensional chi-square with the classification variables being stimulus (same or different), response (same or different), visual field (LVF, bilateral, RVF) and responding hand (left or right). While J.P.’s overall accuracy was significantly depressed compared to the controls, $F(1, 9) = 16.46, p = .003$ (see Figure 3.5), there was a highly significant effect of stimulus on response selection, $\chi^2(1, N = 432) = 44.24, p < .001$, indicating that J.P. was able to discriminate same from different pairs of dot locations. There was no evidence that discrimination was worse with bilateral than with unilateral presentation, $\chi^2(1, N = 432) = 0.12, ns$.

M.M.’s overall accuracy was also significantly depressed compared to control subjects, $F(1, 9) = 12.25, p = .007$ (see Figure 3.5). However, she showed a highly significant effect of stimulus on response selection, $\chi^2(1, N = 432) = 63.79, p < .001$, indicating good stimulus discrimination. Although the combined interaction of stimulus, visual field and hand on response selection was non-significant, $\chi^2(1, N = 432) = 1.39, ns$, M.M.’s performance with her left hand to RVF stimuli failed to better chance, $\chi^2(1, N = 72) = 2.01, ns$. 
Line-Alignment Task

Data from all subjects were first analyzed in terms of the proportion of “misaligned” responses as a function of the degree of actual misalignment. Responses were collapsed across hands as neither the control subjects, nor J.P. or M.M., showed any effect of hand. As seen in Figure 3.6, the psychometric function was steep for the controls indicating reasonably good discrimination under all conditions. Percentages of correct trials were then subjected to an ANOVA for the within-subjects factors of responding hand, stimuli location (LVF, bilateral and RVF) and degree of misalignment.

The control subjects showed a highly significant effect of degree of misalignment, $F(3, 24) = 153.10, p < .001$, reflecting their ability to discriminate among the different misalignments. There was also a significant interaction between visual field location and misalignment, $F(6, 48) = 3.72, p < .05$, that was due to a unilateral versus bilateral field difference in misalignment, $F(3, 24) = 6.58, p < .01$. As can be seen in Figure 3.6, the bilateral function is steeper than the unilateral functions and levels out more in the two conditions of greatest misalignment, indicating higher discriminative accuracy.

Figure 3.5  Mean Accuracy of Responses by Hand and Visual Field in Dot-Location Task in Experiment 3. Error Bars represent Standard Deviation of the Mean.
Figure 3.6  Mean Percentage of “Misaligned” Responses as a Function of Actual Misalignment and Field Location in the Line-Alignment Task in Experiment 3. Error Bars represent Standard Error of the Mean.

The responses of J.P. and M.M. were analyzed using multidimensional chi-square with the main variable being degree of misalignment (0, 0.37, 0.73 or 1.1°) response (aligned or misaligned), visual field (LVF, bilateral, RVF) and responding hand (left or right). While J.P.’s performance was much worse than that of the controls, $F(1, 9) = 4492.91, p < .001$, she still showed a significant effect of stimulus on response selection, $\chi^2(3, N = 192) = 11.83, p < .01$, indicating that she was able to discriminate aligned and misaligned stimuli. The effect of visual field on accuracy (interaction between stimulus, response and visual field) was non-significant, $\chi^2(6, N = 192) = 4.75, ns$, and there were no other significant effects.

M.M.’s performance was also much poorer than that of the controls, $F(1, 9) = 2261.81, p < .001$, and chi-square analysis between stimulus type and response shows that M.M. was unable to discriminate between stimulus types, $\chi^2(3, N = 192) = 5.71, ns$, at better than chance. The interaction between stimulus, response and visual field was non-significant, $\chi^2(6, N = 192) = 4.36, ns$, and there were no other significant effects.
Discussion

On the dot-location task, both J.P. and M.M. performed at better than chance, but at a level that was significantly lower than that of the control sample. While M.M. ’s performance in the crossed RVF-left hand condition was no greater than chance, neither acallosal showed any evidence of disconnection on bilateral trials, suggesting that their poor performance was not obviously related to any difficulty with interhemispheric transfer.

On the line-alignment task both J.P. and M.M. performed at a level that was again significantly lower than that of the control sample. However, while J.P. was able to discriminate between aligned and misaligned stimuli, M.M. was unable to do so and performed the task indiscriminately. As this occurred across all conditions, this inability may not be directly related to any disconnection between the hemispheres, and may have been due to the lack of feedback provided on this task.

This experiment did not show the pattern of the previous experiments, in which M.M. showed interhemispheric disconnection while J.P. did not. This lends some support to Martin’s (1985) conclusion that the anterior commissure does not play a role in the transfer of locational information in these subjects. While it is possible that the tectal commissure is involved in the transfer of locational and orientational information, neither of the acallosal subjects in this study showed evidence of disconnection in this experiment; instead, their performance was depressed for both unilateral and bilateral displays. This may reflect some general consequence of callosal agenesis rather than specific deficits in interhemispheric transfer.

General Discussion

While J.P. showed no signs of disconnection on any of the tasks, M.M. had considerable difficulty matching colours or letters between visual fields, but relatively little difficulty matching them within fields. Since J.P. has an enlarged anterior commissure, while M.M.’s is within normal limits, this confirms
previous suggestions that the anterior commissure may compensate for the absence of the corpus callosum in callosal agenesis, but perhaps only in cases where it is anatomically enlarged (cf. Martin, 1985). There is evidence that a large number—roughly 70% in both the cat (Innocenti, 1986) and the monkey (LaMantia & Rakic, 1984)—of the callosal fibres present at birth are eliminated during maturation, and LaMantia and Rakic (1994) have also shown this pattern of axon overproduction and elimination to be true for the anterior commissure in monkeys. One theory is that the elimination of axons in the anterior commissure is reduced in some acallosal individuals, explaining the increase in cross-sectional area. However, differences in size could be due to a number of factors other than an increase in the number of axons or axonal diameters (Di Virgilio et al., 1999).

The anterior commissure may play relatively little role in those acallosals, like M.M., whose anterior commissures are within the normal range. Nevertheless, the functional disconnection evident in these individuals still appears to be less severe than in those with surgical section of the corpus callosum (cf. Corballis & Corballis, 2001; Johnson, 1984). It is possible that the anterior commissure still plays a compensatory role, or else that there is compensation via subcortical commissures. In fact, subcortical commissures must play a role in those individuals in whom some evidence of information transfer is found even though the anterior commissure is completely absent (Caillé et al., 1999). One subcortical candidate is the tectal commissure connecting the superior colliculi, which are part of the subcortical visual system, known to have retinal input and to be retinotopically organized (Meredith & Stein, 1990). They also have connections to parietal visual association cortex, part of the dorsal “where” stream (Milner & Goodale, 1995).

In one respect, M.M. shows slightly less evidence of disconnection than J.P., despite her smaller anterior commissure - she was nearly perfect in naming both colours and letters in both visual fields. It seems unlikely that this was due to the transfer of nominal information, since she was poor at matching letter names between visual fields in Experiment 2. However there are also reasons to doubt that it can be attributed to bilateral speech. Corballis and Finlay (2000) tested her with letter strings that straddled the midline; each string consisted of six letters, three in each visual field, and each could be read either
as two three-letter words or as a single six-letter word (e.g., FATHER). M.M. always pronounced the string as a whole ("father"), never as two three-letter words ("fat", "her"), suggesting that the string was integrated and identified within a single hemisphere—presumably the left. She also had little difficulty articulating six-letter words presented wholly in one or other visual field.

A similar dissociation between naming and matching has also been observed in cases of surgical disconnection of the hemispheres. One study, for example, revealed one commissuromized man (L.B.) to be capable of naming stimuli in either visual field, and even able to name bilateral pairs, but unable to match the same stimuli between fields, while a commissuromized woman (N.G.) could match between fields but could not name stimuli in the LVF (Johnson, 1984). Although the reasons for this double dissociation remain obscure, it suggests that the commissural routes for simple naming and for interhemispheric matching may be distinct.

The experiments reported here illustrate the differences that can arise between individuals with callosal agenesis. The two acallosal women who served as subjects were of the roughly the same age, handedness, and general ability, yet they showed markedly different patterns of disconnection. One source of variation, but probably not the only one, may be the size of the anterior commissure.
Unilateral LVF trial
Correct response: “same”

Bilateral trial
Correct response: “different”
CHAPTER FOUR

Redundancy Gain in the Acallosal Brain

Abstract

Simple reaction time (RT) was recorded to visual stimuli, presented either singly to one or the other visual field or in bilaterally presented pairs, to two women, J.P. and M.M., with callosal agenesis. The stimuli were either white against a black background, or gray against an equiluminant yellow background. RTs to bilateral pairs were decreased beyond predictions based on a simple race between independent unilateral processes, implying interhemispheric neural summation. This effect was enhanced under equiluminance in the subject M.M. whose anterior commissure was within normal limits, but not in the subject J.P. whose anterior commissure was enlarged. The anterior commissure may act, relative to its size, to inhibit cortical activation to bilateral pairs, which then acts to decrease subcortical neural summation.

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1 This chapter is similar to a published journal article: Barr, M.S. & Corballis, M.C. (2003). Redundancy gain in the acallosal brain. *Neuropsychology, 17*(2), 213-220.
An enhanced redundancy gain implying neural summation, and a lack of cortical inhibition, has been demonstrated in three people with agenesis of the corpus callosum (Corballis, 1998; Corballis et al., 2002; Iacoboni et al., 2000; Roser & Corballis, 2002), although it was not evident in a fourth person with callosal agenesis (Iacoboni et al., 2000).

As described in Chapter One, the retinotectal visual pathway is thought to be largely restricted to magnocellular information, which is unable to process colour information. This is confirmed by the finding that the transfer of colour information in the surgically split brain is largely negative (see review in Chapter Three). Stimuli presented under conditions of equiluminance should therefore restrict processing to the retino-geniculo-striate parvocellular system, which in the split brain is disconnected. In keeping with this, Corballis (1998) found that when the stimuli were equiluminant with the background, the enhanced redundancy gain was largely eliminated in people who had undergone callosotomies, consistent with subcortical summation. Rather surprisingly, however, the effect was if anything increased in a man with agenesis of the corpus callosum when the stimuli were equiluminant.

