J. Physiol. (1987), **384**, *pp.* 619–632
With 7 text-figures
Printed in Great Britain

THE TRANSFER OF VISUAL INFORMATION ACROSS THE CORPUS CALLOSUM: SPATIAL AND TEMPORAL PROPERTIES IN THE CAT

BY NICOLETTA BERARDI, SILVIA BISTI AND L. MAFFEI
From the Istituto di Neurofisiologia del C.N.R., Via S. Zeno 51, 56100 Pisa, Italy

(*Received 6 May 1986*)

SUMMARY

1. The spatial and temporal characteristics of the visual information transmitted across the corpus callosum have been studied in normal cats by recording directly from the corpus callosum and in split-chiasm cats by means of visual evoked potentials (v.e.p.s) and single-unit recordings at the 17/18 border.

2. The modulation transfer functions (m.t.f.s) obtained by recording from the corpus callosum are comparable to the m.t.f.s evaluated by various techniques for the whole visual system of the cat. The spatial and temporal acuities, however, do not reach the values obtained behaviourally or estimated with cortical evoked potentials.

3. In split-chiasm cats, both v.e.p.s and single-unit recordings indicate that the contrast gain of the callosal pathway is considerably lower than the gain of the direct, geniculo-cortical system. Spatial and temporal acuities are lower for the callosal than for the direct system.

4. The same differences in contrast gain between the spatial m.t.f. obtained for the callosal and the direct system have been found in alert split-chiasm cats.

5. Our data suggest that the cross-talk between the hemispheres taking place across the corpus callosum is nearly abolished at low contrasts and high spatial and temporal frequencies.

INTRODUCTION

The role of the callosal connexions at the level of the 17/18 border is currently associated with the necessity of binding together the two halves of the visual field represented separately in the two hemispheres in order to grant perceptual continuity across the vertical meridian and/or to subserve binocular functions such as depth perception (Choudhury, Whitteridge & Wilson, 1965; Hubel & Wiesel, 1967; Berlucchi & Rizzolatti, 1968; Blakemore, 1969, 1970; Mitchell & Blakemore, 1970; Berlucchi, 1972; Bishop, 1973; Blakemore, Diao, Pu, Wang & Xiao, 1983; Payne, Pearson & Berman, 1984).

In fact, both electrophysiological and anatomical data indicate that the receptive fields of neurones connected via the corpus callosum are distributed along the vertical meridian (Whitteridge, 1965; Hubel & Wiesel, 1967; Berlucchi, Gazzaniga & Rizzolatti, 1967; Toyama, Matsunami & Ohno, 1969; Shatz, 1977*a*; Harvey, 1980; Innocenti, 1980).

In addition, behavioural experiments in split-chiasm cats (see Berlucchi & Marzi, 1982, and Berlucchi & Sprague, 1981, for references) indicate that the corpus callosum can mediate the interhemispheric transfer of learning in visual pattern discriminations with visual inputs restricted to one hemisphere.

Knowledge of the neurophysiological substrate for this interhemispheric transfer, however, is rather limited. It is known that neurones projecting across the corpus callosum can belong to any class of cortical cells (simple, complex and hypercomplex) and that most of them are binocular (Berlucchi *et al.* 1967; Hubel & Wiesel, 1967; Shatz, 1977*a*; Harvey, 1980; Innocenti, 1980). The site of origin of callosal connexions is also known (Shatz, 1977*b*; Harvey, 1980; Innocenti, 1980; Symonds, 1982). What is not known is what type of visual information is transmitted across the corpus callosum.

In this paper we have addressed this important problem quantitatively by investigating the spatial and temporal characteristics of the callosal line.

METHODS

Experiments were performed in sixteen cats. Four cats were intact (recordings from the corpus callosum), eleven cats had been subjected 30–40 days in advance to surgical split of the optic chiasm via an oral approach, and one cat had been subjected to section of the right optic tract. The surgery was done under pentobarbitone anaesthesia and in aseptic conditions. In split-chiasm preparations the optic fibres which cross to the opposite site of the brain are severed, thus restricting the visual input from one eye to the ipsilateral hemisphere: the only route by which visual input from one eye can reach the opposite hemisphere is through the corpus callosum.

For visual evoked potentials (v.e.p.s) and single-unit recordings, anaesthesia was induced with Althesin (alfaxalone–alfadolone, 0·18 %; Glaxo), 1·5 ml/kg. A small opening was made in the skull over the appropriate cortical region, the dura removed and the animal paralysed with intravenous injection of Pavulon (pancuronium bromide, 0·2 %; N.V. Organon), 0·1–0·2 ml/(kg h), and artificially ventilated. At the end of the surgical procedure all operated areas were infiltrated with local anaesthetic (Novocaine). During the recording session, anaesthesia was maintained with a continuous injection of Althesin, 0·3 ml/(kg h).

Electroencephalogram (e.e.g.), electrocardiogram (e.c.g.) and P_{CO_2} (4–4·2 %) were continuously monitored throughout the experiment and the body temperature was maintained at 38 °C.

Pupils were dilated with atropine sulphate (1 %) and contact lenses with artificial pupils of 3 mm diameter were applied. The refraction of the cat's eyes was determined by means of retinoscopy and corrected with suitable spectacle lenses placed in front of the eyes. The position of the papillae and the areae centrales was determined at the beginning of the experiment and checked again periodically using the technique described by Fernald & Chase (1971).

A micropipette filled with either sodium chloride (3 M) or Pontamine Sky Blue in sodium acetate (0·5M) was inserted either in the splenium of the corpus callosum (under visual inspection) between Horsley–Clark (H–C) coordinates P2 and P6 or in the visual cortex, area 17 or 18, in correspondence with the representation of the vertical meridian, within H–C coordinates P1–P4 and L2–L4. A solution of agar–agar in saline was used to prevent drying of the cortex.

