Effective binocular integration at the midline requires the corpus callosum

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Abstract

To study the role of the corpus callosum (CC) in midline binocular integration, the effects of late callosotomy and congenital CC agenesis on the ability to perceive dichoptic plaid motion was assessed. Coherent motion was well perceived at all locations in the visual field under diotic viewing but not along the vertical meridian (VM) when the components were dichoptically presented. This deficit was totally abolished in the agenesis subject and reduced in the callosotomized individual when stimulus size was increased beyond the VM. Electrophysiological correlates were also examined by recording visual evoked potentials and these showed that the P1/N2 components were abnormal for small dichoptic stimuli presented on the midline. These findings attest to the importance of the contribution of CC to midline binocular integration and the effects of cerebral plasticity.

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1. Introduction

Visual information is highly lateralized such that each hemifield projects to the contralateral hemisphere. Yet our perception of an object crossing or abutting the midline is neither disrupted nor disjointed. It has been proposed that the corpus callosum (CC), the most important cortical commissure allowing for interhemispheric communication (Antonini, Berlucchi, & Lepore, 1983; Antonini, Berlucchi, Marzi, & Sprague, 1979; Choudhury & Whitteridge, 1965; Gazzaniga, 1966; Myers, 1956), may mediate the unification of the two visual hemifields (Berlucchi, 1981). This midline fusion hypothesis, as it has invariably been called, has been strongly yet indirectly supported by anatomical and electrophysiological studies in animals. The latter show that callosal recipient or projecting cells are generally located on the retinotopic representation of the midline and their receptive fields abut or straddle the vertical meridian (VM) (Berlucchi & Rizzolatti, 1968; Berlucchi, Sprague, Antonini, & Simoni, 1979; Hubel & Wiesel, 1967; Innocenti, 1980). This midline function of CC probably constitutes a general rule for highly lateralized sensory systems, since similar results have been demonstrated for the somatosensory system (Guillemot, Lepore, Prevost, Richer, & Guilbert, 1988; Guillemot, Richer, Prevost, Pito, & Lepore, 1987; Guillemot, Richer, Pito, Guilbert, & Lepore, 1992; Manzoni, Barbaresi, Bellardini, & Caminiti, 1980).

Midline fusion does not constitute the sole function of the CC related to sensory processing. Animals studies show that transection of the CC or the unilateral cooling of the border regions of areas 17/18, where commissural cells abound, leads to a reduction of bilaterally activated cells in the contralateral hemisphere in visual (Blakemore, 1983; Dreher & Cottee, 1975; Lepore & Guillemot, 1982) and somatosensory (Petit, Lepore, Picard, & Guillemot, 1990; Picard, Lepore, Ptito, & Guillemot, 1990) systems. This suggests that, for binocular vision, the CC may facilitate the integration at midline of the information coming from the two eyes.

In humans, there is no conclusive evidence that the CC plays either of these special roles in vision. Hence, Mitchell and Blakemore (1970) reported deficits in midline stereopsis in a callosotomized subject: when stimuli having coarse horizontal disparities (2°) were presented in peripheral visual field, depth was perceived on 16/20 trials whereas presentation next to the VM yielded only a discrimination of depth of 7/20. They argued that this performance was not significantly different from chance level, a somewhat hazardous conclusion based on few trials. The same subject, however, tested with random dot stereograms having disparities of 5' and 40' did not show stereoscopic deficits (Hamilton &
Vermeire, 1986). This contrasting result suggests that the type of disparity (coarse versus fine) might involve different mechanisms. Large disparities could require the CC whereas fine disparities might be coded by other structures (Bishop & Henry, 1971), such as the retinal nasotemporal overlap, characterized by intermingled ganglion cell projections to the cortex: temporal hemiretina cells send their axons to the ipsilateral hemisphere while others atypically project to the contralateral hemisphere (Stone, Leicester, & Sherman, 1973). Midline nasal hemiretina also has cells which project to the two hemispheres, although misrouting is slightly more abundant (Fukuda, Sawai, Watanabe, Wakakuwa, & Morigiwa, 1989). This might explain why callosotomized cats and monkey do not show marked deficits in stereopsis, relative to normal subjects, when tested with fine disparities (Cowey & Wilkinson, 1991; Lepore, Pito, & Lassonde, 1986; Timney, Elberger, & Vandewater, 1985). In addition to the magnitude of the disparity, the type (uncrossed versus crossed) could also be a confounding factor for the understanding of the role of CC in binocularity. Although published only in abstract form (LeDoux, Deutsch, Wilson, & Gazzaniga, 1977), the data showed no impairment of midline stereoscopic discrimination in a subject having a section of CC but an intact anterior commissure. Based on this report, it has been suggested that the coding of uncrossed midline disparity requires the splenium whereas crossed disparity integration might rely on the anterior commissure (Jeeves, 1991).