The main purpose of the present study was to examine redundancy gain in two women, J.P. and M.M., with agenesis of the corpus callosum, under conditions of both luminance contrast and equiluminance. As described previously, these two subjects differ with respect to the size of the anterior commissure, which is greatly enlarged in J.P. but within normal limits in M.M. Previous experiments, discussed in Chapter Three, have shown the interhemispheric matching of colours and letters to be impaired in M.M. relative to that in J.P., suggesting that enlargement of the anterior commissure may facilitate interhemispheric transfer in some people with callosal agenesis. Another earlier study also showed that redundancy gain is somewhat more marked in M.M. than in J.P. (Roser & Corballis, 2002), implying that the larger anterior commissure in J.P. may have resulted in a higher level of cortical inhibition. A major aim of the present study was to determine whether equiluminance would have a different effect on redundancy gain in these two subjects.
Experiment 1: Luminance Contrast

Method

Subjects

There were two subjects, J.P. and M.M. The details of these subjects were given in Chapter Two.

Stimuli and apparatus

The stimuli consisted of filled circular discs, 0.88 cm in diameter, flashed onto the screen for 133 ms. They appeared 5.11 cm from a central fixation cross, either unilaterally to the left or right of the cross, or bilaterally, and were white against a black background. The screen was viewed from a distance of 57 cm, so that 1 cm on the screen represented 1° of visual angle. A chin rest was used to reduce any movement of the head by the subject, ensuring that her eyes were at a constant distance from the computer screen. On a given block there were 99 trials; 30 unilateral trials to the left visual field (LVF), 30 unilateral trials to the right visual field (RVF), 30 bilateral trials to both visual fields simultaneously, and nine 'catch' trials in which no stimuli were presented.

On initiation of a block of trials, a fixation cross appeared in the middle of the screen and remained there for the duration of the block. After 1 s, a 250-Hz tone sounded for 200 ms, and then on trials where stimuli were presented there was a variable interval of 300, 400, 500, 600 or 700 ms prior to presentation of the stimuli. The subject was allowed 1 s in which to respond. On catch trials, the subject was required to withhold the response for 1.7 s following the tone. After either the subject’s response, or the 'time-out' period on catch trials, there was a further period of 1 s before the tone sounded for the next trial. Each of the five variable intervals between tone and stimulus was paired six times with each stimulus condition to generate the 90 trials on which stimuli appeared. These were then randomly presented along with the nine catch trials. For J.P., any error trials, that is either responses to catch trials or non-responses to trials where stimuli were presented, were rerun. Error trials were not rerun for M.M.

Responses were made on a keyboard positioned by the subject for the most comfortable responding. Stimuli were presented on a fast-fade videographics adapter (VGA) screen.

Procedure

Each subject received a block of 10 practice trials and two blocks of 99 experimental trials with each responding hand. Both subjects completed the blocks in the following order: practice right, right, practice left, left, left, right hand. Each block was initiated by the experimenter. The subjects were instructed to fixate on the cross and respond as quickly as possible when they saw the stimuli, but to refrain from responding if no stimulus appeared. Responses were made by pressing the N key, with RTs recorded in milliseconds from the onset of the stimuli.
Results

Table 4.1 shows the percentage of trials on which the subjects failed to respond within 1 s if a stimulus appeared ('misses') or responded within this time frame when no stimulus appeared ('false alarms'). It is clear that both subjects responded reasonably accurately.

Table 4.2 shows median RTs under each of the stimulus conditions. Crossed-uncrossed differences (CUDs) were also computed by subtracting median RTs for uncrossed hand/field conditions (left-hand responses to unilateral LVF stimuli, right-hand responses to unilateral RVF stimuli) from median RTs for crossed conditions (right hand to LVF, left hand to RVF). The CUD can be considered a measure of interhemispheric transfer time (Poffenberger, 1912), and the values shown in Table 4.2 confirm that the CUD is elevated in callosal agenesis relative to that in normal subjects, in whom the CUD is normally between 2 and 6 ms (Aglioti et al., 1993; Berlucchi et al., 1971; Braun, 1992; Corballis, 2002; Iacoboni & Zaidel, 1995). The CUD is typically longer again in those with section of the corpus callosum.

Table 4.1  Percentages of Missed Stimuli and False Responses to Catch Trials in Experiment 1 and Experiment 2

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Left hand response, stimulus in</th>
<th>Right hand response, stimulus in</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LVFa</td>
<td>RVFa</td>
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<tr>
<td></td>
<td>LVFa</td>
<td>RVFa</td>
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<tr>
<td>Experiment 1</td>
<td></td>
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</tr>
<tr>
<td>J.P.</td>
<td>0</td>
<td>0</td>
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<tr>
<td>M.M.</td>
<td>5.00</td>
<td>1.67</td>
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</tbody>
</table>
### Table 4.2  
**Median Reaction Times (RTs) and Transfer Indices in Experiments 1 and 2**

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Left hand RT (ms)</th>
<th>Right hand RT (ms)</th>
<th>Transfer Indices</th>
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<tbody>
<tr>
<td>J.P.</td>
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<tr>
<td>M.M.</td>
<td>3.33</td>
<td>1.67</td>
<td>0</td>
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<tr>
<th>Experiment 2</th>
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<thead>
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<th>Subjects</th>
<th>Left hand RT (ms)</th>
<th>Right hand RT (ms)</th>
<th>Transfer Indices</th>
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<tbody>
<tr>
<td>J.P.</td>
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<tr>
<td>M.M.</td>
<td>3.33</td>
<td>1.67</td>
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*Percentages in these columns refer to missed stimuli*

*Percentages in these columns refer to false responses to catch trials*
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<tr>
<th></th>
<th>LVF</th>
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<td>CUD</td>
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### Experiment 1

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### Experiment 2

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<td>382</td>
<td>348</td>
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<th>M.M.</th>
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A rough measure of redundancy gain was obtained by subtracting the median RT to bilateral stimuli from the shorter of the two median RTs to unilateral stimuli, and these are also shown in Table 4.2.

TESTING THE RACE MODEL
The next question, then, is whether the redundancy gain exceeds that expected from a simple race model. If RT to bilateral presentations simply depends on the winner of a race between independent processes initiated by the unilateral stimuli, then at any given time t the probability $p_B$ that a response will have occurred is given by:

$$p_B = p_L + p_R - (p_L \cdot p_R),$$

where $p_L$ is the probability of a response having occurred to the stimulus in the LVF alone, and $p_R$ is the probability of a response having occurred to the stimulus in the RVF alone. This can be tested by plotting the cumulative probability over time of ($p_B - (p_L + p_R - p_L \cdot p_R)$). If at any point the expression exceeds zero, we can conclude that the race model is violated$^2$.

Cumulative functions were computed for each subject as follows. With each hand, each subject received 180 stimuli (plus 18 blank trials), 60 in the LVF alone, 60 in the RVF alone, and 60 bilateral pairs. RTs to the stimuli were ranked, and then assigned to 18 bins of 10, with the first bin containing the 10 shortest RTs, the second containing the 20 shortest, and so on, cumulatively. The RTs in each bin were then assigned to the three conditions (LVF, RVF, bilateral), and the numbers converted to probabilities by dividing by 60. The expression ($p_B - (p_L + p_R - p_L \cdot p_R)$) was then computed for each bin for each subject with

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$^2$ The data was also tested with the more conservative race model inequality with violations still found over all subjects and experiments
each hand in turn. Figure 4.1 shows both the cumulative RT distributions for each condition and the value of the expression \((p_B - (p_L + p_R - p_L.p_R))\) over the response bins.
Figure 4.1
Cumulative RT Distributions and Distributions of the Violation Function, defined by the expression $(p_{B} - (p_{B}L + p_{R} - p_{L}p_{R}))$, for each of the Subjects under Conditions of Luminance Contrast (Experiment 1).
It is clear that both subjects showed some violation of the race model, although the violation is marginal in the case of M.M.’s right-hand responses. Previous research using exactly the same task with 58 normal subjects, 38 women and 20 men, whose ages ranged from 19 to 51 years, showed the corresponding mean violations to be more than 1 standard deviation below zero, indicating that the redundancy effect was significantly less than that predicted by the race model (Corballis, 2002). The two subjects tested therefore show a larger summation effect than normal. Contrary to the results reported by Roser and Corballis (2002), the redundancy gain was not obviously larger in M.M. than in J.P., as predicted by the difference in the size of the anterior commissure, and in both cases the effect was somewhat less pronounced than that shown by the acallosal subject described in the study by Corballis (1998).

**Experiment 2: Equiluminance**

The next question is whether the summation effect persists under equiluminance.

**Method**

**Subjects**

The subjects were the same as in Experiment 1. All had previously taken part in that experiment.

**Stimuli and procedure**

The stimuli and procedure were identical to those of Experiment 1, except that the stimuli were pale gray against a bright yellow background, generated according to the technique described by Cavanagh, Adelson, and Heard (1992; see also Corballis, 1998). This is not only a robust technique for approximating equiluminance; it also effectively eliminates colour-defined borders detectable by the magnocellular system (Cavanagh et al., 1992).

**Results**

Table 4.1 shows the percentages of misses and false alarms. Although the percentage of false alarms was notably higher than in Experiment 1, both subjects maintained reasonably high accuracy. Table 4.2 shows the median RTs under each condition for each hand, along with measures of CUD and redundancy gain, computed as in Experiment 1. According to these measures J.P. showed a marked increase in CUD, but little change in redundancy gain, under equiluminance. M.M., in contrast, showed a marked increase in redundancy gain.