Visual stimuli were generated by a computer on a cathode ray tube (c.r.t.) screen (22 by 25 cm, mean luminance 7 cd/m^2) placed either at 57 or 40 cm from the cat's eyes. Stimuli used were sinusoidal gratings of various spatial frequency, contrast and orientation. Contrast was defined as:

$$(L_{max} - L_{min})/(L_{max} + L_{min}),$$

where L_{max} and L_{min} are the maximum and minimum luminance, respectively.

For visual evoked potential (v.e.p.) recording, stationary gratings phase-reversed at temporal frequencies ranging from 2 to 8 Hz (4–16 reversals/s) were used. The signals from the micro-electrode were filtered with an active bandpass filter (1–60 Hz). The v.e.p.s recorded in response to phase-reversed gratings result in a periodic wave form (approximately sinusoidal, Campbell & Maffei, 1970) with periodicity corresponding to the second harmonic of the stimulus

frequency. The signal was averaged on-line by a Digital PDP11/03 computer over at least 100 stimulus periods in order to improve the signal-to-noise ratio. The averaged responses at any given spatial frequency were Fourier analysed on-line and the amplitude of the second harmonic was used to evaluate the response of the system to that visual stimulus. As a measure of the visual acuity we took the highest spatial frequency at which a potential reliably exceeding the noise level could be obtained in response to a square-wave grating of maximum contrast. For other details of the v.e.p. procedure see Bisti & Carmignoto (1986).

In v.e.p. recordings from area 17 of split-chiasm cats the position of the receptive field from multi-unit recordings was assessed before the beginning of the recording session. In all cases the receptive fields were adjacent to the vertical meridian and within 10 deg of the area centralis.

For single-neurone recordings, gratings either drifted laterally in the cell's preferred direction or phase-reversed at various temporal frequencies. Cell responses were fed to the PDP11/03 computer, which stored the raw sequence of nervous impulses and computed on-line the peristimulus time histogram of the cell responses.

On isolating a single unit the experimental procedure was the following.

(1) The cell's receptive field was mapped on a tangent screen and the c.r.t. screen centred with respect to the receptive field.

(2) The cell's ocular dominance, preferred orientation and direction of movement were assessed by means of hand-held bar stimuli.

(3) A drifting grating of optimum orientation was used to evaluate the cell's optimum spatial frequency and drift velocity for the ipsilateral and the contralateral input (ipsilateral and contralateral eye, respectively).

(4) The cell's contrast threshold for the optimum stimulus presented to the ipsilateral or the contralateral eye was evaluated with the method of adjustment, listening to the cell's discharge through a loudspeaker.

(5) A contrast–response curve was obtained for both the ipsilateral and the contralateral input at least for a grating of optimum spatial frequency.

(6) A spatial-frequency tuning curve was measured for the ipsilateral and the contralateral input, using a sinusoidal grating drifting at the optimum temporal frequency and of contrast 4–6 times the contrast threshold evaluated for each input. The spatial acuity for each input was estimated using square-wave gratings of maximum contrast and determining the highest spatial frequency of the grating which still elicited a response from the cell when presented to the ipsilateral or the contralateral eye.

(7) A temporal-frequency tuning curve and a temporal resolution were evaluated in a similar way for each input.

Crucial points of steps 5, 6 and 7 were repeated several times in order to minimize the effects of variability in cell responsiveness. The whole procedure took, on average, 70–80 min to be completed.

To evaluate the contrast threshold and the slope of the contrast–response curve, data were fitted linearly by the method of least squares; experimental points in the range of saturation were not included in the fit. We considered a curve well-fitted by a straight line when the correlation coefficient was greater than 0·9.

For each animal at least two penetrations, either for v.e.p.s or single-unit recordings, were performed for each hemisphere. All the penetrations performed with micropipettes containing Pontamine were marked for subsequent histological reconstruction (for details see Berardi, Bisti, Cattaneo, Fiorentini & Maffei, 1982).

At the end of the recording session the animal was given a lethal dose of pentobarbitone and the eyes were quickly removed for a whole-mount preparation of the retina (Stone, 1965) to control for the complete section of the optic chiasm. The animal was subsequently perfused through the heart with saline and formol saline, and the brain removed and stored in fixative for 2 days. Blocks of frozen tissue were then cut (40 μm) and counter-stained with neutral red for the histological reconstruction of the penetrations.

Classification of the cells as simple or complex in area 17 and simple-like or complex-like in area 18 was performed on the basis of their response to drifting gratings. Cells which responded to a drifting grating with a modulation of their discharge were classified as simple (simple-like in area 18); cells which responded to a drifting grating with an unmodulated increase of their discharge were classified as complex (see Bisti, Carmignoto, Galli & Maffei, 1985, for references).

The noise level for simple and simple-like cells was taken as the amplitude of the first harmonic in the cell's spontaneous discharge.

We have performed altogether four v.e.p. recording sessions from the corpus callosum, ten v.e.p. recording sessions from area 17 of split-chiasm cats and two from the deafferented hemisphere of the optic-tract-sectioned cat. Three v.e.p. recording sessions have been performed in the alert split-chiasm cat.

We have recorded from fifty-six neurones in area 18 of split-chiasm cats, all with receptive fields within 3–4 deg of the vertical meridian and 5 deg of the area centralis.

Only data gathered in animals where the section of the optic tract was complete or the section of the optic chiasm was complete and fairly symmetrical were included in our sample. No difference has been found betwen recordings performed in the right and the left hemisphere.