Therefore, the evidence attempting to demonstrate the implication of CC on binocular function, especially at midline, based on stereopsis is insufficient and unclear. In the present study, we used dichoptic plaid motion stimuli to try and define the special role of the callosum in binocular integration at midline. This permitted us to circumvent the issues raised by the stereopsis studies. Plaid motion is, moreover, an ideal stimulus to study binocular integration since it can be perceived, on the one hand, diopically, i.e. both eyes view both components (Adelson & Movshon, 1982) and, on the other, under dichoptic viewing (Andrews & Blakemore, 1999; Cobo-Lewis, Gilroy, & Smallwood, 2000), i.e. each eye views one component. Coherent plaid motion perception in this case would imply binocular integration of the two gratings. Using this novel paradigm (Fig. 1A), we extensively investigated one subject with callosal agenesis and one having been callosotomized as an adult, both having an intact anterior commissure (Fig. 1B). Two questions were examined: first, what is the ability of these subjects to integrate binocular information in the absence of CC? Second, given that the agenesis subject developed without a CC whereas the other subject was callosotomized at adulthood, are there evidences that some neuronal plasticity or from having anatomically different set of interhemispheric connexions might have operated in the former resulting in superior perceptual abilities? Behavioral and electrophysiological investigations were carried out to examine the hypothesis that the CC is specifically implicated in midline binocular integration.

2. Method

2.1. Subjects

Observers had corrected or normal visual acuity. They gave their informed consent to the experimental protocols in conformity with the Université de Montréal ethics committee. Two male acallosal subjects were tested: one was born without a CC (S.P.) and the other (M.L.) underwent an adult section of the CC because of untreatable epilepsy. S.P. and M.L. were 26 and 34 years old, respectively. Four control observers matched for sex and age participated in the psychophysical experiments. Two additional subjects having comparable dioptic and dichoptic motion performance were added to the control group for the VEP study.
2.2. Stimuli

Drifting squarewave gratings (spatial frequency: 5 cycles per degree; velocity: 2° s⁻¹; contrast: 10%) were generated on a Power Macintosh computer with VPixx™ software and displayed on a ViewSonic P815 monitor (1600 H × 1200 V pixels). Contrast was defined by: \( \frac{L_{\text{max}} - L_{\text{min}}}{L_{\text{max}} + L_{\text{min}}} \times 100 \), where \( L_{\text{max}} \) is the maximum luminance and \( L_{\text{min}} \) is the minimum luminance of the stimulus. The centers of the stimuli were presented at different eccentricities (0°, ±0.75°, ±1.5°, and ±4.5°) and viewed through different circular apertures (0.75°, 1.5°, 3°, and 4.5°) from a distance of 114 cm in a dark room. In some experiments, the duty-cycle was modified by reducing the spatial frequency (and consequently, the temporal frequency, to keep velocity constant) in the aperture when the stimulus size was increased (3° and 4.5°). Motion stimulation could be local (one grating) or global (two superimposed orthogonal gratings). The two components forming the plaid pattern were presented either superimposed to one eye (monoptic condition), superimposed to both eyes (diotic condition) or separately to each eye (dichoptic condition). Stimulation parameters were optimal to maximize binocular summation of the two orthogonal gratings when presented dichoptically (Liu, Tyler, & Schor, 1992). Dichoptic presentations were delivered through liquid crystal shutter-glasses (Crystaleyes, StereoGraphics Corporation, CA, USA). Goggles switched in synchronization with alternating left and right image fields of the monitor at 120 Hz, so that when the monitor displayed the left eye’s image, the left eye’s shutter was transparent and the right eye’s shutter was opaque, and vice versa for the right eye’s image. Thus, the image presented to each eye was refreshed at 60 Hz, which provided flicker-free viewing. In the monoptic and diotic conditions, observers also wore the shutter-glasses, which were open either for the viewing eye or for both eyes, respectively, in order to keep the mean luminance of the stimuli (6 cd/m²) constant among all conditions.