**Testing the race model**

Cumulative distributions and the expression \( \frac{p_B}{B} - (p_L + p_R - p_L p_R) \) were computed as in Experiment 1, and are plotted in Figure 4.2. In this case the results are in accord with the expectation based on the size of the anterior commissure: The violation is clearly larger in the case of M.M., whose commissure is within normal limits, than in the case of J.P., whose commissure is enlarged. Moreover, in M.M. the violation exceeds that observed in Experiment 1, consistent with evidence from another person with callosal agenesis that the violation is greater under conditions of equiluminance than under conditions of luminance contrast (Corballis, 1998). In J.P., by contrast, the violation was if anything slightly reduced...
in this experiment, despite the fact that her CUD was increased relative to that in Experiment 1.
A notable feature of the violations of the race model is that they occurred primarily toward the beginning of the cumulative distributions, that is, for shorter rather than longer RTs. At longer RTs, the value of the race-model expression \((p_B - (p_L + p_R - p_Lp_R))\) dips below zero, suggesting inhibition. This implies that there may be a delayed inhibitory influence, perhaps due to delayed interhemispheric transfer. However, this delay may not be directly related to the delay represented by the CUD. There is evidence from normal subjects that the CUD and redundancy gain are unrelated (Corballis, 2002), and in the present study the prolonged...
CUD shown by J.P. under the equiluminance condition was not accompanied by an increase in redundancy gain (which was if anything reduced relative to that under luminance contrast). Conversely, in M.M. the CUD was slightly reduced under equiluminance, yet the redundancy gain was substantially increased.

It was expected that, of the two subjects, J.P. might show the weaker redundancy gain, due to the enlargement of her anterior commissure. Although a previous study suggested that this was so (Roser & Corballis, 2002), this was not borne out by Experiment 1, in which the stimuli were shown under luminance contrast. It was, however, clearly evident in Experiment 2, where the stimuli were displayed under equiluminance. Moreover, the increase in redundancy gain under equiluminance shown by M.M. is consistent with that shown by another person with agenesis of the corpus callosum (R.B. in the study by Corballis, 1998).

It might be questioned whether J.P. failed to show enhanced redundancy gain in the equiluminance condition (Experiment 2) because of a prolonged CUD (35 ms as compared to 15 ms for M.M.—see Table 4.2), which may have attenuated any neural summation. This is unlikely, since the prolongation was restricted to the right hand (57 ms as against 13 ms for the left hand), yet Figure 4.2 shows that violation (or its lack) of the race model is about the same for the two hands. For M.M., too, the CUD under equiluminance was longer for the right hand (21 ms) than for the left hand (10 ms), yet the violation was again about the same for the two hands. Moreover, there is evidence that the CUD is uncorrelated with redundancy effects in normal subjects (Corballis, 2002), suggesting that they tap different aspects of interhemispheric transfer. It is perhaps also worth noting that the CUD was longer for the right hand than for the left hand in Experiment 1 as well as in Experiment 2, which is opposite to the result reported by Marzi et al. (1991) in a meta-analysis of results from normal subjects.

Why should redundancy gain be especially enhanced under equiluminance? There is evidence that, even in normal subjects, redundancy gain under equiluminance may be dissociated from that under luminance contrast (Corballis, 2002). In the case of callosal agenesis, inhibition of cortical activation may depend on the anterior commissure and, as explained above, its inhibitory effect may be delayed relative to that produced by callosal transfer in normals. And in some cases, such as M.M. and R.B., the inhibition may be largely restricted to the magnocellular system, and ineffective in the case of equiluminance. In cases like J.P., where the anterior commissure is enlarged, inhibitory transfer may include parvocellular information, which is why the redundancy was somewhat reduced for both luminance contrast and equiluminance (see Livingstone & Hubel, 1987, for an account of the different characteristics of the magnocellular and parvocellular systems). Previous studies (see both Chapter Three and Corballis & Finlay, 2000) have shown that J.P. is relatively unimpaired in matching colours across the visual fields, whereas M.M. performed barely above chance—although she was well above chance in matching colours within visual fields.

The enhanced redundancy gain in the split brain does not appear to depend on topographical correspondence between the visual fields (Corballis et al., 2002; Roser & Corballis, 2002), and also occurs when the stimuli are staggered in time by as much as 50 ms (Reuter-Lorenz et al., 1995). These properties suggest that the summation may occur in the reticular formation. It might arise from corticofugal activation, but the cortical response
is normally inhibited by the corpus callosum, which perhaps has to do with a focus of attention on one or other of the double stimuli, but not both. This can explain why the effect is much more pronounced in people with section of the corpus callosum. In those with callosal agenesis, the anterior commissure may take over some of this inhibitory role, so that the redundancy gain exceeds that observed in neurologically intact people, but is somewhat less than that observed in those with surgical section of the corpus callosum. This inhibition may be relatively ineffective with stimuli that are equiluminant with the background, which is why redundancy gain is further enhanced under equiluminance in at least some people with agenesis of the corpus callosum. In one of the subjects of the present study (J.P.), however, the anterior commissure was greatly enlarged, perhaps resulting in interhemispheric inhibition between equiluminant stimuli as well as between stimuli defined by luminance contrast.

An alternative explanation to this inhibitory theory is that proposed by Reuter-Lorenz et al. (1995) and later, in a slightly modified version, by Roser and Corballis (2002). This theory suggests that transfer of information via an intact corpus callosum in neurologically intact individuals ensures bilateral activation even when stimuli presentation is unilateral, essentially creating bilateral input in all conditions. In this scenario, the ‘appearance’ of a redundancy gain in the surgically or congenitally split-brain is actually due to either reduced or absent information transfer in unilateral conditions, resulting in either less or absent neural summation. RTs to unilateral input would then be slower than RTs to bilateral input, in which neural summation, presumably at a subcortical level, would be possible. This theory, unlike that based on interhemispheric inhibition in the normal brain, attributes redundancy gain in the split brain to a slowing of RTs to unilateral stimuli, rather than to a speeding of RTs to bilateral stimuli.

If this theory is correct, it may be that the anterior commissure is mediating some transfer of information in both J.P. and M.M., but that this information is restricted to the magnocellular system in M.M., hence the larger redundancy gain in the equiluminant condition. In J.P., with an enlarged anterior commissure that seems able to mediate the transfer of colour information (see Chapter Three), the anterior commissure may also have the capacity to transfer information arising in the parvocellular system.
CHAPTER FIVE

Early Visual Evoked Potentials in Callosal Agenesis

Abstract

Three subjects with callosal agenesis and twelve neurologically normal subjects were tested on a simple reaction time task, with visual evoked potentials collected using a high-density 128 channel system. Independent-components analyses were performed to isolate the visual components of interest. Contrary to previous research with acallosals, evidence of ipsilateral activation was present in all three subjects. While ipsilateral visual components were present in all four unilateral conditions in the two related acallosal subjects, in the third these were present only in the crossed visual field/hand conditions and not in the uncrossed conditions. Suggestions are made as to why these results differ from previous findings and as to the neural mechanisms facilitating this ipsilateral activation.

1 This chapter is similar to a submitted journal article: Barr, M.S., Hamm, J.P., Kirk, I.J. & Corballis, M.C. Early visual evoked potentials in callosal agenesis.
Numerous studies have shown that individuals with agenesis of the corpus callosum are able to react to stimuli displayed in the visual field opposite to the responding hand (e.g. Ettlinger et al., 1972, 1974; Sauerwein & Lassonde, 1983). As the hemisphere contralateral to that controlling the motor response receives the visual information in this scenario, this act has been presumed to involve the interhemispheric transfer of information. In individuals lacking a corpus callosum the question has been what alternative pathway or pathways they are using, with both cortical and subcortical routes being suggested for different types of information transfer.

The most likely cortical alternative to the corpus callosum is the anterior commissure, which is present in most individuals with callosal agenesis (Rauch & Jinkins, 1994), and is known to connect areas involved in processing visual information (Di Virgilio et al., 1999). As discussed by Milner (1994), some subcortical transfer must be also be possible as evidenced by the transfer of visual information, albeit limited, by some individuals with full forebrain commissurotomies. The intertectal commissure, connecting the superior colliculi, is the subcortical pathway usually suggested, although the posterior commissure, connecting the posterior pretectal nuclei, is also a possibility (Milner, 1994).

An alternative scenario, however, is that in acallosal people the incoming visual pathways may differ from normal, with ipsilateral sensory pathways allowing the information from each visual field to be available to both sides of the brain, therefore eliminating the need for hemispheric transfer. It has often been suggested that acallosals have enhanced ipsilateral projections in the somatosensory system (Nebes & Sperry, 1971; Dennis, 1976; Vanasse et al., 1994), and it therefore seems reasonable to investigate whether ipsilateral pathways also exist in the visual system.

One possibility is to use electroencephalography (EEG) to record the visual evoked potentials (VEPs) to lateralized stimuli presentations. In normal subjects this technique has identified a number of VEP components in the 50-250 ms time range, most notably the C1, P1 and N1 components (Clark, Fan & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis & Hillyard, 2001; Jeffreys & Axford, 1972a,b). The C1 component occurs at approximately 50-80 ms post-stimulus and is thought to be of primary visual (striate) cortical origin. This part of cortex is known to be retinotopically organized and the observation that the polarity and topography of the C1 potential changes with the retinal location of the stimulus is in keeping with this. The P1 component (called C2 by Jeffreys & Axford, 1972a,b) is comprised of an earlier contralateral phase and a later bilateral phase that peak around 100 and 130 ms respectively. Dipole models place the P1 generators in extrastriate cortex, in agreement with the finding that stimulus location had little effect on these potentials. The N1 is actually a collection of negative components occurring around 140 to 200 ms post-stimulus and generated from multiple sources. While different authors find components that differ slightly both temporally and spatially, there seems a general pattern of separate early contralateral components in both frontal and occipito-parietal areas, followed slightly later by a component in more temporal areas, and a late ipsilateral component in occipito-parietal/occipito-temporal areas (Clark et al., 1995; Di Russo et al., 2001).

In general, a lateralized stimulus results in activation in both hemispheres, although a consistent hemispheric difference is found, with the contralateral components having shorter latencies and larger amplitudes than ipsilateral components. It is suggested that the latency difference is due to the time required for the information to cross from the directly activated hemisphere to the indirectly activated hemisphere via the corpus callosum, and the smaller
amplitude due to the reduction in signal strength that occurs with this transfer (Rugg et al., 1985).