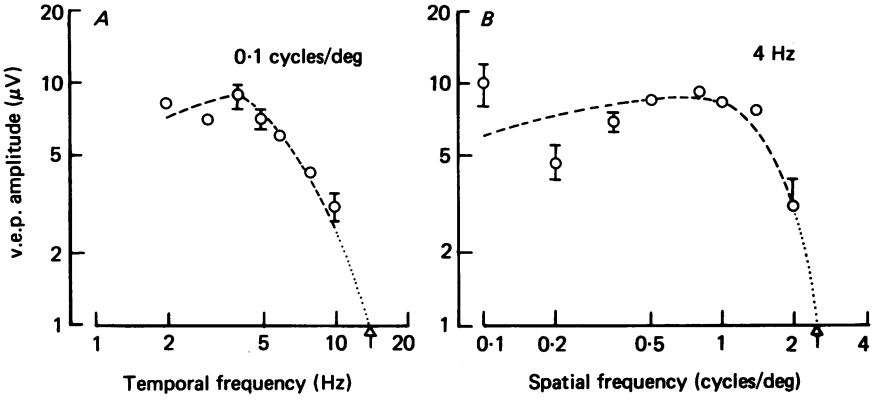

Fig. 1. V.e.p.s recorded from the corpus callosum. The v.e.p. amplitude is shown as a function of the temporal (*A*) and spatial (*B*) frequency of the visual stimuli, which are sinusoidal gratings of either fixed spatial frequency (0·1 cycles/deg) in the case of the temporal m.t.f. or fixed temporal frequency (4 Hz) in the case of the spatial m.t.f. The temporal frequency refers to the rate of alternation. In both cases the contrast used was 18%. The arrows on the abscissae mark the spatial and temporal acuities, evaluated with maximum contrast gratings (75%). Experimental data have been interpolated by eye (interrupted curves). The standard deviations of several experimental points are shown to give an idea of the signal variability.

RESULTS

Electrophysiological recordings from the corpus callosum

The first attempt to determine the type of information transmitted through the corpus callosum has been to measure the modulation transfer function (m.t.f.) of the callosal system, both in the space and the time domain, recording the mass activity with a micro-electrode inserted in the corpus callosum.

Fig. 1 shows an m.t.f. in the time (*A*) and the space domain (*B*) obtained for one cat. The amplitude of the v.e.p.s is shown as a function of the temporal (*A*) or spatial (*B*) frequency of the stimuli, which are sinusoidal gratings of either fixed spatial frequency (in the case of the temporal m.t.f.) or fixed temporal frequency (in the case of the spatial m.t.f.). The temporal m.t.f. reported was obtained for gratings of spatial frequency 0·1 cycles/deg; similar results can be obtained using other spatial frequencies in the region of approximately one decade where the spatial m.t.f. is rather flat, i.e. where the dependence of the signal amplitude on the stimulus spatial frequency is weak or absent. The spatial m.t.f. that we report was obtained for a rate of grating alternation of 4 Hz. Similar results can be obtained for alternation rates ranging from 2 to 6 Hz.

At first sight, the m.t.f.s of the callosal system are roughly comparable to the m.t.f.s evaluated with various techniques for the whole visual system of the cat, both in shape and in frequency range. However, it has to be noted that both the spatial and temporal acuities do not reach the values obtained behaviourally or estimated with cortical evoked potentials (Campbell, Maffei & Piccolino, 1973; Bisti & Maffei, 1974; Berkeley, Loop & Evinger, 1975).

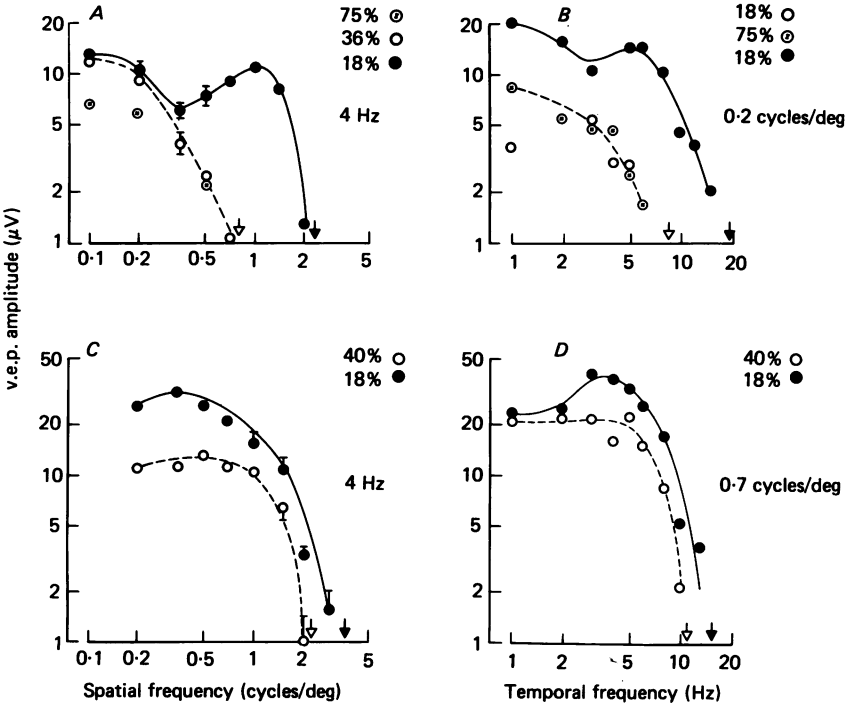

Fig. 2. V.e.p.s in area 17 of split-chiasm cats. M.t.f.s in the space (*A* and *C*) and the time domain (*B* and *D*) recorded in area 17 of two split-chiasm cats, cat CH5 (*A* and *B*) and cat CH2 (*C* and *D*). The spatial and temporal frequencies of the gratings used to evaluate, respectively, the temporal and spatial m.t.f.s are indicated in the Figure. Filled circles, data obtained for the ipsilateral eye; open circles, data obtained for the contralateral eye. The contrasts of the stimuli are indicated on the Figure. Only the data obtained with 36% contrast in *A* and 75% contrast in *B* have been interpolated. The filled and open arrows on the abscissae mark the acuity values obtained for the ipsilateral and the contralateral eye, respectively. Noise levels: 0·8 μV (*A*), 0·5 μV (*B*), 0·6 μV (*C*) and 0·9 μV (*D*).

The fact that the callosal visual system exhibits lower resolution values than the whole visual system has been confirmed by v.e.p.s recorded from a visual cortical area (area 17) in the deafferented hemisphere of a cat with section of the optic tract: both spatial and temporal resolution values were lower than those normally found for v.e.p. recordings in area 17, particularly the spatial acuity.