2.3. Psychophysical testing

The subject’s task was to discriminate between five motion directions of the moving pattern by depressing the appropriate key (control subjects) or by verbal and gestural reports (acallosal subjects). Global motion drifted in the upward oblique, horizontal or downward oblique direction while local motion drifted in one of these three directions as well as upward and downward (Fig. 1A). Observers initiated each trial while looking steadily at a fixation point (0.25°). The fixation point and short trial duration (250 ms) were used to minimize eye movements. A blank field with the same mean luminance as the stimuli was presented for at least 2.5 s between each presentation. For each direction, global and local motions were presented 30 times (two blocks of 15 trials per direction) in random order. Thus, plaid motion discrimination was calculated as a percentage of correct responses for 90 trials (30 trials × 3 directions).

2.4. Electrophysiological testing

Stimuli were basically the same as in the psychophysical experiments. Motion-onset VEPs were recorded from Oz, O3 and O4 derivations according to 10–20 international system (Jasper, 1958) and referred to linked earlobes. Recordings were carried out with Ag–AgCl electrodes. Their impedance was kept below 5 kΩ. The EEG signal was amplified with a gain of 20,000 and bandpass-filtered at 0.03–100 Hz (Grass, model 79D). The digitization rate was 1000 Hz. Sixty-nine stimuli were randomly presented, which include the different directions. The relatively small number of trials, which is nonetheless above the minimum suggested by the International Society for Clinical Electrophysiology of Vision (Harding, Odom, Spileers, & Spekreijse, 1996), was used to reduce testing duration considering the comparatively limited attentional capacities of the acallosal subjects, and especially M.L. Trials where the response was higher than 50 mV were rejected before averaging. Motion-onset consisted of an initial stationary period of 1550 ms followed by an abrupt onset of motion (duration: 250 ms; velocity: 2° s⁻¹). Such a duty-cycle (14%) typically produces a P1/N2 waveform complex where N2 is the dominant component. Latencies of the P1 and N2 were determined from the maximum deflection whereas the amplitudes were determined using a peak-to-peak standard procedure. The deviation of acallosal subjects from the mean of control subjects was evaluated by one-tailed t-test.

3. Results

3.1. Stimulus location

A pilot study was performed to make certain that control as well as acallosal subjects could correctly discriminate local motion composed of a single grating having the same parameters as the components used for the global motion experiments. Results indicated that all subjects perceived the correct direction of the moving stimuli at least 90% of the time regardless of the location in the visual field.

3.1.1. Azimuthal discriminations

The subjects were assessed in their ability to discriminate between three plaid motion directions through an aperture of 1.5° in central and lateral visual fields. The average percentage correct responses for diotic and dichoptic plaid motion on the azimuth are presented in Fig. 2A. The data of the four control subjects (Fig. 2A, top) have been pooled together since individual scores were quite similar. The mean performance in the diotic condition was excellent for presentations in the left hemifield, the central location and the right hemifield. In the dichoptic condition, the direction of the plaid pattern was also correctly discriminated by control subjects at all eccentricities. However, the subjects reported that the dichoptic motion was not as salient as for the diotic
Fig. 2. Discrimination of plaid motion direction as a function of eccentricity. Percent of correct responses are illustrated for: average of four control subjects (top), CC agenesis subject (middle) and callosotomized subject (bottom). (A) Performances on azimuth. (B) Performances on vertical meridian in the lower visual field. (C) Performances on central location. Dichoptic: white, diotic: gray, monoptic: black.

