

## INTERHEMISPHERIC TRANSFER OF VISUAL INFORMATION IN HUMANS: SPATIAL CHARACTERISTICS

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### SUMMARY

1. The problem of the interhemispheric transfer of visual information in humans has been approached psychophysically, making use of a visual discrimination task that shows a clear left field advantage and is subject to the phenomenon of perceptual learning.

2. For this task (discrimination of complex gratings differing only by the relative spatial phase of their harmonic components) there is a left field advantage and a lack of interhemispheric transfer of learning effects at all spatial frequencies tested for stimuli removed at least 5 deg from either side of the vertical meridian.

3. For stimuli close to the vertical meridian, the left field advantage disappears and there is a complete transfer of learning effects, provided the fundamental spatial frequency is 2 cycles/deg or lower.

4. At higher spatial frequencies the left field advantage is maintained and the learning effects do not transfer from one visual hemifield to the other, even at  $\pm 0.5$  deg from the vertical meridian, unless the contrast is very high.

5. The transfer of learning effects obtained for spatial frequencies of 2 cycles/deg or lower is peculiar to regions placed close to the vertical meridian and symmetrically located on either side of it. No transfer is obtained between non-overlapping regions on the same side of the vertical meridian.

6. These findings are consistent with an interhemispheric transfer of visual information, preferential for low spatial frequencies and high contrasts, in agreement with that found for callosal transfer in the cat (Berardi, Bisti & Maffei, 1987).

### INTRODUCTION

It has been known for a long time that in higher mammals, and particularly in primates, most visual areas in the two hemispheres are connected through the corpus callosum. Only in the last 20 years, however, has the physiological role of the corpus callosum come to be understood. Anatomical and electrophysiological data agree in indicating that, with few exceptions, callosal connexions between visual cortical areas are restricted to a strip along the projection of the vertical meridian and contribute to the representation of the portion of the ipsilateral visual hemifield which is found in each hemisphere (see for instance Berlucchi, 1981; van Essen, Newsome & Bixby, 1982). This has suggested that a possible role of callosal connexions is to grant

perceptual continuity across the vertical meridian (Choudhury, Whitteridge & Wilson, 1965; Hubel & Wiesel, 1967; Berlucchi & Rizzolatti, 1968).

In addition, behavioural experiments in split-chiasm animals demonstrate that there is interocular (interhemispheric) transfer of learning effects in discrimination tasks with visual stimuli restricted to one hemisphere, provided that the corpus callosum is intact (see Berlucchi & Marzi, 1982, for references).

Relatively little is known about the informational content of the neural messages transmitted through the callosal connexions. Recent electrophysiological experiments in the cat (Berardi *et al.* 1987) have suggested that information about visual stimuli of low spatial and temporal frequency and high contrast are preferentially transmitted through the corpus callosum, while high spatial and temporal frequencies are almost completely filtered out in the process of interhemispheric callosal transfer.

We thought it of interest to investigate whether in man similar limitations are imposed on the interhemispheric transfer of visual information.

We have approached the problem psychophysically, making use of a visual discrimination task that shows a clear lateralization (discrimination is better performed when the stimuli are presented in the left than in the right visual hemifield) (Fiorentini & Berardi, 1984) and is subject to a striking phenomenon of perceptual learning (Fiorentini & Berardi, 1980, 1981).

Our experimental paradigm has been to investigate whether the lateralization (left field advantage) and the lack of transfer of learning effects found for stimuli removed 5 deg or more from the vertical meridian still hold at smaller distances from the vertical meridian, i.e. in a region of the visual field likely to correspond to callosal zones of the cortical areas. The discriminanda were complex gratings differing in the relative spatial phase of their harmonic components. They were therefore suitable to use in investigating whether a possible interhemispheric transfer is contingent upon the stimulus spatial frequency and contrast.