V.e.p. recordings in split-chiasm cats: m.t.f.s in the space and the time domain

To allow a *direct* comparison of the information transmitted through the corpus callosum with that transmitted through the direct geniculo-cortical system, we recorded v.e.p.s in area 17 of cats with the optic chiasm sectioned. In such a

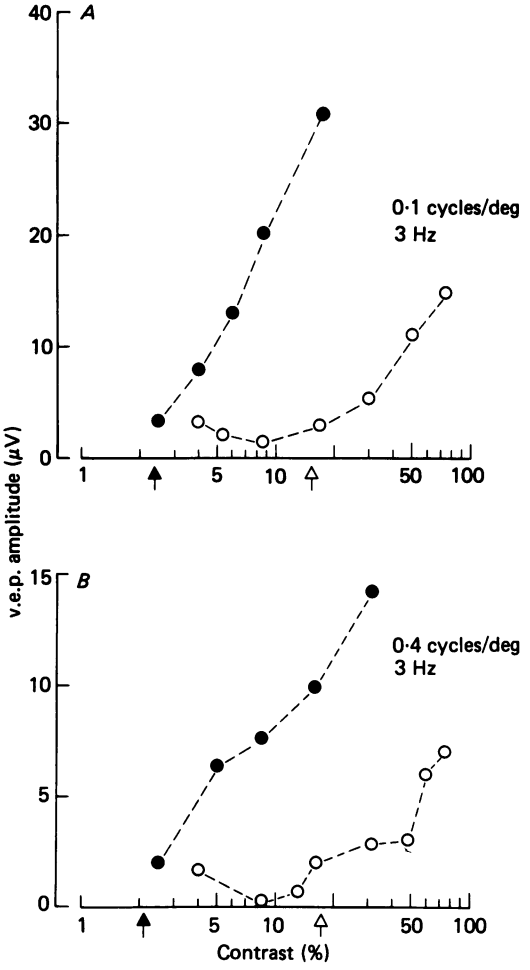

Fig. 3. Contrast–v.e.p. amplitude curves in area 17 of split-chiasm cats. The v.e.p. amplitude recorded in area 17 of a split-chiasm cat is shown as a function of the logarithm of the stimulus contrast for two spatial frequencies of the sinusoidal grating used (*A*, 0·1 cycles/deg, and *B*, 0·4 cycles/deg). The rate of alternation of the gratings was 3 Hz in both cases. Open symbols, data obtained from the contralateral eye; filled symbols, data obtained from the ipsilateral eye. The arrows on the abscissae mark the extrapolated contrast thresholds: 2·3 % for the ipsilateral and 15·2 % for the contralateral eye, with the 0·1 cycles/deg grating, and 2 % for the ipsilateral and 17 % for the contralateral eye, with the 0·4 cycles/deg grating. Noise levels: 1 μV (*A*) and 0·8 μV (*B*).

preparation the optic fibres which cross to the opposite side of the brain are severed, and the only way by which the visual input from one eye can reach the contralateral hemisphere is through the corpus callosum. By comparing the m.t.f.s of v.e.p.s obtained by stimulation of the ipsilateral and the contralateral eye it is possible to compare the characteristics of the direct geniculo-cortical system with those of the callosal system. It has to be remembered that while v.e.p.s from the corpus callosum give the characteristics of the whole visual callosal input transmitted to the contralateral hemisphere, v.e.p.s recorded from area 17 give information about the

callosal input to area 17, with the additional contribution of local intracortical activity. Fig. 2 shows the m.t.f.s obtained for two split-chiasm cats (*A* and *B*, cat CH5; *C* and *D*, cat CH2) in the space domain (*A* and *C*) and the time domain (*B* and *D*).

The first finding worth noting is that in both cats the contrast of the stimulus presented to the contralateral eye had invariably to be set at high values in order

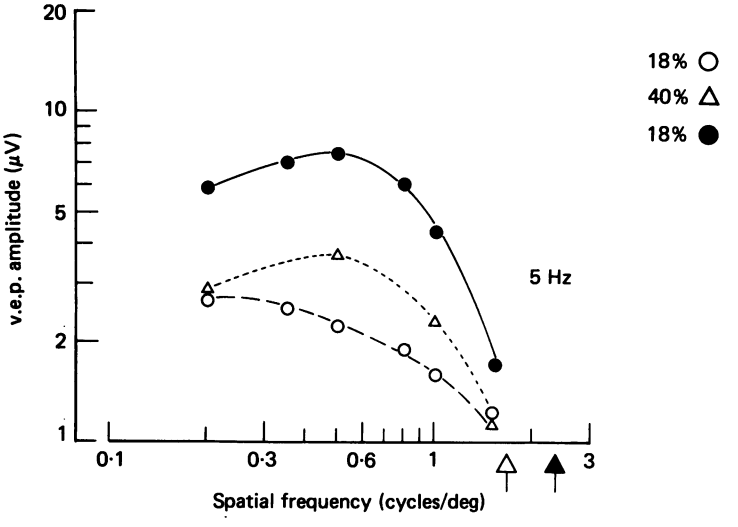

Fig. 4. V.e.p.s in area 17 of alert split-chiasm cats. M.t.f. in the space domain recorded from area 17 of an alert split-chiasm cat for the contralateral (open symbols) and the ipsilateral (filled symbols) eye. The contrasts of the stimuli are indicated on Figure. Fixed temporal frequency, 5 Hz. Arrows have the same meaning as in Fig. 2. Noise level, $1{\cdot}5 \pm 0{\cdot}3\ \mu V$.

to obtain a reliable response from the callosal pathway. Despite the higher contrast used, in both cats the amplitude of the signals evoked by the callosal input is lower than that evoked by the direct input, even when the maximum available stimulus contrast is used (Fig. 2*A* and *B*).