Three studies have previously investigated VEPs in people lacking a corpus callosum. Rugg et al. (1985) tested two acallosals and found no evidence of an ipsilateral N160 in the same time window as that found in their control sample. They concluded that this potential is generated from information transferred from the contralateral hemisphere via the corpus callosum, information unavailable in the acallosal brain. Similarly, an abstract by Mangun et al. (1991) suggests absent ipsilateral P1 and N1 potentials in four surgically callosotomized individuals, although little further detail is given. Finally, Brown et al. (1999) tested four complete acallosals, two partial acallosals (missing the posterior callosum) and one commissurotomized person and also found a lack of ipsilateral visual evoked potentials. Further analysis using latency-adjusted VEP averaging also failed to reveal any ipsilateral components (Brown et al., 1998), with the authors concluding that the integrity of the posterior callosum is necessary for the interhemispheric transfer of the P1 and N1 visual potentials.

Although Rugg et al. (1985) concluded that normal ipsilateral activation was absent in the acallosal subjects, there was evidence of ipsilateral stimulus-evoked activity at a longer latency than found in controls. The authors suggest a number of possible reasons, some artifactual and some involving compensatory commissural systems. In contrast, Brown et al. (1999) found only a positive ipsilateral wave at a slightly longer latency than the contralateral N1 in their acallosal subjects. As this wave was not seen in the callosotomized subject (whose anterior commissure is also thought to have been transected), the authors suggest that the intact anterior commissures of the acallosals may have been sufficient to mediate some transfer of information, although not the complete P1/N1 complex.

An important limitation in the two studies that included acallosal subjects, however, is that they both used only a very limited set of recording electrodes, with seven in the Rugg et al. (1985) study and three in the Brown et al. (1999) study. It is therefore possible that they may have missed ipsilateral activation if it is located even slightly differently from normal. This is a real possibility in people congenitally lacking a corpus callosum who have been shown in previous research to have remarkably little functional disconnection, implying some neural compensatory mechanism/s.

Another well-established finding regarding interhemispheric interaction is that in simple visual RT tasks, RTs are shorter to bilateral stimuli than unilateral stimuli, a phenomenon known as redundancy gain. In neurologically normal people, this redundancy gain is usually less than that predicted by simple probability summation, where the RT of two stimuli racing to be the first to arrive at a response will on average be shorter than the average RT to either stimuli presented alone (Corballis, 2002; Raab, 1962). In individuals lacking a corpus callosum, however, the redundancy gain has been found to exceed that predicted by probability summation, implying some interhemispheric neural summation of the responses to the two stimuli (Corballis, 1998; Iacoboni et al., 2000; Reuter-Lorenz et al., 1995; Roser & Corballis, 2002). This was also shown in Chapter Four with two of the three subjects tested in this experiment.

As this neural summation occurs in the absence of a corpus callosum and also following hemispherectomy (Tomaiuolo et al., 1997), the site at which it occurs is presumably subcortical. However, the testing with J.P. and M.M. described in Chapter Four has suggested that there is also a cortical role in the redundancy gain. While both subjects showed a redundancy gain exceeding that predicted by probability when the stimuli were
white dots on a black background, when equiluminant stimuli were used the effect was enhanced in M.M., who has a normal-sized anterior commissure, but not in J.P., who has an enlarged anterior commissure. It was suggested on the basis of this that the anterior commissure may have a role, relative to its size, of inhibiting cortical activation to bilateral stimuli, thereby decreasing subcortical neural summation.

This study investigates the early visual potentials in three subjects with callosal agenesis, with the aim of extending the current body of knowledge by using a dense electrode array of 128 channels, allowing a more comprehensive picture of what is occurring in the acallosal brain. A simple reaction time task was used with both unilateral and bilateral stimuli presentations and each hand used in turn.

Of the three acallosals tested, both J.P. and A.L.M. have been shown by MRI to have enlarged anterior commissures, while M.M.’s is within normal limits. Chapter Three has suggested that J.P.’s enlarged anterior commissure may play an enhanced role in the transfer of color and letter information compared to the performance of M.M., and it is possible it may also play a role here in the transfer of VEPs. Only the P1 and N1 potentials are examined in this study, as the C1 is only visible when stimuli are presented above or below the horizontal retinal midline, whereas our stimuli were all on the midline.

Method

Subjects

Three subjects with agenesis of the corpus callosum - J.P., M.M. and A.L.M., were tested. The details of these subjects are given in Chapter Two. In addition, there were twelve control subjects. All the control subjects were right-handed and participated voluntarily. There were six males and six females, with ages ranging from 20 to 43 years and an average age of 30.0 years. The aim was not to provide precise age- and gender-matched controls for the acallosal subjects, but instead to gain a general impression of how normal adults would perform.

Experimental Setup

Subjects were seated in a quiet, electrically shielded room and monitored continuously with a closed circuit video camera. The experiment was run using a Pentium II/200 computer and stimuli were displayed on a Phillips flat-screen monitor with a resolution of 640 x 480 pixels. A chin rest was used to minimize head movements and ensure that the subject’s eyes were at a constant distance from the computer screen. TTL pulses generated via the parallel port of the display computer provided synchronization of stimulus and response events with EEG acquisition. Millisecond timing routines and synchronization of the triggers with the top of the stimulus are described in Hamm (2001). The methods developed by Heathcote (1988) were used to synchronize stimulus presentation with the raster scan.

EEG

The EEG was recorded using Electrical Geodesics 128 channel Ag/AgCl electrode nets (Tucker, 1993). Electrode positioning on the head is shown in Figure 5.1. For individual subjects the position of Cz is calculated using anatomical measurements. All other electrode positions are determined by the layout of the sensor net, with the nasion electrode and ear
markers on the net helping to ensure correct positioning. It should be noted here that subject A.L.M. had an unusually high cranial vault, which meant that the electrodes did not extend as low on the head as normal, with the ear markers sitting approximately 1.5 cm higher than is customary.
Leave room about here for figure 5.1
During testing the EEG was recorded continuously with a sampling rate of 250 Hz and an analogue bandpass of 0.1-100 Hz. The signal was amplified using Electrical Geodesics amplifiers (200M input impedance) and was recorded using Electrical Geodesics acquisition software on a Power Macintosh 9600/200 computer with a National Instruments PCI-1200 12 bit analogue to digital conversion card. Electrode impedance ranged from 10 to 50kΩ. A common vertex (Cz) reference was used during acquisition.

**Stimuli**

The stimuli consisted of solid white circular discs that were flashed onto a black background for 133 ms. They had a diameter spanning 0.88° of visual angle, and appeared 5.11° from a central fixation cross, either unilaterally to the left or right of the cross, or bilaterally. The computer screen was viewed from a distance of 57 cm, so that 1 cm on the screen represented 1° of visual angle.

For the control subjects, there were 200 trials in each block; 50 unilateral trials to the left visual field (LVF), 50 unilateral trials to the right visual field (RVF), 50 bilateral trials where stimuli appeared in both visual fields simultaneously, and 50 'catch' trials in which no stimuli were presented. However, the number of trials in each condition was increased for the acallosal subjects to ensure that sufficient numbers of trials were available for analysis. M.M. and J.P. were presented with 400 trials (100 trials in each condition), while A.L.M. was presented with 300 trials (75 in each condition). Trial presentation was completely randomized and subjects were given the opportunity to take a break every 50 trials.

On initiation of a block of trials, a fixation cross appeared in the middle of the screen and remained there for the duration of the block (except during break periods). After 1000 ms, a 100-Hz tone sounded for 200 ms, and then on trials where stimuli were presented, the stimuli appeared 500 ms after tone onset. The subject was allowed 1000 ms in which to respond. On catch trials, the subject was required to withhold the response for 1500 ms following the onset of the tone. After either the subject’s response, or the ‘time-out’ period on catch trials, there was a further period of 1000 ms before the tone sounded for the next trial. A correct response resulted in the reappearance of the fixation cross; an incorrect response led to a tone followed by the fixation cross. Any error trials, that is either responses to catch trials or non-responses to trials where stimuli were presented, were rerun.

**Procedure**

The task comprised one block of experimental trials preceded by one block of 16 practice trials for each responding hand. Half of the control subjects responded first with the left hand (LH), while the other half responded first with the right hand (RH). For the acallosal subjects, M.M. and A.L.M. responded first with their LH, while J.P. responded first with her RH.

Each block was initiated by the experimenter. Subjects were instructed to fixate on the cross and respond as quickly as possible when they saw the stimuli, but to refrain from responding if no stimulus appeared. Responses were made using the index finger on a response box positioned at the subject’s midline and angled for the most comfortable responding. The subject’s wrist and forearm were lightly restrained to reduce the likelihood of muscles other than the distal finger muscles being involved in responding. RTs were recorded in milliseconds from the onset of the stimuli.
Results

Behavioural Statistics

Table 5.1 shows the percentage of errors under all conditions. It is clear that all subjects responded highly accurately, except that A.L.M. incorrectly responded to the catch trials approximately 11 percent of the time. These errors occurred equally with both hands and appeared to be due to lapses in concentration.

Table 5.1 Percentages of Missed Stimuli and False Responses to Catch Trials

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Left hand response, stimulus in</th>
<th>Right hand response, stimulus in</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LVF&lt;sup&gt;a&lt;/sup&gt;</td>
<td>RVF&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Both&lt;sup&gt;a&lt;/sup&gt;</td>
<td>LVF&lt;sup&gt;a&lt;/sup&gt;</td>
<td>RVF&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>J.P.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>M.M.</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<sup>a</sup> LVF: Left Visual Field, RVF: Right Visual Field, Neither: Neither hand responded.