We shall show that, when the stimuli are presented close to the vertical meridian, the left field advantage disappears and there is a complete transfer of learning effects, provided that the spatial frequency is not too high and the contrast is not too low. These findings will be shown to be consistent with the hypothesis of an interhemispheric callosal transfer limited to stimuli of sufficiently high contrast and/or low spatial frequency.

A preliminary account of these findings has been given elsewhere (Berardi & Fiorentini, 1985).

#### METHODS

##### *Stimuli*

Compound gratings generated by a Digital PDP 11/03 computer were displayed on a Tektronix oscilloscope, 34 cd/m<sup>2</sup> mean luminance. The luminance profile of the grating was the sum of two sinusoids of spatial frequency  $f$  and  $3f$  with contrast ratio 3:1, like the fundamental and third harmonic of a square wave. The relative spatial phase of the  $3f$  component could be pre-set at any value between 0 deg (peak-subtract) and 180 deg (peak-add) under computer control. A piece of white cardboard with a window 8 × 8 cm (illuminated at the same mean luminance as the oscilloscope) was set immediately in front of the oscilloscope screen and used to limit the size of the stimulus. To assure fixation and correct focusing at the grating distance a black diamond (4 mm side) was applied at a chosen (variable) position on the cardboard. Unless otherwise stated, the fixation spot was centred with respect to the vertical side of the stimulus grating and removed laterally, so that the grating appeared either in the right or in the left visual field.

The viewing distance was 1.2 or 2.4 m. The fundamental spatial frequency of the grating was 2 or 4 cycles/deg, respectively, at the two viewing distances. Lower spatial frequencies were obtained by varying the period of the grating.

The contrast and time of presentation of the gratings were under computer control. The orientation could be varied by rotating the oscilloscope behind the cardboard mask. When oblique gratings were used, the mask had an octagonal shape (see inset in Fig. 7).

### *Procedure*

*Experiment 1 – spatial phase thresholds.* In this experiment, pairs of compound gratings were compared. In one of them, the spatial phase of the third harmonic was 0 deg (peak-subtract); in the other it was variable. In each trial the two gratings were presented successively, each for a given time (usually 100–250 ms; see Results) with a time interval of 1 s, according to a forced-choice procedure. The subject initiated the trial by pressing a button. The stimulus presentation followed, each grating being accompanied by a sound. Then the subject pressed one of two other buttons to indicate whether the grating with spatial phase of 0 deg had been presented first or second.

The variable spatial phase of one of the discriminanda was varied according to a double staircase procedure, converging to 71 % correct performance level (Badcock, 1984).

As to the definition of spatial phase threshold, it has been argued that the discrimination of complex gratings, as in the present experiments, is the result of local contrast detection rather than true spatial phase discrimination. This argument, however, is irrelevant to the scope and findings of our experiments.

The spatial phase thresholds (minimum relative spatial phase discriminable from a spatial phase of 0 deg; Burr, 1980) were determined for gratings of fundamental spatial frequencies 2 or 4 cycles/deg, of various contrasts and at different eccentricities (distances of the inner side of the grating from the vertical meridian of the visual field) in either visual hemifield.

A similar procedure was used to evaluate the contrast threshold of sinusoidal gratings of spatial frequency 3f at various eccentricities. In this case, the staircase variable was the grating contrast. The stimulus contrasts used to evaluate the spatial phase thresholds were such that the contrast of the third harmonic exceeded its threshold by at least a factor of about 1.3.

*Experiment 2 – learning of spatial phase discrimination.* The aim of this experiment was to investigate whether the improvement in the performance of forced-choice spatial phase discriminations resulting from repetition of trials (Fiorentini & Berardi, 1980, 1981) transferred from one region of the visual field to another.