plaids, although it was still coherent. The performances observed at ±6° may somewhat underestimate the perceptual abilities of the control subjects because of their reduced visual acuity in the periphery, considering the stimulus parameters (contrast: 10%; size: 1.5°; spatial frequency: 5 cycles per degree). An index was derived to quantify the amount of binocular integration independently of absolute performances. The index consists of the ratio obtained by dividing the dichoptic by diotic scores. The binocular integration indexes (BIIs) for the control group were ≥0.85 for all locations. A BII of ≤0.5 was arbitrarily considered to indicate deficient integration abilities.

Dioptic plaid perception of the CC agenesis subject (S.P.) was similar to that of the control group for all eccentricities, although performance was slightly lower (Fig. 2A, middle). However, the performance found in the dichoptic condition was extremely deficient for stimuli on or abutting the VM. Indeed, motion detection was at chance on the midline and gradually increased as the stimuli were presented more laterally in the left or right hemifields. These results were quite exceptional in confirming the importance of CC in midline function. We, thus, wanted to be absolutely certain that they reflected the true performance of this subject. The dichoptic experiment was therefore repeated two weeks later. The two testing sessions gave remarkably similar results (Table 1). The bars in the histogram plotted in Fig. 2A represent the mean score obtained in the two dichoptic testing sessions. The BIIs also confirm the gradation in performance accuracy: it was <0.5 at mid-line and greater than this cut-off point at more eccentric positions.

The callosotomized subject (M.L.) showed a similar pattern of responses for both viewing conditions (Fig. 2A, bottom). The performance found in the diotic condition was almost identical to that of S.P. Dichoptic plaid
discrimination was also evaluated twice and results obtained in each testing session were analogous (Table 1). Again, discrimination was also evaluated twice and results obtained

<table>
<thead>
<tr>
<th>Location (◦)</th>
<th>S.P.</th>
<th>M.L.</th>
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<tbody>
<tr>
<td>−6</td>
<td>66</td>
<td>67</td>
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<tr>
<td>−1.5</td>
<td>66</td>
<td>69</td>
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<tr>
<td>−0.75</td>
<td>53</td>
<td>51</td>
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<tr>
<td>0</td>
<td>35</td>
<td>39</td>
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<tr>
<td>0.75</td>
<td>51</td>
<td>47</td>
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<tr>
<td>1.5</td>
<td>59</td>
<td>44</td>
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<tr>
<td>6</td>
<td>51</td>
<td>55</td>
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3.1.3. Binocular integration or summation?

In the experiments presented above, it may be argued that the reduced dichoptic performances were caused by a lack of binocular summation, which is defined simply as the fact that perception using two eyes is better than the one using only one eye (Howard & Rogers, 1995). We, therefore, carried out an additional experiment, where the two components determining plaid motion were presented monoptically in the central visual field of the dominant eye in both the control and acallosal subjects. Results showed that plaid motion perception either under monoptic or dichoptic viewing was both excellent and equivalent for all subjects (Fig. 2C). This finding suggests thus that the perceptual deficit of acallosal subjects for dichoptic plaid was not caused by the fact that each eye received only one component, and hence only one copy of the plaid was generated in the brain, as opposed to the dichoptic presentation, where the plaid is represented twice.

3.2. Spatial summation

The perceptual deficits of the acallosal subjects observed above suggest that the dichoptic coding for a small zone straddling the midline (from 0° to ±0.75°) is especially perturbed. As the stimulus was presented more eccentrically, performance improved. We thus examined whether increasing the size of the centrally located stimulus, thereby recruiting additional visual cortex, and especially cortex beyond the callosal projection zones, would allow the acallosal subjects to overcome their deficit along VM.