<sup>b</sup> Values in parentheses indicate lapses in concentration.
<p>| | | | | |</p>
<table>
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<tbody>
<tr>
<td>5.00</td>
<td>1.67</td>
<td>0</td>
<td>0</td>
<td>1.67</td>
</tr>
<tr>
<td>0</td>
<td>1.67</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>A.L.M.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.32</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10.71</td>
</tr>
<tr>
<td></td>
<td>1.32</td>
<td>1.32</td>
<td>0</td>
<td>11.76</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Controls</td>
<td>Mean</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.32</td>
<td>0.49</td>
<td>0.48</td>
<td>2.05</td>
<td>0.16</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2.68</td>
</tr>
</tbody>
</table>

*aPercentages in these columns refer to missed stimuli

*bPercentages in these columns refer to false responses to catch trials
Table 5.2 shows median RTs under each of the stimulus conditions. Crossed-uncrossed differences (CUDs) were calculated by subtracting median RTs for uncrossed hand/field conditions (LVF stimuli responded to by the LH, RVF stimuli responded to by the RH) from median RTs for crossed conditions (LVF/RH, RVF/LH). The mean CUD of 3 for the control subjects is within the range of 2-6 ms derived in previous experiments (see Braun, 1992 for a review), and all three acallosals have CUDs longer than the controls, a finding that has been shown previously both with other acallosal people (e.g. Aglioti et al., 1993; Caillé et al., 1999, Clarke & Zaidel, 1989; Corballis, 1998) and with two of our subjects J.P. and M.M. (Barr & Corballis, 2003). However, while the CUD of M.M. is within 1 SD of the controls’ mean, the CUD is not considered a very stable measure unless large numbers of trials are performed. Iacoboni and Zaidel (2000) suggest that to obtain a reproducible CUD in a single individual, approximately 2000 trials are needed. As the individual acallosals tested here had 400 to 600 trials the CUD needs to be interpreted with caution.

Table 5.2 Median Reaction Times (RTs) and Transfer Indices

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Left hand RT (ms)</th>
<th>Right hand RT (ms)</th>
<th>Transfer Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>LVF</td>
</tr>
<tr>
<td>J.P.</td>
<td>304</td>
<td>300</td>
<td>287</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M.M.</td>
<td>296</td>
<td>281</td>
<td>289</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
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</table>
A rough measure of redundancy gain was also obtained by subtracting the median RT to bilateral stimuli from the shorter of the two median RTs to unilateral stimuli, and these are also shown in Table 5.2.

Testing the Race Model

The next question, then, is whether the redundancy gain exceeds that expected from a simple race model. If RT to bilateral presentations simply depends on the winner of a race between independent processes initiated by the unilateral stimuli, then at any given time $t$ the probability $p_B$ that a response will have occurred is given by:

$$p_B = p_L + p_R - (p_L \cdot p_R),$$

where $p_L$ is the probability of a response having occurred to the stimulus in the LVF alone, and $p_R$ is the probability of a response having occurred to the stimulus in the RVF alone. This can be tested by plotting the cumulative probability over time of $(p_B - (p_L + p_R - p_L \cdot p_R))$. If at any point the expression exceeds zero, we can conclude that the race model is violated.

Cumulative functions were computed for subjects as follows. With each hand, each control subject received 150 stimuli (plus 16 blank trials), 50 in the LVF alone, 50 in the RVF alone, and 50 bilateral pairs. RTs to the stimuli were ranked, and then assigned to 15 bins of 10,
with the first bin containing the 10 shortest RTs, the second containing the 20 shortest, and so on, cumulatively. As J.P. and M.M. had 100 trials in each stimuli condition, their RTs were assigned to 30 bins of 10, while A.L.M. with 75 trials in each condition had 22 bins of 10 and a 23rd bin with the remaining 5 trials. The RTs in each bin were then assigned to the three conditions (LVF, RVF, bilateral), and the numbers converted to probabilities by dividing by the number of trials in each condition. The expression \((p_B - (p_L + p_R - p_{L,R}))\) was then computed for each bin for each subject with each hand in turn. Figure 2 shows the value of the expression \((p_B - (p_L + p_R - p_{L,R}))\) or ‘violation’ over the response bins for both the controls and individual acallosal subjects.

Figure 5.2 shows that the values of the expression were below zero for all bins for the averaged control data, indicating that the redundancy gain is actually less than that predicted by the race model. In contrast, all three acallosal subjects clearly showed an enhanced redundancy gain, although the violation was unusual in the case of A.L.M.’s left-hand responses as the violation did not appear until the tenth bin. Again, this confirms previous findings with acallosal subjects in general (e.g. Corballis, 1998; Iacoboni et al., 2000) and also the findings with J.P. and M.M. in Chapter Four.
Visual Evoked Potentials EEG files were segmented offline with respect to event triggers, with the data presented here cut into 1700 ms epochs beginning 700 ms before onset of the visual stimulus. Segments containing artefact (eye-movement, muscle, etc) were rejected and omitted from the ERP calculation. On average, about 26 percent of the control subjects' trials were rejected for violating these criteria, while 19 percent for M.M., 24 percent for J.P. and 21 percent for A.L.M. were rejected. Rejection rates were high for some individual subjects as they had difficulty in refraining from blinking for the long periods required. Remaining epochs were then averaged into groups based on stimulus condition – LVF trials, RVF trials and bilaterally presented stimuli trials – for each responding hand. Grand averages were constructed for the control subjects' data, while the three acallosal subjects were analyzed individually. To further reduce high-frequency noise the averaged epochs were low-pass filtered at 30 Hz using custom-built visualization software (Hamm, 2000). Data were referenced to average reference.
The acallosal subjects were particularly difficult to analyze as their data were exceptionally noisy with large amounts of alpha waveforms that masked the potentials of interest. Further analysis was therefore carried out in order to isolate the components of interest from this noise. Firstly, principle component analyses (PCAs) were performed for each average to ascertain the number of components that individually explained at least 1 percent of the variance in the data set. Independent components analyses (ICA) (Makeig, Bell, Jung & Sejnowski, 1996) were then carried out on the averaged segments using MATLAB 5.3 software, with the number of independent components set to the number of principle components detected above. These components were visually inspected and only those representing early visual activity were selected for further investigation. Topographic scalp maps of the data were made using EMSE software and Loreta (low-resolution tomographical analysis; Pascual-Marqui, Michel & Lehmann, 1994) software was used for source estimation. To illustrate, Figure 5.3 shows the overlaid raw waveform and the six independent components for the control subjects’ grand averaged data for the bilateral stimuli/LH condition, while Figure 5.4A
shows the scalp map for the raw waveform. Visual inspection suggested that in this particular case component 3 was the only component of interest, with scalp maps showing this to have a prominent negative peak with a bilateral occipital distribution at a latency of 164 ms (see Figure 5.4B). Components 5 and 6 were identified as noise, 2 as an auditory component in response to the tone, and 1 and 4 as late visual components (P324 and P240 respectively) outside of the time of interest.

Figures 5.5 to 5.8 show the earliest identifiable visual components for each stimulus-hand condition for the averaged data from the control subjects and each individual acallosal subject. For each condition three figures are shown: a topographical scalp map projecting the component onto a spherical head, and two horizontal MRI slices from a standard brain showing the main sources of this activation. Tables 5.3 to 5.6 give the complete list of sources of each component with their coordinates in Talaraich space. It should be noted that while Talaraich coordinates are given for the acallosal subjects as well as the controls, the main focus is whether sources are localized to the left, right or both hemispheres. Care is required in trying to locate more specifically than this for the acallosal subjects, as it is possible that their pathology may have altered the geometry or conductivity of their VEP generators. The Loreta source localization program assumes a standard head model whereas the acallosals may have quite different brain organization and structure. For example they may have a greater proportion of CSF because of the missing callosal brain tissue which may alter the conduction of electrical activity to the scalp.
CONTROL SUBJECTS
The results for the control subjects can be seen in Figure 5.5 and Table 5.3. In all four unilateral conditions the scalp maps show a visual component with a negative polarity in the latency range 152-156 ms post-stimulus. While these maps suggest that the components may have a purely contralateral locus, source localization shows that there is also ipsilateral activation, although in all but the RVF/LH condition the contralateral sources are clearly larger. The components in the bilateral conditions are also negative, with latencies of 164 and 160 ms for the left and right hand respectively. They also have similar source loci to the unilateral components, the difference being that there are also two clearly distinguishable areas of activation on the scalp maps, one in each hemisphere. The distribution and latency of these 6 components suggests that they are part of the N1 complex discussed by Clark et al. (1995) and Di Russo et al. (2001).

J.P.
Figure 5.6 and Table 5.4 show the results for the acallosal subject J.P. As for the control subjects, the earliest identifiable visual components are also N1 components, although at slightly later time points (164-180 ms). J.P. also shows a similar pattern to controls on the scalp maps with clear contralateral visual components in the four unilateral conditions and bilateral components to bilateral stimuli, although source localization data presents a different pattern. While the two crossed conditions (LVF/RH and RVF/LH) and the two bilateral conditions show bilateral sources, the two uncrossed conditions (LVF/LH and RVF/RH) have only contralateral sources.

M.M.
The results for M.M. can be seen in Figure 5.7 and Table 5.5. The earliest identifiable visual components, unlike those of the other subjects, were positive with latencies between 164-180 ms. While the peak latencies of these components are outside of the range usually seen for P1s, both the scalp maps and source localization data show these components to be in visual areas and as M.M.’s reaction times are slowed compared to controls, it may be that for M.M. the slowing occurs early on in the visual pathways. Both the scalp maps and the source localization data clearly show bilaterally produced components for all stimuli presentations, but in the unilateral conditions the activation tends to be larger in the hemisphere contralateral to the stimulus presentation.