To do this, pairs of gratings of different relative spatial phases of their harmonics (0 and 90 deg, or 0 and 75 deg), of fixed contrast, duration, spatial frequency and orientation, were presented according to a forced-choice procedure in successive blocks of forty (or twenty) trials each. After each block of trials the percentage of correct responses for that block was displayed on the computer monitor. Several blocks of trials (usually ten) were run for a given eccentricity in one visual hemifield, until the percentage of correct responses stabilized around a constant value. If necessary the procedure was repeated in a subsequent session. Then the fixation spot was moved to a different position, so that the gratings appeared in a different portion of the visual field (for instance, on the opposite side of the vertical meridian). A number (at least five) of blocks of trials was carried out in the new position. In some experiments, a further series of trials was run in which the two grating positions (left and right visual field) were alternated between blocks.

Since the effects of practice in spatial phase discrimination are selective for the orientation and spatial frequency of the gratings, the grating orientation (or spatial frequency) was changed when the same subject had to be tested successively for transfer of learning relative to various areas of the visual fields (i.e. various lateral eccentricities, or upper *vs.* lower field, etc.). It has to be mentioned that when Experiment 1 was performed, the subjects had already reached a stable performance level in the discrimination of gratings of 0 and 90 deg spatial phase, and of the same orientation, spatial frequency and eccentricity as used in Experiment 1. (In fact Experiment 1 was performed after a part of Experiment 2 had been completed).

### *Subjects*

The subjects were the authors (N. B. and A. F.) and a male student (E. C.), unaware of the scope of the experiment. Another subject (E. M.), a female student, participated in a part of Experiment 2.

All subjects were corrected at 20/20, at least for the viewing distance of 1.2 or 2.4 m. Correct focusing was found to be very important for a stable performance in the discrimination of spatial phase, especially at the higher spatial frequency.

During the experiments with the naive subjects, an operator, standing behind the screen, checked by inspection that fixation was maintained during trials.

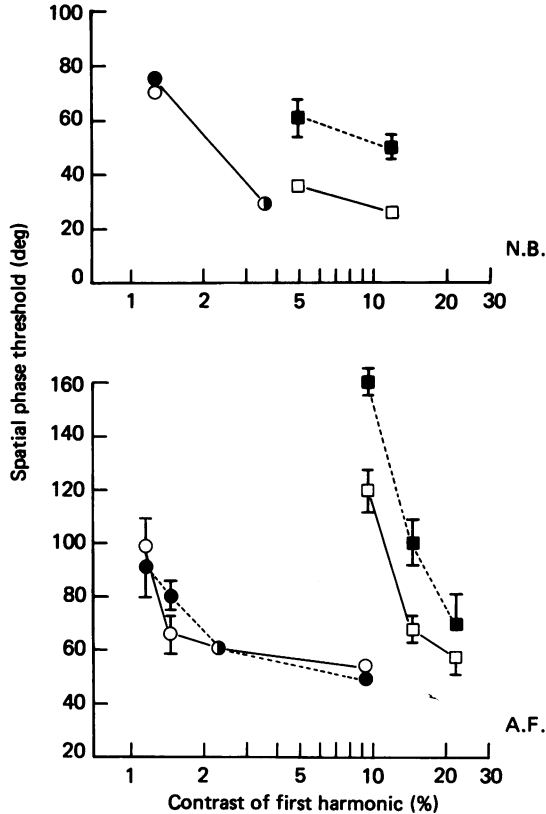


Fig. 1. Spatial phase threshold at 1 deg (circles) and 5 deg (squares) from the vertical meridian in the right (filled symbols) and left (open symbols) visual hemifield, plotted against the contrast of the first harmonic (2 cycles/deg) of the two complex gratings to be discriminated. Data from two subjects. Each point is the mean of at least four threshold evaluations. Standard errors exceeding the size of the symbols are indicated by the vertical bars.

## RESULTS

### *Spatial phase discrimination in the left and right visual fields at different distances from the vertical meridian*

To test for the existence of a lateralization in visual discrimination tasks it is common procedure to present the stimuli some degrees either to the left or to the right of the vertical meridian in order to avoid the possible involvement of callosal connexions. Accordingly, when we explored in our previous work the existence of a lateralization in complex gratings discrimination, we placed our stimuli at least 5 deg from the vertical meridian. In this situation we found a left field advantage.