In addition, the spatial and temporal acuities of the callosal system are lower than those of the direct system. The ratio between the values of the acuity (direct/callosal) is 3 for the spatial and 2·5 for the temporal acuity of cat CH5, 1·9 for the spatial and 1·5 for the temporal acuity of cat CH2.

On average, the ratios obtained are 2 ± 1 ($n = 8$) for the spatial acuity and $2{\cdot}0 \pm 0{\cdot}7$ for the temporal acuity ($n = 7$).

V.e.p.s in split-chiasm cats: contrast–response curves

An interesting point would be to see whether the difference in signal amplitude observed between the callosal and the direct pathways for suprathreshold stimulus contrasts is present also at threshold stimulus contrast.

It has been reported (Campbell & Maffei, 1970) that a linear relationship exists between the v.e.p. amplitude (voltage) and the logarithm of the stimulus contrast, and that the contrast threshold for a given spatial frequency can be evaluated by

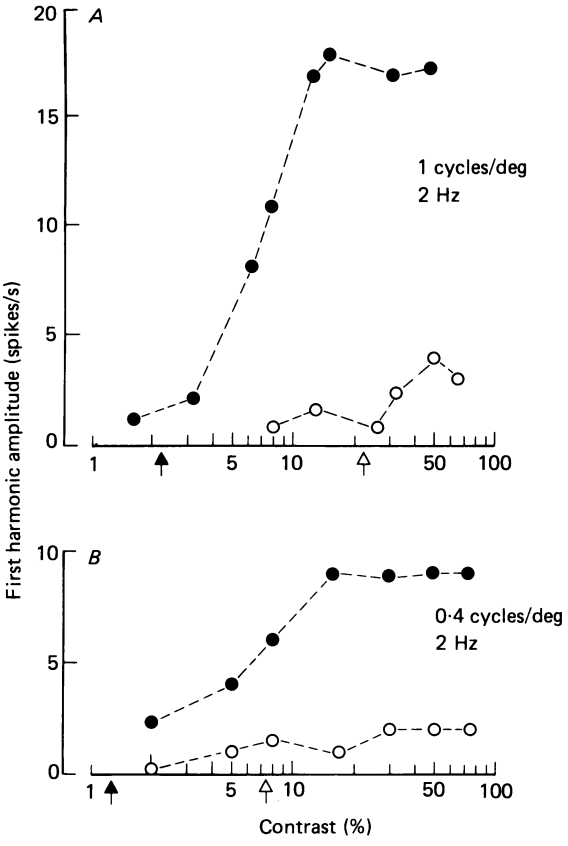

Fig. 5. Contrast–response curves for single cells of area 17 in split-chiasm cats. The first harmonic amplitude of the modulation of the cell discharge is shown as a function of the logarithm of the stimulus contrast for two simple cells of area 17 in a split-chiasm cat. Filled symbols, data obtained for the ipsilateral eye; open symbols, data obtained for the contralateral eye. The stimulus was a drifting sinusoidal grating (temporal frequency, 2 Hz) of optimum spatial frequency for each cell (*A*, 1 cycle/deg; *B*, 0·4 cycles/deg). The extrapolated contrast thresholds (marked by arrows on the abscissae) are: *A*, 2·2 % for the ipsilateral and 22 % for the contralateral eye; *B*, 1·2 % for the ipsilateral and 7·4 % for the contralateral eye. Noise levels: *A*, 0·6 spikes/s; *B*, 0·5 spikes/s.

extrapolating to zero response (noise level) the regression line for the contrast–response relation obtained for a grating of that spatial frequency.

An example of two contrast–response curves is shown in Fig. 3 for two spatial frequencies (*A*, 0·1 cycles/deg and *B*, 0·4 cycles/deg). The extrapolated contrast thresholds are marked by arrows: it is evident that the contrast threshold for the callosal input (open circles) is much higher than that for the direct input (filled circles) by nearly a factor of 7 for 0·1 cycles/deg and by a factor of 8 for 0·4 cycles/deg. The average ratio between the threshold for the callosal and direct pathways for all the contrast–response curves measured is 5 ± 3 ($n = 7$). The slope of the linear-regression line can be taken as a measure of the contrast gain; the ratio of the gains for the direct and indirect callosal pathway is 1·8 for 0·1 cycles/deg and 1·5 for 0·4 cycles/deg. The average ratio is $1{\cdot}7 \pm 0{\cdot}2$ ($n = 7$).

V.e.p.s in alert split-chiasm cats

The difference in contrast sensitivity observed between the signals transmitted through the direct and callosal pathways could be due to a differential effect of anaesthesia on the callosal *vs.* the direct pathway. In order to check this possibility we have performed an experiment where v.e.p.s were recorded from area 17 of an alert split-chiasm cat.

The results are reported in Fig. 4 for the spatial domain. It has to be noted that: first, the amplitude of the signals for the direct pathway is higher than that for the callosal pathway by nearly a factor of 2 at every frequency tested, and secondly, the signal from the callosal pathway becomes indistinguishable from the noise level beyond 1 cycle/deg. The spatial acuities are 1·6 cycles/deg for the callosal and 2·5 cycles/deg for the direct pathway. The ratio between the two values is 1·5, a value which is in the range of ratios found in our sample of anaesthetized animals.

Single-cell recordings in area 17 of split-chiasm cats

We recorded fifty-six cells in area 17 and thirty-seven cells in area 18 of split-chiasm cats. As previously reported (Maffei, Berardi & Bisti, 1986), the percentage of binocular units in area 18 is higher than in area 17 (73 % against 52 %) and the two ocular dominance distributions are different. Indeed, in area 17, binocular cells are distributed predominantly between ocular dominance classes 6 and 5, with no cells in classes 3–2 (see also Cynader, Gardner, Dobbin, Lepore & Ghiemo, 1986) whereas binocular neurones of area 18 are distributed more evenly amongst classes 6–2. The subject of area-18 callosal input will be briefly taken up again at the end of the Results section.