3.2.1. Size of the aperture

The stimulus aperture, which measured 1.5° in the experiments described above, was thus increased in size so that it covered either 3° or 4.5°. Discrimination of motion direction as a function of stimulus size is illustrated in Fig. 3. Using the larger stimuli, control subjects still showed very

Table 1

Percent of correct responses for the agenesis (S.P.) and callosotomized (M.L.) subjects observed at the two testing sessions
good discrimination for either the 3° or the 4.5° stimulus size for both diotic and dichoptic presentations (Fig. 3A, top). Surprisingly, the dichoptic performance of callosal agenesis subject S.P. improved only slightly as the stimulus size increased and was still well below the diotic level for both the 3° and 4.5° stimuli (Fig. 3A, middle). Callosotomized subject M.L. showed a similar pattern for the 3° and 4.5° stimulus (Fig. 3A, bottom).

3.2.2. Constancy of the duty cycle

Although control subjects showed excellent performance, they reported that the motion perceived through the 3° or 4.5° aperture was not as “strong” or salient as the motion seen through the 1.5° aperture. Because duration, velocity and spatial frequency were initially kept constant, motion viewed through the different aperture sizes were all produced by the drifting of 2.5 cycles stimulus. Since the number of cycles is much larger within a large aperture than a small one, the perceived shift of the pattern within a large aperture is reduced. Thus, the spatial duty cycle was modified by reducing the spatial frequency of the grating when the aperture size was increased. As a result, the number of cycles in the aperture, and consequently the phenomenological impression of motion, remained constant whatever the stimulus size used (1.5°, 3° or 4.5°). This procedure (Fig. 3B) did not produce changes in the performance of the control group. The diotic and dichoptic performances of S.P., however, improved dramatically, becoming comparable to those of the control group for the 3° (BII: 0.92) and 4.5° (BII: 0.97) stimuli. This suggests that the recruitment of additional visual cortex by increasing stimulus size, added to the increase of stimulus saliency, can compensate for the reduced efficacy around the midline. The performance of callosotomized subject M.L. also improved. However, it still failed to reach the diotic level with stimuli of 3° (BII: 0.65) and 4.5° (BII: 0.67). Unfortunately, potential confounding effects did not allow us to test M.L. with larger sizes to confirm that performance recovers when stimuli extend far enough away from the VM. Indeed, binocular integration of two orthogonal gratings is optimal with relatively low contrast and high SF (Liu et al., 1992). In comparison with the initial SF (5 cpd) was reduced to 2 cpd for the 4.5° aperture to adjust the duty cycle. Dichoptic paid patterns with lower SFs, for instance 1 cpd for an aperture of 9°, induced binocular rivalry effects and thus underestimated the beneficial effect of aperture size.

3.2.3. Masking the central stimulus

The improved performance in the acallosal subjects, especially subject S.P., obtained with the larger stimuli was interpreted as indicating that recruitment of cortex surrounding the most central representation of the visual field can compensate for the reduced integration carried out in this cortical region. It implies that these recruited regions can in fact integrate the binocular inputs and that the deficit mainly concerns cells representing the VM. To verify this, we carried out an additional experiment whereby the central portion of the 4.5° stimulus was occluded by a mask of 1.5°. The BII of both subjects remained basically the same (S.P.: 0.94; M.L.: 0.75) despite the presence of this mask. These results indicate that the improved performance shown in Fig. 3B is in fact due to these recruited structures.

3.2.4. Lack of interhemispheric cooperation?

We carried out a fourth experiment to confront two opposing explanations for our results: on the one hand, we have hypothesized above that dichoptic perception at midline in the acallosal subjects varies around a threshold level. Thus, larger stimuli which recruit more cells and changes in the duty cycle which modify saliency improve performance. This ‘activation strength’ explanation can account for data in Fig. 3B. On the other hand, poor performance by acallosal subjects using the small stimuli, and particularly the 1.5° stimulus, might have an alternative explanation. One may claim that each hemisphere in these subjects receives a stimulus that is half the size of the original stimulus (i.e. 0.75°), without any possibility of combining the two halves
to achieve a 1.5° stimulus, as is the case for control subjects having a functional callosum. So the poor performance of the acallosals may simply be due to the fact that the stimulus that has to be analyzed in each hemisphere is too small. The latter explanation is unlikely because, as mentioned before, it was easy for control as well acallosal subjects to perceive dioptric motion through an aperture of 0.75° presented on the VM. Nevertheless, we tried to exclude the ‘size’ explanation by presenting the 0.75° stimuli only in the right hemifield just abutting the midline. With this presentation, the left hemisphere of the acallosals received a stimulus equal to that it would receive were a 1.5° stimulus to be presented on the VM. As shown in Fig. 3C, the results indicate that size was not a factor in explaining the poor performance of the acallosals. Control subjects performed extremely well in both conditions. The acallosals, on the other hand, showed good performance under dioptric presentations and were still deficient in the dichoptic condition.