In the present experiment our aim was to investigate a possible role for the corpus callosum in compensating for this left field advantage. Therefore, we tested the discrimination performance with stimuli located close to the vertical meridian. This was done for stimuli of various spatial frequencies and contrasts.

Our task required the subject to discriminate between two complex gratings differing in the relative spatial phase of their harmonic components  $f$  and  $3f$ . The accuracy in the performance of the task was evaluated by determining the spatial phase threshold, i.e. the minimum phase difference between the relative spatial phase of  $f$  and  $3f$  that could be discriminated from a phase difference of 0 deg (see Methods).

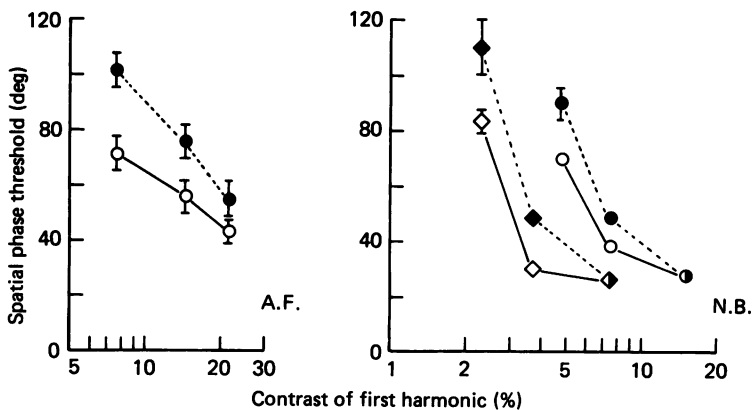


Fig. 2. Spatial phase thresholds for gratings of fundamental spatial frequency 4 cycles/deg at 1 deg (circles) and 0.5 deg (diamonds) from the vertical meridian in the right (filled symbols) and left (open symbols) visual hemifield. Each point is the mean of at least four threshold evaluations.

The rationale of the experiment was first to confirm the left field superiority in spatial phase discrimination for stimuli 5 deg from the vertical meridian, extending these findings to stimuli of various contrasts, and then to repeat the experiment at 1 deg from the vertical meridian.

The results for gratings of fundamental spatial frequency 2 cycles/deg are presented in Fig. 1. It is evident from the results (Fig. 1, squares) that the phase threshold in the right hemifield at 5 deg from the vertical meridian (filled squares) remains larger than in the left hemifield (open squares) for all contrasts tested in both subjects.

Closer to the vertical meridian (Fig. 1, closed and filled circles) no difference was found between the phase thresholds in the two hemifields for either subject, whatever the contrast of the gratings.

At a higher spatial frequency, on the other hand (4 cycles/deg), the contrast of the gratings seems to be an important parameter in determining the presence of a left field advantage for stimuli presented close to the vertical meridian. Indeed, with this spatial frequency there is a left field advantage even at 1 deg eccentricity if the contrast is low; this advantage decreases with increasing contrast and may even disappear for very high contrasts. This is shown in Fig. 2 (circles).

The same dependence on stimulus contrast for gratings of 4 cycles/deg holds at smaller distances from the vertical meridian (0.5 deg; Fig. 2, diamonds).

In conclusion, the left field superiority in the discrimination of spatial phase, previously observed for stimuli removed 5 deg laterally from the vertical meridian, is not present for stimuli extending 1–5 deg from the meridian, unless the contrast is low and the spatial frequency sufficiently high.

#### *Interhemispheric transfer of learning in spatial phase discrimination*

Another approach to the study of interhemispheric transfer is to investigate whether learning of visual discrimination tasks can transfer from one hemisphere to the other (Berlucchi & Marzi, 1982). Spatial phase discrimination offers two possibilities for investigating interhemispheric transfer; one was illustrated in the previous section, namely the lateralization of the task. The other is a perceptual learning effect (Fiorentini & Berardi, 1980, 1981). In this section we report the results of experiments in which the phenomenon of learning in spatial phase discriminations has been used to study the interhemispheric transfer.