Contrast–response curves. In *all* area-17 cells where the callosal input was present, this was always weaker than the direct input; that is, the amplitude of the cell response to a stimulus presented to the contralateral eye was invariably lower than that obtained presenting the same stimulus to the ipsilateral eye. To evaluate this difference in signal amplitude more quantitatively, in terms of contrast threshold and contrast gain, we have measured a complete contrast–response curve for both inputs in eight cells. An example for two simple cells is presented in Fig. 5. It has to be noted that for both cells the contrast threshold is higher, and the contrast–response relation is much shallower, for the callosal than for the direct input. Similar results have been obtained for all the other cells. The mean ratio between the thresholds of the two inputs (callosal/direct) is 6 ± 2, ($n = 8$), with values as high as 10; the mean ratio between the slopes of the best regression lines through the two sets of data (direct/callosal) is 3 ± 1 ($n = 6$). Only those regression lines with correlation coefficient greater than 0·9 have been included in the sample (see Methods).

Thus, not only does the callosal input need a higher stimulus contrast in order to evoke a response from a neurone (higher threshold), but the response amplitude barely increases with increasing contrast (lower gain); it is therefore not surprising that the contrast of the stimulus had invariably to be set at very high levels to obtain a reliable response from the contralateral eye.

Spatial characteristics of the callosal vs. the direct input. In area 17 the spatial characteristics have been carefully documented both for the direct and the callosal input in eight cells.

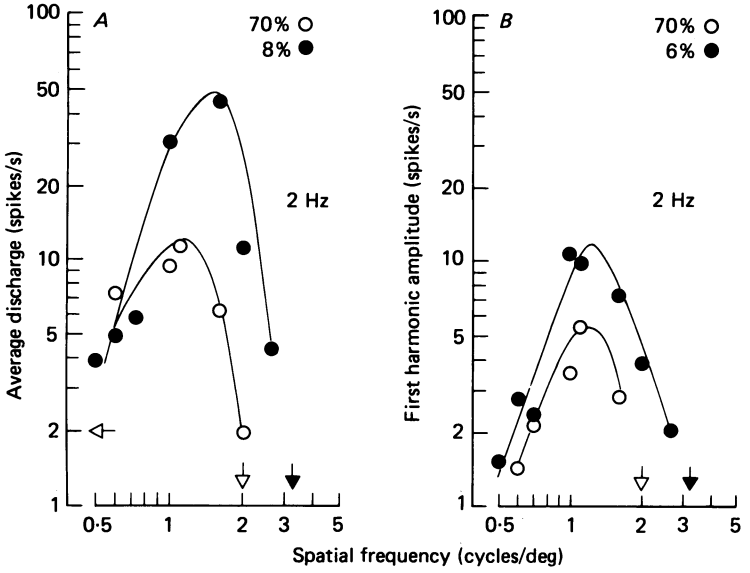

Fig. 6. Spatial-frequency tuning curves for the callosal and the direct input for neurones in area 17 of split-chiasm cats. The dependence of the cell response (*A*, average discharge; *B*, first harmonic amplitude) is shown as a function of the stimulus spatial frequency for a complex cell (*A*) and a simple cell (*B*) in area 17 of two split-chiasm cats. Arrows on the abscissae have same meaning as in Fig. 2. The spontaneous discharge level of the complex cell is marked by the arrow on the ordinate. The contrasts of the stimuli are indicated on Figure. Fixed temporal frequency, 2 Hz. Noise level for the simple cell, 0·7 spikes/s.

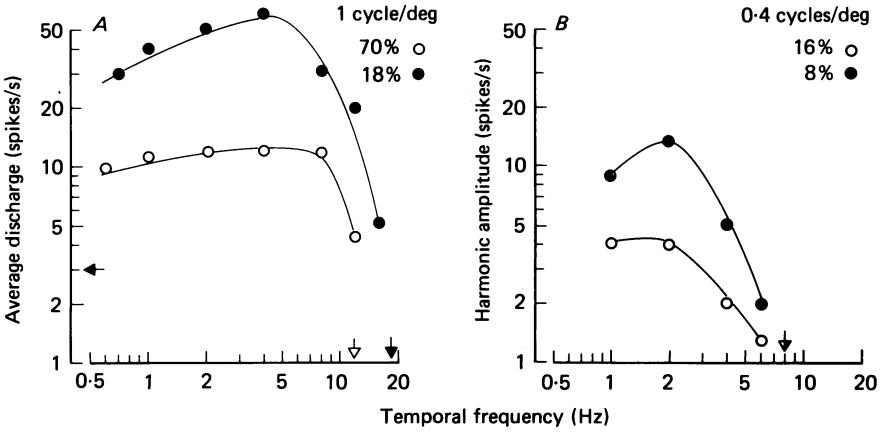

Fig. 7. Temporal tuning curves for the direct and callosal input for neurones of area 17 in split-chiasm cats. The response of a complex (*A*) and a simple cell (*B*) in area 17 of two split-chiasm cats is shown as a function of the temporal frequency of the stimulus. Arrows on the abscissae have same meaning as in Fig. 2. The spontaneous discharge of the complex cell is marked by the arrow on the ordinate. The contrasts of the stimuli and the fixed spatial frequencies are shown on the Figure. Noise level for the simple cell, 0·5 spikes/s.

Fig. 6 shows two spatial-frequency tuning curves measured for a complex (*A*) and a simple cell (*B*). It is evident that: (1) the bands of spatial frequencies transmitted through the two inputs are largely superimposed and there is no striking difference in the position of the optimum spatial frequency and in the low spatial-frequency cut-off; this observation is confirmed in all the other cells of our sample, (2) the spatial acuity for the direct input is higher than that of the callosal input for both cells shown in Fig. 6; this result has been observed in six out of eight cells (mean ratio for the ipsilateral/contralateral spatial acuity is 2 ± 1) and is more striking for those cells with acuities higher than 2 cycles/deg, and (3) the response amplitude for the contralateral input is noticeably lower than the ipsilateral input, despite the contrasts used being 6–8 % for the direct and 70 % for the callosal pathway.