A.L.M.
Figure 5.8 and Table 5.6 show the results for A.L.M. These results had a similar topographical pattern to control subjects, although at much longer latencies. The earliest identifiable components were negative and although unilateral on the scalp in response to unilateral stimuli, all 6 conditions were bilaterally sourced. The only clear asymmetry was that for LVF stimuli the activation tended to be larger in the right hemisphere. Although the peak latencies were much longer than controls at 216 ms for all conditions, the components are distributed similarly enough to suppose that they are also part of the N1 complex.
Leave room for Figure 5.5
Leave room for Figure 5.6
Leave room for Figure 5.7
Leave room for Figure 5.8
Leave room for Table 5.3
Leave room for Table 5.4
Leave room for Table 5.5
Leave room for Table 5.6
Discussion

This experiment found that in all three acallosal subjects unilateral visual information was available to both hemispheres in some instances. In two of the subjects this occurred in all conditions, while in one subject this occurred only in the bilateral conditions or in crossed hand/field conditions. These findings are at odds with those of earlier studies with acallosal subjects that concluded there was no evidence of ipsilateral N1s in their acallosal subjects (Rugg et al., 1985; Brown et al., 1998; Brown et al., 1999).

Consistent with previous research, all three acallosal subjects showed an enhanced redundancy gain on the reaction time data whereas there was no evidence of a redundancy gain above that explained by simple probability models in the control subjects. The control subjects also showed the expected pattern in their VEP data, with ICA analysis isolating N1 components in all stimulus/hand conditions. Further analysis using source localization revealed these components to have bilateral sources, suggesting that for these neurologically normal subjects the visual information in the unilateral stimulus conditions is transferred interhemispherically prior to the latency at which these components occur.

It was on the VEP data that our results with the acallosal subjects differ both from controls and from what has been previously found in the acallosal literature. A.L.M. was most like controls with a similar pattern of bilaterally sourced N1 components for all conditions, but at a much longer latency, around 50 ms later in most conditions. However, her reaction times were faster than those of the control subjects in all but one condition, and the latencies of her N1 potentials were quite close to the reaction times, and in one condition they were identical. As there is a corticomuscular conduction time of approximately 20 ms to the first dorsal interosseous (Kloten, Meyer, Britton & Benecke, 1992), this suggests that the information must be available bilaterally earlier than the time of the N1 component identified.

M.M. also showed bilateral early VEPs but in her case the earliest identifiable component was the P1. Like A.L.M., the latencies of these components are longer than is usual for P1s to simple stimuli, but it is clear that information was available to both the contralateral and ipsilateral hemispheres from early on in visual processing.

J.P. was the only subject not to show bilateral VEPs in all conditions. Bilateral components were seen only in the bilateral conditions or in crossed hand/field conditions where the hemisphere receiving the visual information was not the hemisphere that controlled the finger making the response. When the hemisphere receiving the visual input was the same as that making the response there was no sign of interhemispheric transfer. For J.P. it may be that while interhemispheric transfer of visual information is possible, it is not as automatic as for neurologically normal individuals and only occurs when the information is needed by the ipsilateral hemisphere.

There may be a number of reasons why ipsilateral potentials have not been found previously. Firstly it is possible that the other studies may have failed to find activation in the ipsilateral hemisphere for methodological reasons. As discussed earlier, the previous acallosal studies had very few recording electrodes and it is possible that ipsilateral activation may have been missed. Secondly, as this research attests, acallosal subjects cannot be considered a homogeneous group and it is possible that the two subjects tested by Rugg et al. (1985) and the four tested by Brown et al. (1999) were different from the three tested here. Two of the three tested here (M.M. and A.L.M.) were related and possibly more likely to have a similar pathology, and indeed their results were more similar to each other than to J.P.’s results.
Also of importance is that while Brown et al. (1999) found no evidence of ipsilateral activity at any latency, Rugg et al. (1985) were only focused on the presence or absence of a normal ipsilateral N1 at the same latency as found in their control subjects. Although they did not find any evidence of this, these results do not necessarily imply that there is no transfer of visual information in acallosals. If other, possibly less efficient, mechanisms are used by the acallosal brain it is possible that the ipsilateral potential, if it exists, may look quite different. It may have a different latency, as has been found in this study, and even a different scalp distribution.

Without further research we can only speculate as to the mechanism/s generating the ipsilateral activation in these acallosals. At least for M.M., ipsilateral activation can be seen early on in visual processing in the P1 component. As the P1 is thought to be generated in extrastriate cortex, and the splenium is the only cortical commissure connecting these areas, either the transfer must be subcortical and then projected to the cortex, or else there must be compensatory ipsilateral sensory pathways. While J.P. and A.L.M. may also have bilateral P1s, as these were not isolated by the ICA methodology we can only be sure that ipsilateral information was available at the time of the N1 component. As both of these subjects had enlarged anterior commissures it is possible that they may have facilitated interhemispheric transfer. The N1 potential has multiple sources including the temporal lobes, areas the anterior commissure is known to connect.

In summary, it is clear that the acallosal subjects tested here have developed neural mechanisms to compensate for their lack of a corpus callosum. It is also clear that each individual has done this in different ways and that acallosals should be considered separately when discussing their interhemispheric transfer abilities.
Figure 5.1 Electrode Layout of 128 Channel Sensor Net with Recording Electrodes shown in boxes. Anatomical Landmarks without Recording Electrodes are indicated by circles. Those Electrodes closest to Standard 10-20 Positions (Jasper, 1958) are labelled in red. LIO, Left Infraorbital; RIO, Right Infraorbital; LOC, Left Outer Canthal; ROC Right Outer Canthal; Iz, Inion; Nz, Nasion; M1, Left Mastoid; M2, Right Mastoid. Ground Electrode is located above the Nasion, between Electrodes 22 and 14.
The Earliest Identifiable Visual Components are shown for each Stimulus/hand Combination for the Averaged Data from the Control Subjects. For each Condition three figures are shown: a Topographical Scalp Map projecting the Component onto a Spherical Head, and two Horizontal MRI Slices from a Standard Brain showing the Main Sources of this Activation. The label above the Scalp Map indicates the Polarity of the Component (N = Negative) and the Latency of the Component from Stimuli Onset.

Figure 5.5
Figure 5.6  The Earliest Identifiable Visual Components are shown for each Stimulus/hand Combination for J.P. For each Condition three figures are shown: a Topographical Scalp Map projecting the Component onto a Spherical Head, and two Horizontal MRI Slices from a Standard Brain showing the Main Sources of this Activation. The label above the Scalp Map indicates the Polarity of the Component (N = Negative) and the Latency of the Component from Stimuli Onset.
Figure 5.7 The Earliest Identifiable Visual Components are shown for each Stimulus/hand Combination for M.M. For each Condition three figures are shown: a Topographical Scalp Map projecting the Component onto a Spherical Head, and two Horizontal MRI Slices from a Standard Brain showing the Main Sources of this Activation. The label above the Scalp Map indicates the Polarity of the Component (P = Positive) and the Latency of the Component from Stimuli Onset.
Figure 5.8  The Earliest Identifiable Visual Components are shown for each Stimulus/hand Combination for A.L.M. For each Condition three figures are shown: a Topographical Scalp Map projecting the Component onto a Spherical Head, and two Horizontal MRI Slices from a Standard Brain showing the Main Sources of this Activation. The label above the Scalp Map indicates the Polarity of the Component (N = Negative) and the Latency of the Component from Stimuli Onset.
### Table 5.3  
Brain Regions Activated in each Stimulus/hand Condition for the Control Participants. Anatomical Stereotaxic Coordinates are in Millimeters (R=Right, L= Left). Activations in **Bold** Type indicate Maxima in each Hemisphere.

<table>
<thead>
<tr>
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<th>Right Hand Responding</th>
<th>Coordinates</th>
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<td><strong>LVF Stimuli</strong></td>
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<td>R inferior occipital gyrus</td>
<td>17 -10 -95 -13  2.77 e-0003</td>
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<td><strong>RVF Stimuli</strong></td>
<td></td>
</tr>
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<td>L precuneus/PL</td>
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<td>R superior temporal gyrus</td>
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<td>L fusiform gyrus/TL</td>
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<td>R cuneus/OL</td>
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Table 5.4  Brain Regions Activated in each Stimulus/hand Condition for Participant J.P.  Anatomical Stereotaxic Coordinates are in Millimeters (R=Right, L=Left).  Activations in **Bold** Type indicate Maxima in each Hemisphere.

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<th>Coordinates</th>
<th>Loreta Value</th>
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<td><strong>LVF Stimuli</strong></td>
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<td>7.19 e-0003</td>
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### Table 5.5  Brain Regions Activated in each Stimulus/hand Condition for Participant M.M.  Anatomical Stereotaxic Coordinates are in Millimeters (R=Right, L=Left).  Activations in **Bold** Type indicate Maxima in each Hemisphere.

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<td><strong>Bilateral Stimuli</strong></td>
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Table 5.6  Brain Regions Activated in each Stimulus/hand Condition for Participant A.L.M.  Anatomical Stereotaxic Coordinates are in Millimeters (R=Right, L=Left).  Activations in **Bold** Type indicate Maxima in each Hemisphere.

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CHAPTER SIX

General Discussion

This study has added to our understanding of interhemispheric transfer in agenesis of the corpus callosum. Firstly, it confirmed previous findings that the disconnection syndrome seen so strikingly in surgically split-brain people is much reduced in the congenitally split brain. Secondly, it extended research on the acallosal brain with the testing of one subject never before reported in the literature. Finally, it provided further information on the neural compensatory mechanisms that may be utilized by these individuals in the absence of the corpus callosum.

The first set of experiments, detailed in Chapter Three, were designed to determine what types of visual information can be integrated interhemispherically in individuals with callosal agenesis. As J.P. and M.M. have a substantial difference in the size of their anterior commissures, a further conjecture was that J.P.’s enlarged anterior commissure may be able to compensate for an absent corpus callosum better than M.M.’s normal-sized anterior commissure.

A number of different tasks requiring both intra- and inter-hemispheric matching were presented to the subjects. The tasks involved matching on the basis of either colour, letter, spatial location or alignment information. While J.P. showed no signs of disconnection on any of the tasks, M.M.’s performance was significantly worse (and yet still above chance) on the interhemispheric matching of both colour and letter information. Both subjects performed quite poorly overall on the tasks involving spatial location and alignment.