3.3. Electrophysiological correlates

In order to corroborate the behavioral findings, VEPs were recorded from occipital regions Oz, O3 and O4 using a motion-onset paradigm. Because of artifacts produced by residual epileptic discharges in posterior regions, it was impossible to analyze the VEPs recorded from callosotomized subject M.L. Only the results from agenesis subject S.P. are therefore presented. Components P1/N2 are particularly sensitive to motion onset stimuli and their amplitude and latency were evaluated in controls and the acallosal subject while they viewed plaid motion.

The experiment presented above showed that it is possible to cancel the midline deficit in acallosal subjects by increasing the size of the stimulus, especially for S.P. Thus, the motion-onset potentials were evoked from stimuli in central location viewed dioptrically and dichoptrically through the aperture sizes of 1.5° and 4.5° having the same spatial duty cycle. Results obtained for S.P and six control subjects (grand mean average) are illustrated in Fig. 4 from the three derivations. When viewed through the 1.5° aperture, S.P. showed normal VEPs for P1 and N2 for dioptric stimulation (Fig. 4A). Indeed, no significant differences from the control group were observed for latencies of the P1 (O3: z = 0.31; Oz: z = −0.30; O4: z = −1.5) and N2 components (O3: z = 0.43; Oz: z = −0.18; O4: z = 0.81) as well as peak-to-peak amplitudes (O3: z = −0.43; Oz: z = −0.49; O4: z = −0.84). However, the P1/N2 amplitudes were significantly different in the dichoptric condition (Fig. 4B), with the exception of site O3, although even at this derivation it was close to being significant (O3: z = −1.47, P = 0.07; Oz: z = −1.98, P < 0.05; O4: z = −1.83, P < 0.05). The latencies of the P1 and N2 components, however, were generally comparable to those of the control group, except for N2 at O3, which was delayed (z = 3.25, P < 0.001).

![Fig. 4. Motion-onset VEPs obtained from the CC agenesis subject (thick) and the averaged six control subjects (thin) from Oz (middle), O3 (left) and O4 (right). (A) When small stimuli were presented dioptrically, amplitudes and latencies of the P1/N2 complex were normal. (B) VEPs from dichoptric stimuli of 1.5° show abnormal amplitudes and latencies. Both waveforms were comparable when large stimuli (4.5°) were used either under dioptric (C) and dichoptric (D) conditions. Positive and negative deflections are up and down, respectively.](image-url)
Amplitudes and latencies obtained using the larger stimulus (4.5°) were not significantly different between S.P. and the control group, either when the stimulus was presented dioptrically or dichoptically (Figs. 4C and D).

4. Discussion

In the present report, acallosal subjects had normal dioptric motion discrimination regardless of the location of the stimulus in the visual field whereas their performance was at chance for stimuli dichoptically presented on the VM. This binocular integration deficit gradually decreased as the stimuli were presented at more eccentric positions on the azimuth. Moreover, the lack of discrimination on the VM is not due to a lack of interhemispheric cooperation to compute the plaid motion because the performance of the acallosal subjects was normal under monoptic or dioptic viewing. The midline deficits reported here are thus not associated with a lack of hemispheric communication but rather with a deficit in binocular integration.