Temporal characteristics of the callosal vs. the direct input. In area 17 the temporal characteristics of six cells have been documented both for the direct and the callosal pathway. The frequency ranges spanned by the two inputs are largely superimposed, again showing a difference in resolution, present in five out of six cells (mean ratio for the ipsilateral/contralateral acuity is $2{\cdot}0 \pm 1$). Fig. 7 shows the temporal tuning curves for two cells, a simple and a complex cell. The cell shown in *B* is the only cell in which the temporal resolution values were identical for both pathways.

The callosal input to area 18. We found in area 18 cells with a contralateral input comparable in strength to the ipsilateral input, at variance with area 17. The evaluation of contrast–response curves for the callosal and the direct input in area 18 confirmed that the callosal input to area 18 seems to be 'stronger' than in area 17 (see also Maffei *et al.* 1986). We found that only five out of fourteen cells in area 18 had a lower contrast threshold for the direct than the callosal input. As for the spatial and temporal characteristics, fewer cells in area 18 exhibit a difference in spatial and temporal resolution values (five out of ten).

DISCUSSION

We have shown both with v.e.p.s and single-unit recordings that the corpus callosum transmits a large portion of the information relayed to the cortex by the lateral geniculate nucleus. However, the contrast gain of the callosal pathway is considerably lower than the gain of the direct, geniculo-cortical system, with ratios of signal amplitude as low as 0·1 for the same stimulus contrast. In addition, high spatial and temporal frequencies are strongly attenuated in the process of callosal transfer.

Within our sample of neurones in split-chiasm cats, the difference in signal amplitude between the callosal and the direct input is much stronger for area 17 than for area 18 cells.

The relevance of these findings is strengthened by the results obtained in the alert split-chiasm cat, which show that the differences between the callosal and the direct pathway are not the consequence of a higher susceptibility of the former to anaesthetics, but reflect different properties of the two pathways.

It would be interesting to find out from where these properties of the callosal m.t.f. arise. For instance, the lower signal amplitude and the high spatial frequency attenuation observed for the callosal recipient cells in split-chiasm cats by stimulation of the contralateral eye could be already present at the level of the input fibres, i.e.

the callosal fibres, or could be due to the integration processes in the recipient hemisphere.

The mass recordings from the corpus callosum (Fig. 1) indicate that an attenuation in high spatial and temporal frequencies shows up already at the level of the input fibres; however, from our mass recordings it is impossible to trace back the contrast gain of the single callosal fibres.

Implications for the physiological role of the corpus callosum

One of the most important observations reported in this paper is that in split-chiasm preparations the callosal input can be activated only for high contrasts and low spatial frequencies.

A consequence of these results would be that the cross-talk between the hemispheres taking place across the corpus callosum at the 17/18 border is nearly abolished at low contrasts and high spatial frequencies. (Some behavioural data concerning the callosal transfer of complex forms seem to be explained by these present results; personal communication by J. Sprague.)

If one assumes that the m.t.f.s for the callosal input to the visual areas involved in the transfer of learning and discrimination have similar properties of attenuation to those of area 17, one would predict that in behavioural experiments in split-chiasm cats the performance level attained monocularly for a visual discrimination task should be more easily retained in the process of interocular (interhemispheric) transfer when the patterns to be discriminated have relatively high contrasts. On the other hand, retention should be impaired or even absent in the transfer of pattern discrimination with patterns of low contrast. Experiments are in progress to verify this hypothesis.

If our physiological results on the transfer of information across the corpus callosum could be extended from cats to humans, one would predict that only neural signals elicited by stimuli of low spatial frequency and high contrast would be transferred from one hemisphere to the other. Indeed, Berardi & Fiorentini (1985, 1987) have found psychophysical results consistent with this hypothesis. They have shown that the right hemisphere superiority found in the discrimination of complex gratings differing in the spatial phase of their harmonic components (Fiorentini & Berardi, 1985) disappears when patterns of low spatial frequency and high contrast are presented close (1 deg) to the vertical meridian, i.e. in a region of the visual field where the presence of callosal connexions has been demonstrated, at least in monkeys. For the discrimination of gratings of high spatial frequency and low contrast, a right hemisphere superiority is present also at the same small distance from the vertical meridian.

We thank Dr A. Fiorentini for critical reading of the manuscript and A. Antoni, G. C. Cappagli, A. Tacchi and P. Taccini for technical assistance. N. B. is a Research Fellow of Scuola Normale Superiore, Pisa.

REFERENCES

BERARDI, N., BISTI, S., CATTANEO, A., FIORENTINI, A. & MAFFEI, L. (1982). Correlation between the preferred orientation and spatial frequency of neurones in visual areas 17 and 18 of the cat. *Journal of Physiology* **323**, 603–618.

BERARDI, N. & FIORENTINI, A. (1985). Possible role of interhemispheric information transfer in the discrimination of complex gratings. *Perception* **14**, A6.

BERARDI, N. & FIORENTINI, A. (1987). Interhemispheric transfer of visual information in humans: spatial characteristics. *Journal of Physiology* **384**, 633–647.

BERKELEY, M. A., LOOP, M. S. & EVINGER, C. (1975). Temporal modulation sensitivity in the cat. II. Evoked potentials measures. *Vision Research* **15**, 563–568.

BERLUCCHI, G. (1972). Anatomical and physiological aspects of visual functions of corpus callosum. *Brain Research* **37**, 371–392.

BERLUCCHI, G., GAZZANIGA, M. S. & RIZZOLATTI, G. (1967). Microelectrode analysis of transfer of visual information by the corpus callosum. *Archives italiennes de biologie* **105**, 583–596.

BERLUCCHI, G. & MARZI, C. A. (1982). Interocular and interhemispheric transfer of visual discrimination in the cat. In *Analysis of Visual Behaviour*, ed. INGLE, D. J., GOODALE, M. A. & MANSFIELD, R. J. W., pp. 719–750. Cambridge, MA, U.S.A.: M.I.T. Press.