These results suggest that J.P.’s enlarged anterior commissure was able to compensate for an absent corpus callosum on the colour and letter tasks. As discussed in Chapter One, the anterior commissure connects areas of the ventral visual pathway which process identity or “what” information (Di Virgilio et al., 1999). The enlarged anterior commissure of J.P. may therefore be able to mediate the transfer of a greater quantity or quality of identity information, such as the colour, shape or name of an object, than the normal-sized commissure of M.M. For M.M., transfer of limited identity information may be mediated either by subcortical pathways such as the intertectal commissure, which is not known to transfer complex shape information, or by a less richly connected anterior commissure. As both subjects showed no disconnection on the spatial tasks and the anterior commissure does not connect areas of the cortex known to be involved with visuospatial functions, it is suggested that this function may be mediated by subcortical pathways such as the intertectal commissure which joins the superior colliculi. The superior colliculi are part of the subcortical visual system and are known to have retinal input and to be retinotopically organized (Meredith & Stein, 1990). They also have connections to parietal visual association cortex, part of the dorsal visual pathway which processes spatial or “where” information (Milner & Goodale, 1995).

Chapter Four reports two experiments designed to extend the current research on the redundancy gain in the acallosal brain. Both experiments used a simple reaction-time paradigm, with the stimuli presented under conditions of luminance contrast in the first
experiment and under conditions of equiluminance in the second. Both J.P. and M.M. showed an enhanced redundancy gain to bilateral stimuli in the first experiment in keeping with previous research with acallosals. However, while this redundancy gain was further enhanced in M.M. under conditions of equiluminance, it was if anything reduced in J.P.

As in Chapter Three, it was again suggested that in the equiluminant condition the enlarged anterior commissure of J.P. may be able to mediate more of the functions of the absent corpus callosum than the normal-sized anterior commissure of M.M. Depending then on whether the dual-attention theory or that of Reuter-Lorenz et al. (1995) and Roser and Corballis (2002) is correct, the anterior commissure may be either inhibiting or mediating, relative to its size, a transfer process affecting subcortical neural summation.

The study described in Chapter Five was designed to replicate the simple reaction-time task used in Experiment One of Chapter Four whilst simultaneously providing event-related potential data. Both of the previous studies investigating early visual evoked potentials in acallosal subjects had suggested that there is only contralateral visual activation to unilateral stimulus presentations (Brown et al., 1999; Rugg et al., 1985), at odds with the findings in neurologically intact individuals of a delayed ipsilateral activation. This study was designed both to extend the research to three more subjects and also to address any methodological limitations of the previous research by using a high-density, 128-electrode EEG system that allows a more extensive coverage of the scalp area.

In contrast to what had been found previously, this experiment found evidence of ipsilateral activation in all three acallosal subjects tested. For M.M. and A.L.M. this occurred across all stimuli conditions, while for J.P. it occurred only on the bilateral and crossed hand/field conditions. A number of reasons were suggested for the difference between these results and those found previously. Firstly, the small number of electrodes used in the Rugg et al. (1985) and Brown et al. (1999) studies (seven and three respectively) may have led to ipsilateral activation being missed. It is also possible that the ipsilateral potential may be located differently from the normal brain, and as found in this study, it may also have a different latency, factors suggesting that a broader set of criteria may be needed when looking for ipsilateral activation. Finally, different acallosal subjects appear to have compensated for the lack of a corpus callosum in different ways, and it is therefore possible that the three subjects tested here have developed mechanisms that differ from those in the six subjects tested previously.

**Individual Differences in Compensation**

It is becoming clear from the literature on people with agenesis of the corpus callosum that they cannot be considered a homogeneous group. Although there are similarities in that many people with this condition have Probst’s bundles and some associated decrease in mental functioning (Wisniewski & Jeret, 1994), there are many differences as well. Also, while the Aicardi, Andermann, Shapiro, Acrocallosal and Menkes Syndromes are usually comorbid with callosal agenesis, there are many other disease entities that are also seen with rates of callosal agenesis higher than can be explained solely by chance (see Wisniewski & Jeret, 1994). It is important, therefore, to keep in mind the aetiology, associated pathologies and clinical presentation of those being tested when looking for similarities in their cognitive functioning.

There are a number of possible compensatory mechanisms that may reduce the disconnection between the cerebral hemispheres in the absence of the corpus callosum. These have been discussed in detail in Chapter One, but include enhanced ipsilateral sensory
or motor pathways, and the use of non-callosal pathways such as the anterior commissure or the subcortical intertectal commissure.

For as yet unknown reasons, different mechanisms may be operating in different individuals with resulting differences in the pattern of disconnection deficits. In order to understand the nature of any one individual’s compensation extensive case studies are suggested. By gathering comprehensive information about their abilities and deficits we can build up a clear picture of what that person’s pattern of disconnection is and make reasonable speculations about their mechanisms of compensation. Although the three acallosal subjects examined in this thesis were not investigated using a case study approach, it is important to collect together all that is known of each person. Doing this may well reveal patterns in their cognitive presentation as well as suggest areas of future examination. Therefore each of the subjects will now be examined in turn.

Case Studies

J.P.

As described more completely in Chapter Two, J.P. is a woman who was aged in her early-to-mid-thirties during the time of the testing described in this thesis. She was diagnosed with complete callosal agenesis by CT scan in 1998 after presentation with medical problems that have since been resolved. An MRI scan in 1999 confirmed diagnosis and also revealed prominent Probst’s bundles and a greatly enlarged anterior commissure. J.P.’s functioning on the WAIS-III was in the borderline and extremely low ranges, although an episode of major depression at the time of testing may have deflated the scores. J.P. is right-handed with a laterality quotient of 77 on the Edinburgh Handedness Inventory.

Besides the articles stemming from work presented in this thesis, there have now been two other articles published with data from J.P. (see Roser & Corballis, 2002; Roser & Corballis, 2003). At present, therefore, the data available to build up a comprehensive picture of her disconnection syndrome is still limited. The only same-different tasks that J.P. has been tested on are those described in Chapter Three. The results of these experiments suggest that J.P. is able to transfer colour and letter information interhemispherically. Her performance on the colour-matching task was indistinguishable from that of the control sample and, while performance on the two letter-matching tasks was somewhat depressed compared to controls, this was not due to any disconnection between the hemispheres. On the basis of these results it was hypothesized (for a number of reasons discussed both above and in Chapter Three) that her enlarged anterior commissure may be mediating the transfer of this information.

While J.P.’s performance on the dot-location and line-alignment tasks was depressed compared to controls, again there were no signs of worse performance on the interhemispheric compared to the intrahemispheric conditions. As the anterior commissure does not connect areas known to be involved in visuospatial functions, it was suggested that the intertectal commissure, connecting the superior colliculi, was able to transfer a degraded form of this type of information.

The other four studies that have involved J.P. have all used simple reaction-time tasks. In Chapters Four and Five in this thesis and in the Roser and Corballis (2003) study, stimuli were presented unilaterally to either the left or right visual field or bilaterally to both visual fields. In the Roser and Corballis (2002) study unilateral or bilateral stimuli were again presented, but the stimuli could be presented in either of two positions in each visual field.
allowing for bilateral conditions that were either symmetrical or asymmetrical around the vertical meridian. All four studies found evidence for an enhanced redundancy gain in J.P., although in the Roser and Corballis (2002) study it was not significantly different from the control data when averaged over all stimulus conditions. Further, this redundancy gain was not affected by manipulations of the stimuli in any of the studies. While this was also true of the other congenitally- and surgically-split subjects in the Roser and Corballis (2002) study, this was not the case in Chapter Four where the second acallosal subject, M.M., had a further enhancement of the redundancy gain under conditions of equiluminance. The results of Chapter Five provided evidence of bilateral visual evoked potentials to unilateral stimuli presentations in J.P., suggesting either that the transfer of visual information between hemispheres occurs through a non-callosal route or that ipsilateral sensory pathways have developed, allowing information to be available to both hemispheres. As J.P. differed from the other two acallosal subjects (who are mother and daughter) in that bilateral components were identified only in the bilateral or crossed hand-field conditions, it is suggested that interhemispheric transfer is the most likely explanation. Activation was only seen in the ipsilateral hemisphere when its presence was necessary to complete the task, i.e. the ipsilateral hemisphere was the one controlling the motor response, and it seems unlikely that if ipsilateral sensory pathways were the compensatory mechanism that they would be influenced by this downstream prerequisite. J.P.’s anterior commissure may be the compensatory mechanism mediating this transfer, as it is known to be enlarged and has already been proposed as a compensatory mechanism in Chapters Three and Four. In Chapter Three it has been implicated in the transfer of colour and letter information, far more complex information than need be transferred in this task. Further, the ipsilateral components identified in J.P. were N1s, at latencies between 164 and 180 ms post-stimulus. The N1 is known to have multiple generators, some of these located in the temporal lobes (Clark et al., 1995; Di Russo et al., 2001), areas which are connected, in part, by the anterior commissure. In summary then, J.P.’s enlarged anterior commissure is posited as the compensatory mechanism in all three experimental chapters in this thesis. Further testing with other types of tasks will add more information and hopefully allow more definitive conclusions to be reached. For example can digit and quantity information be transferred? What about more complex tasks such as shape- and face-matching? Also, as performance by both acallosal subjects on the visuospatial tasks in Chapter Three was depressed compared to controls, it would be expedient to test these functions further to see how they perform on other tests tapping similar abilities.

M.M.

M.M. is a woman who was aged in her late thirties to early forties during the time of the testing described in this thesis. A brief description follows, with more detailed information contained in Chapter Two. M.M. was assessed for agenesis of the corpus callosum, after her fifth child, A.L.M., was diagnosed with the condition as a newborn. Her fourth child has since also been diagnosed. M.M. was discovered as having complete callosal agenesis by MRI scan, which also revealed prominent Probst’s bundles. There were no other cerebral abnormalities and M.M.’s anterior commissure was within normal size limits. Her functioning on the WAIS-R was in
the borderline and low-average ranges, and she is right-handed with a laterality quotient of 64 on the Edinburgh Handedness Inventory.