The fact that the performance of M.L. was not as good as S.P. as the stimulus size was increased suggests that the binocular representation of the midline is more disturbed by the late callosotomy than by a congenital absence of CC. In agreement with the general consensus that brain reorganization is linked to the functional maturity of the lesioned structure at the time of the insult (Goldman-Rakic, 1980; Lassonde, Sauerwein, McCabe, Laurencelle, & Geoffroy, 1988; Piito & Lepore, 1983) the differential effects of callosotomy and CC agenesis reflect the smaller cerebral plasticity in the adult brain. Thus, compensation for the lack of interhemispheric interaction might be greater in the congenital acallosal than in the callosotomized subject. Numerous plastic changes can occur in the CC agenesis brain. For example, hypertrophy of non-callosal pathways, such as the anterior commissure, has been reported (Stefanko & Schenk, 1979). We carried out a gross anatomical analysis of the MRI scans of the CC subject and did not notice larger residual commissures in S.P. However, the possibility that the anterior commissure is functionally more efficient can not be discarded. Since we do not know the fine functional changes in brain structures in our subjects which would result from changes in cell density, fiber myelination, or synaptogenesis, we conclude that the CC agenesis subject showed greater cerebral plasticity.

The receptive fields of cells at the V1/V2 border in primates, that is known to contain abundant callosal afferences and efferences, are small (less than 1°) and represent 0°–2° on the azimuth lateral to the midline (Kennedy, Martin, Orban, & Whitteridge, 1985). Thus, the different stimulus sizes used in the present study, especially the smaller ones, stimulated preferentially potential dysfunctional zones. In fact, the performance increased as a function of stimulus size in both subjects, although in a limited fashion for M.L. Hence, spatial summation can activate a sufficient number of binocular cells in V1/V2 and/or additional neurons from extrastriate areas representing this portion of the visual field because of their larger receptive fields (Maunsell & Newsome, 1987). On the other hand, it is difficult to conclude about the effect of the nasotemporal overlap on binocular integration. Although not yet confirmed anatomically, behavioral evidence of the existence of a nasotemporal overlap in humans has been obtained from callosotomy subjects (Fendrich, Wessinger, & Gazzaniga, 1996). Here, the results observed in acallosal subjects with 0.75° stimuli, which should fall within the overlap, still showed deficient integration for dichoptically presented plaids. However, the performance was slightly higher than chance level, suggesting some contribution of the overlap. On the other hand, as reported by control subjects, such a stimulus had better saliency than the 1.5° plaids and is easily perceptible. This confounding effect makes it difficult to estimate the contribution of the nasotemporal overlap to binocular integration at midline.

It is probable that the midline deficits observed in the two acallosal subjects resulted mainly from a dysfunction of binocular neurons located at the V1/V2 border. Callosotomy in adult monkeys produced neuronal changes consisting of a reduction in the number and/or the shrinking of large pyramidal cells in layer III of the portion of area 18 just bordering striate cortex (Glickstein & Whitteridge, 1976). This corresponds to the retinotopic representation of midline. A similar reduction of pyramidal cells at the 17/18 border has also been observed in CC agenesis humans (Shoumura, Ando, & Kato, 1975). Our electrophysiological data support the idea that early processing in the visual cortex is dysfunctional. Indeed, lower amplitudes for dichoptic midline stimulation suggest a reduction of activation of binocular cells in occipital cortex. The abnormal VEPs observed from O3 and O4 sites probably result mainly from a dysfunction at the V1/V2 border regions rather than of extrastriate cortex such as V5. Indeed, analysis of motion is generally sequential when stimuli are presented at speeds below 6° s⁻¹ and the activation of motion extrastriate cortex is largely dependent on primary visual cortex (Fytche, Guy, & Zeki, 1995; Kaufman & Williamson, 1990; Raiguel, Lagae, Gulyas, & Orban, 1989). This was probably the case in our study because the velocity of the plaids was 2° s⁻¹. We also did not find, somewhat unexpectedly, that the latencies obtained from O3/O4 were significantly different from those derived from Oz in the control group. But VEPs are an indirect measure of brain activity and are inappropriate for studying connectivity between different cortical areas closely situated.