This phenomenon consists of an increase in the percentage of correct responses with increasing numbers of trials in forced-choice discrimination of complex gratings. This effect of practice is specific for the parameters of the stimulus (orientation and spatial frequency), and does not transfer from the lower to the upper portion of the visual field, although it shows interocular transfer (Fiorentini & Berardi, 1981). All these properties put together may indicate that the effect of learning is restricted to the populations of neurones selectively activated by the stimulus. One would expect, therefore, that the effect of learning in spatial phase discrimination will not transfer from one hemisphere to the other, at least at a sufficiently large distance from the vertical meridian.

The findings reported in Fig. 3A–C for 5 deg eccentricity show that this is indeed the case. Each point represents the percentage of correct responses in a block of forty trials of forced-choice discrimination between two compound gratings (spatial frequency 2 cycles/deg) differing in the relative spatial phase of their harmonics. For all subjects there is a clear improvement in performance with increasing numbers of trials for the visual field tested first (Fig. 3, left field, open symbols) until a stable performance level is reached. This effect of learning, however, is not retained when the stimuli are removed from the left to the right hemifield (filled symbols). It is indeed clear that in the new situation there is initially a drop in performance (that for two subjects falls to levels near chance) followed by a progressive improvement. A stable performance level is again reached after approximately the same number of trials as for the visual field tested first. The final level reached in the right hemifield is significantly lower than in the left, confirming our previous findings.

The results obtained closer to the vertical meridian (1 deg eccentricity) are quite different. In this case the effects of learning are transferred from one visual field to the other, and the final levels attained in the two hemifields are comparable. This is shown in Fig. 3D for subject E.C. After a first learning session with stimuli presented in the left visual field (open symbols) a second session was run 3 days later. The first six blocks of discrimination trials performed in the same visual field show that the effect of previous learning had been largely maintained. When the stimuli

were removed to the right visual field the performance was very stable from the beginning, with no sign of improvement within 200 trials, and the average performance levels were practically equal in the two hemifields.

These results have been repeatedly confirmed in the other two subjects (see e.g. Figs. 4 and 5) for fundamental spatial frequencies of 2 cycles/deg or lower.