BERLUCCHI, G. & RIZZOLATTI, G. (1968). Binocularly driven neurons in visual cortex of split chiasm cats. *Science* **159**, 308–310.

BERLUCCHI, G. & SPRAGUE, J. M. (1981). The cerebral cortex in visual learning and memory, and in interhemispheric transfer in the cat. In *The Organization of the Cerebral Cortex*, ed. SCHMITT, F. O., WORDEN, F. G., ADELMAN, G. & DENNIS, J. G., pp. 415–440. Cambridge, MA, U.S.A.: M.I.T. Press.

BISHOP, P. O. (1973). Neurophysiology of binocular single vision and stereopsis. In *Handbook of Sensory Physiology*, vol. VII/3A, *Central Processing of Visual Information*, ed. JUNG, R., pp. 256–305. Berlin: Springer-Verlag.

BISTI, S. & CARMIGNOTO, G. (1986). Monocular deprivation in kittens differently affects crossed and uncrossed visual pathways. *Vision Research* **26**, 875–884.

BISTI, S., CARMIGNOTO, G., GALLI, L. & MAFFEI, L. (1985). Spatial-frequency characteristics of neurones of area 18 in the cat: dependence on the velocity of the visual stimulus. *Journal of Physiology* **359**, 259–268.

BISTI, S. & MAFFEI, L. (1974). Behavioural contrast sensitivity of the cat in various visual meridians. *Journal of Physiology* **241**, 201–210.

BLAKEMORE, C. (1969). Binocular depth discrimination and the nasotemporal division. *Journal of Physiology* **205**, 471–497.

BLAKEMORE, C. (1970). Binocular depth perception and the optic chiasm. *Vision Research* **10**, 43–47.

BLAKEMORE, C., DIAO, Y., PU, M., WANG, Y. & XIAO, Y. (1983). Possible functions of the interhemispheric connexions between visual cortical areas in the cat. *Journal of Physiology* **337**, 331–349.

CAMPBELL, F. W. & MAFFEI, L. (1970). Electrophysiological evidence for the existence of orientation and size detectors in the human visual system. *Journal of Physiology* **207**, 635–652.

CAMPBELL, F. W., MAFFEI, L. & PICCOLINO, M. (1973). The contrast sensitivity of the cat. *Journal of Physiology* **229**, 719–731.

CHOUDHURY, B. P., WHITTERIDGE, D. & WILSON, M. E. (1965). The functions of the callosal connections of the visual cortex. *Quarterly Journal of Experimental Physiology* **50**, 214–219.

CYNADER, M., GARDNER, I., DOBBIN, A., LEPORE, F. & GHIEMO, J. P. (1986). Interhemispheric communication and binocular vision: functional and developmental aspects. In *Two Hemispheres – One Brain: Functions of the Corpus Callosum*, ed. LEPORE, F., PTITO, M. & JASPER, H. H., pp. 189–209. New York: Alan R. Liss.

FERNALD, R. & CHASE, R. (1971). An improved method for plotting retinal landmarks and focusing the eyes. *Vision Research* **11**, 95–96.

FIORENTINI, A. & BERARDI, N. (1984). Right-hemisphere superiority in the discrimination of spatial phase. *Perception* **13**, 695–708.

HARVEY, A. R. (1980). A physiological analysis of subcortical and commissural projections of areas 17 and 18 of the cat. *Journal of Physiology* **302**, 507–534.

HUBEL, D. H. & WIESEL, T. N. (1967). Cortical and callosal connections concerned with the vertical meridian of visual fields in the cat. *Journal of Neurophysiology* **30**, 1561–1573.

INNOCENTI, G. M. (1980). The primary visual pathway through the corpus callosum: morphological and functional aspects in the cat. *Archives italiennes de biologie* **118**, 124–188.

MAFFEI, L., BERARDI, N. & BISTI, S. (1986). Interocular transfer of adaptation after effect in neurons of area 17 and 18 of split chiasm cats. *Journal of Neurophysiology* **55**, 966–976.

MITCHELL, D. E. & BLAKEMORE, C. (1970). Binocular depth perception and the corpus callosum. *Vision Research* **10**, 49–54.

PAYNE, B. R., PEARSON, H. E. & BERMAN, N. (1984). Role of corpus callosum in functional organization of cat striate cortex. *Journal of Neurophysiology* **52**, 570–594.

SHATZ, C. (1977*a*). Abnormal interhemispheric connections in the visual system of Boston siamese cats: a physiological study. *Journal of Comparative Neurology* **171**, 229–246.

SHATZ, C. (1977*b*). Anatomy of interhemispheric connections in the visual system of Boston siamese and ordinary cats. *Journal of Comparative Neurology* **173**, 497–518.

SINGER, W., TRETTER, F. & CYNADER, M. (1975). Organization of cat striate cortex: a correlation of receptive field properties with afferent and efferent connections. *Journal of Neurophysiology* **38**, 1080–1098.

STONE, J. (1965). A quantitative analysis of the distribution of ganglion cells in the cat's retina. *Journal of Comparative Neurology* **124**, 337–354.

SYMONDS, L. L. (1982). Connections among cortical visual areas in the cat. Ph.D Dissertation. Philadelphia: University of Pennsylvania.

TOYAMA, K., MATSUNAMI, K. & OHNO, T. (1969). Antidromic identification of association, commissural and corticofugal efferent cells in cat visual cortex. *Brain Research* **14**, 518–520.

TOYAMA, K., MATSUNAMI, K., OHNO, T. & TOKASHIKI, S. (1974). An intracellular study of neuronal organization in the visual cortex. *Experimental Brain Research* **21**, 45–66.

WHITTERIDGE, D. (1965). Area 18 and the vertical meridian of the visual field. In *Functions of the Corpus Callosum*, ed. ETTLINGER, E. G., pp. 115–120. London: Churchill.