As regards the VEP amplitudes, one may question the fact that a significantly lower amplitude was only observed for the small dichoptic pattern and not for the larger one, given that the P1/N2 complex is a function of motion-onset and the latter was present when using either stimulus. However, there is evidence showing that VEPs reflect not only the physical stimulus but also the perceptual state of the observer. Hence, dichoptic presentation of random dot stereograms having a horizontal disparity, and thus producing a...
perception of depth, evoked a higher P1 component than the same stimulus, where the horizontal disparity had been removed or replaced by a vertical disparity to prevent stereopsis (Regan & Spekreijse, 1970). More significantly, the amplitude of the N2 wave has been shown to be lower when the coherence of a global motion pattern formed by two random dot components or two plaid components breaks down, suggesting that VEP amplitude elicited by motion onset are closely associated with the consistency of the global motion perception (Niedeggen & Wise, 1998).

Electrical stimulations of callosal fibers can produce excitatory postsynaptic potentials but are somewhat ineffective in driving postsynaptic cells (Singer, Tretter, & Cynader, 1975). In accordance with this observation, it has been proposed that callosal projections could amplify weaker monocular signals to facilitate binocular coding of the inputs coming from each eye (Payne, Pearson, & Berman, 1984). This is supported by results obtained in our laboratory for the visual and somatosensory systems. Hence, optic tract transection (which eliminates callosal projections from the deafferented hemisphere) produces a shift in the ocular dominance distribution: inputs from the ipsilateral eye drive substantially fewer cells in the afferented cortex (Lepore, Samson, & Molotchkinoff, 1983). In the somatosensory system, the same phenomenon manifests itself following callosal section, namely, bilaterally activated cells in SII are less strongly driven by stimulation of ipsilateral body regions (Petit et al., 1990; Picard et al., 1990).

A recent result presented only in abstract form shows that callosal axons mainly project to cell columns innervated through the geniculate layers representing the ipsilateral eye (Alexeenko, Toporova, & Makarov, 2001). Callosal influence on the receptive fields of binocular cells has also been found at the midbrain level (Antonini et al., 1979). Section of the CC in cats with mid sagittal section of the optic chiasm eliminated almost completely the responses of superior colliculus cells to contralateral eye stimulation, although the te- cal commissures were intact. More importantly, the callosal lesion also reduced the number of receptive fields abutting the VM activated through the ipsilateral eye.

Our results from human subjects suggest, therefore, that the role of CC in cortical binocularity is not a winner-take-all process, but a facilitatory one. CC is hence implicated in midline binocular coding by raising the post-synaptic activation of putative binocular cells (mainly for inputs coming from the ipsilateral side) so that they reach more easily firing thresholds. The functional relevance of such a callosal role might be to compensate for a decrease in the binocular activation of cortical neurons caused by the nasotemporal overlap. It is difficult to estimate the proportion of nasotem- ral overlap cells projecting to the “wrong” hemisphere, i.e. ipsilateral for nasal cells and contralateral for tempo- ral cells. However, the proportion of ganglion cells across one hemiretina which reach the “wrong” side of the brain has been estimated in fetal monkey. Very few cells, less than 0.5% of the total ganglion cell population either for temporal or for nasal hemiretina, were found to project to the inappropriate hemisphere (Chalupa & Lía, 1991). The possible consequence of the misrouting of the inputs at the midline of temporal and nasal hemiretina is that binocu-
lar convergence on cortical cells in each hemisphere coding around the midline is reduced. The latter is only true if these ganglion cells do not bifurcate, i.e. send axonal collaterals, and thereby project to both hemispheres. While there is ev- idence of bifurcating cells in rodents (Insausti, Blakemore, & Cowan, 1984; Jeffery & Perry, 1981) in very small num-
bers, other data did not confirm their existence in the cat (Jacobs, Perry, & Hawken, 1984), suggesting the absence of bifurcating cells in higher mammals. Thus, by re-sending the information to the other hemisphere, the CC allows an additional activation leading to increased binocular coding.

The callosal commissure becomes therefore crucial to en-
able adequate binocular integration close the VM.

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