Besides the work presented in this thesis, there have been four other articles published with data from M.M. (Corballis & Finlay, 2000; Finlay et al., 2000; Roser & Corballis, 2002; Roser & Corballis, 2003). Corballis and Finlay (2000) tested M.M. and her two acoalous daughters on their ability to integrate colour, letters, digits and words across the midline. M.M. had little difficulty in reading six-letter words that straddled the midline and was above chance at making same-different judgements about bilaterally presented digits. Curiously, however, while she was highly accurate at making same-different judgements about bilaterally presented letters when the pairs were 5.18 cm apart centred about the midline, her performance dropped below chance when the letters were changed to 15.54 cm apart, even though this was still closer than the digits which were 17.27 cm apart. M.M. was also unable to perform above chance on the interhemispheric matching of colour.

These results may be explained together with those of Chapter Three of this thesis where M.M. showed a significant interhemispheric disconnection on the matching of colour and letters. While the letters were only spaced 5.70 cm apart and the results should be closer to the 5.18 cm spaced condition in the Corballis and Finlay (2000) study, the addition of a third letter and the use of both upper and lowercase versions of those letters makes the tasks more difficult. As the Corballis and Finlay (2000) task could be performed through the transfer of only binary information (as only uppercase ‘A’s and ‘B’s were used), it may be that these results fit on a continuum of task difficulty with stimulus number and eccentricity as factors. However, this is difficult to reconcile with her above-chance performance on the same-different digits task. As there were eight digits in the stimulus set and the stimuli were even more eccentric, this task should have been more difficult than it was. It maybe that digits are a unique case in that they are more commonly seen as single items than letters, which usually appear as part of a word, and are therefore easier to transfer.

As the only known neuroanatomical difference between J.P. and M.M. is in the size of their anterior commissures, it is suggested that M.M.’s averaged-sized commissure is unable to mediate the transfer of the same quantity or quality of information as that of J.P.’s. If we accept that the transfer of binary information is sufficient to explain the high level of performance in the 5.18 cm spaced experiment in Corballis and Finlay (2000), it appears that little colour or letter information can be transferred interhemispherically. This may be due to either transfer through a less richly connected anterior commissure or the intertectal commissure connecting the superior colliculi, a pathway not known to transfer complex shape information.

Like J.P., M.M.’s performance on the dot-location and line-alignment tasks in Chapter Three was depressed compared to controls, with her responding at below chance levels on the line-alignment task. As suggested for J.P., it may be that the intertectal commissure connecting the superior colliculi is able to carry a degraded form of this type of information, but in M.M.’s case does not carry sufficient information for performance of the line-alignment task. Finlay et al. (2000) tested M.M. on the Tactile Localisation Task, in which blindfolded subjects are required to indicate which finger has been touched by the experimenter by touching together the finger and the thumb. M.M. was found to have marked impairment in the interhemispheric condition (where the subject has to respond with the opposite hand) compared to her perfect performance on the intrahemispheric conditions. This may be due to the degradation of spatial information during interhemispheric transfer. As discussed above, M.M. had marked difficulty with the spatial tasks reported in Chapter Three.
The other four studies involving M.M. have all used simple reaction-time tasks. As with J.P., the studies described in Chapters Four and Five of this thesis and in Roser and Corballis (2003) presented stimuli either unilaterally or bilaterally, while the Roser and Corballis (2002) study had two possible positions in each visual field allowing conditions of either symmetrical or asymmetrical stimuli in the bilateral conditions.

All four studies found evidence for an enhanced redundancy gain in M.M. This redundancy gain, both in M.M. and in the other acallosal and split-brain subjects, was not affected by the presence or absence of symmetry in the Roser and Corballis (2002) study, leading the authors to suggest that the (presumably) subcortical summation may not occur at the retinotopically organized superior colliculi, as had been previously suggested (Corballis, 1998). However, the redundancy gain in M.M. was affected by luminance as demonstrated in Chapter Four of this thesis. This finding was in agreement with that of another acallosal subject (R.B.) tested by Corballis (1998), but not with the other acallosal subject (J.P.) tested here. As suggested in Chapter Four it may be that, depending on which redundancy gain model is correct, the anterior commissure may be able to either inhibit or mediate, relative to its size, a transfer process affecting subcortical summation. J.P.’s enlarged anterior commissure has been used as an explanation for the difference between her ability to transfer colour and letter information interhemispherically in Chapter Three and the lack of this ability in M.M., who has a normal sized anterior commissure. The enlarged anterior commissure may well be able to mediate luminance as well as hue information, explaining the difference between J.P. and M.M. on this redundancy gain task. This explanation could also apply to R.B. as it is not mentioned that he has an enlarged anterior commissure (see MRI scan reproduced in Forster and Corballis, 1998).

The results of Chapter Five provided evidence that M.M. shows bilateral visual evoked potentials regardless of whether stimuli are presented unilaterally or bilaterally. In the case of M.M. it may be that ipsilateral sensory pathways are the compensatory mechanism responsible, rather than the interhemispheric transfer via the anterior commissure posited for J.P. Firstly, bilateral activation was seen in all experimental conditions even when it was not necessary for task completion, unlike J.P. where the condition determined whether transfer occurred. Secondly, the bilateral activations isolated by source localization in M.M. were P1 components. These components have been sourced to extrastriate cortex, upstream from the secondary visual areas that the anterior commissure connects. Further, Chapters Three and Four have suggested that the anterior commissure that does not seem to be a compensatory mechanism in M.M.

In summary, then, M.M. may be achieving some limited interhemispheric transfer of information through the anterior and intertectal commissures, although, with a normal-sized anterior commissure transfer is of a lesser quantity or quality than that of J.P. Like J.P., further testing with other tasks will allow a clearer picture to emerge. Ipsilateral sensory pathways may also be a compensatory mechanism in this subject. In order to clarify this question, further research could extend the ERP study in Chapter Five by dividing the visual field into four quadrants and presenting stimuli unilaterally and bilaterally over these four positions. As explained in the introduction to Chapter Five, the earliest identified visual evoked potential, the C1, has a positive or negative polarity dependent on whether the stimulus is below or above the horizontal midline, and is thought to be of primary visual cortex origin. If this potential was also found to be bilateral to unilateral input, it is unlikely that interhemispheric transfer can be considered an explanation
as this part of cortex has no known commissural connections, nor is it connected to the secondary visual pathways.

A.L.M.

As detailed more fully in Chapter Two, A.L.M. is the daughter and fifth child of M.M. She was 13 years old at the time of the testing in Chapter Five. A.L.M. was diagnosed with complete callosal agenesis by CT scan soon after her birth in 1987 in an examination exploring concerns about suckling difficulties and an unusually large head. A later MRI scan found her anterior commissure to be twice normal size with no other cerebral abnormalities noted. A.L.M.’s functioning on the WPPSI at age 6 years 10 months was in the low average range, and she is right-handed with a laterality quotient of 50 on the Edinburgh Handedness Inventory.

Besides the work presented in Chapter Five, there have been two other articles published with data from A.L.M. (see Corballis & Finlay, 2000; Finlay et al., 2000). Finlay et al. (2000) tested A.L.M. on the Tactile Localization Task, and like her mother M.M., she was found to have marked impairment in the interhemispheric condition but perfect performance in the intrahemispheric conditions. Corballis and Finlay (2000) tested the ability to integrate colour, letters, digits and words across the midline. A.L.M. was shown to have perfect performance on the interhemispheric matching of pairs of letters presented 5.18 cm apart centred about the vertical meridian, and near perfect performance on 15.54 cm separated letters and 17.27 cm separated digits. On the tasks involving colour, A.L.M. was at ceiling at naming colours in either visual field, but, while her performance in the colour-matching task was significantly above chance it was worse in the bilateral condition than in the unilateral conditions. Finally, while she was shown to have difficulties with the task of reading six-letter words presented either unilaterally or straddling the midline, this was found to be due to poor reading skills and further testing by the authors suggested there was perceptual integration across the midline.

Overall, then, A.L.M. shows no disconnection on the perception of words across the midline or in integrating letters and digits presented to separate visual fields. Where she does show disconnection is on the interhemispheric transfer of colour and tactile information. A.L.M. differs from her mother in that her performance on colour integration was slightly better and performance on the more eccentric letter-matching task was significantly more accurate. As A.L.M. has been shown by MRI to have an anterior commissure approximately twice the average size it may be that this pathway is able to mediate a higher quantity or quality of information than the normal-sized commissure of M.M. However, her commissure is smaller than that of J.P., who can again perform at a higher level of accuracy than either A.L.M. or M.M.

Chapter Five is the only study to test A.L.M. on a simple reaction-time task. Like the other acallosals tested, A.L.M. showed an enhanced redundancy gain, although the violation was small with the left hand. The visual evoked potential data showed A.L.M. to have a similar topographical pattern to control subjects with bilateral activation in all conditions, but at much longer latencies (216 ms post-stimulus compared to about 160 ms post-stimulus). It is difficult to make any definitive conclusions about the mechanism underlying these bilateral activations when we have so little information from which to draw. While the same different tasks discussed above suggest that her enlarged anterior commissure may mediate more transfer than that of M.M.’s normal-sized commissure, her visual evoked potential data is more like M.M.’s than J.P.’s, although the components isolated were later N1s rather than
the earlier P1s. There is therefore insufficient data to determine whether ipsilateral sensory pathways or interhemispheric transfer via the anterior commissure is the mechanism of compensation.

Due to her young age A.L.M. has not yet been tested very thoroughly. However, since the time of the testing reported here she has also sadly developed a further complication, a Chiari’s malformation, which has complicated her presentation and will probably mean an end to her testing.

Conclusion

It is clear that marked differences exist between these three subjects with agenesis of the corpus callosum. While the differences are greatest between J.P. and the two related subjects, there are still significant differences between M.M. and A.L.M. This highlights the importance of reporting detailed information about individuals when reporting data from acallosal subjects, so that comparisons between subjects can take into account their differences as well as their similarities. It is only by doing this that we will understand the nature of their compensation and their remaining deficits.
References