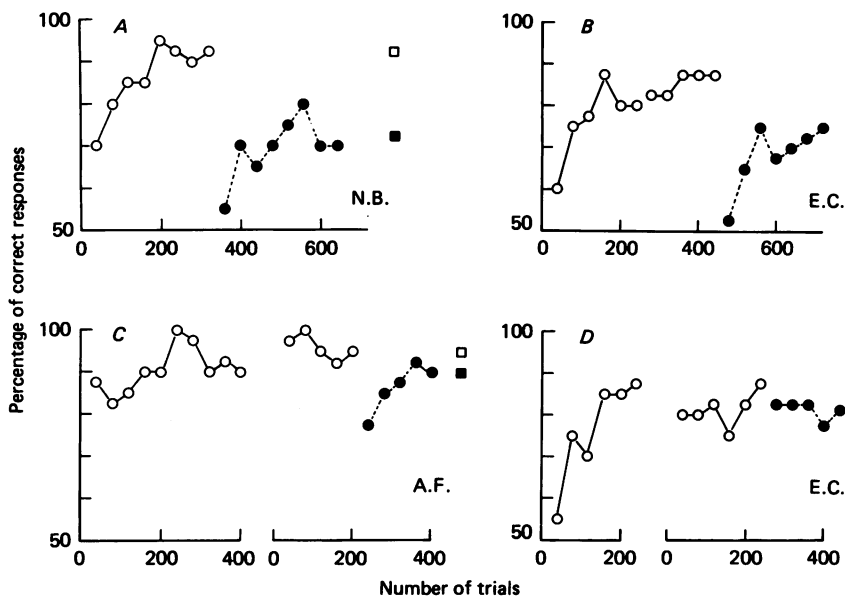


Fig. 3. Learning curves of three subjects for spatial phase discrimination at 5 deg (*A*, *B* and *C*) or 1 deg (*D*) from the vertical meridian in the right (filled symbols) or left (open symbols) hemifield. The relative phases of the  $f$  and  $3f$  components in the gratings to be discriminated were 0 and 75 deg (*A*) or 0 and 90 deg (*B*, *C* and *D*). Each point is the percentage of correct responses in a block of forty trials. Data were obtained in a single daily session (*A* and *B*) or on two different days (*C* and *D*). The squares in *A* and *C* represent the percentage of correct responses obtained by alternating the gratings positions (left and right) between blocks of trials. Stimulus parameters: fundamental spatial frequency, 2 cycles/deg; gratings, horizontal; contrast, 10% (*A*, *C* and *D*) or 15% (*B*); presentation time, 100 ms (*A*, *C* and *D*) or 150 ms (*B*).

Interestingly, the effects of training seemed not to transfer interhemispherically when the training and test grating had different spatial frequencies (2 and 1 cycle/deg, respectively) suggesting that the interhemispheric transfer of learning effects is selective for the stimulus spatial frequency. Subsequently, we have also found that it is selective for the stimulus orientation, in that the effects of training with a grating of 2 cycles/deg were not transferred across the vertical mid line to a test grating of the same spatial frequency orientated perpendicularly.

In these two subjects (N.B. and A.F.) we also tested whether there was a transfer of learning for stimuli (2 cycles/deg) presented at 2 deg from the vertical meridian. The results obtained at this intermediate eccentricity are somewhat intermediate between those obtained for the smaller (1 deg) and higher (5 deg) eccentricity. Although the final performance levels reached in the two hemifields were different,

the left field advantage was smaller than for 5 deg eccentricity and there was also a partial transfer of learning effects.

In the previous section we have shown that the presence of a left field advantage in spatial phase discrimination depends not only upon the distance of the stimuli from the vertical meridian but also upon their spatial frequency. We therefore investigated whether there was a transfer of learning effects in the discrimination of gratings of

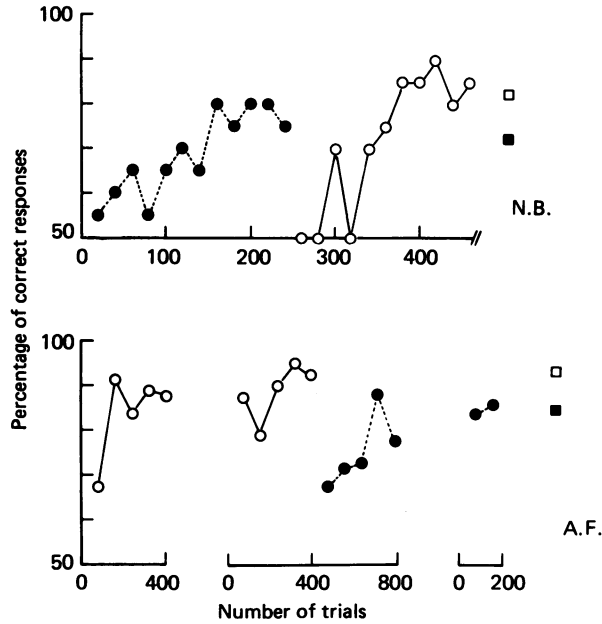


Fig. 4. Learning curves of two subjects for spatial phase discrimination (0 from 75 deg for N. B., 0 from 90 deg for A. F.) at 1 deg from the vertical meridian in the right (filled symbols) or left (open symbols) hemifield. Each point is the percentage of correct responses in a block of twenty (N. B.) or eighty (A. F.) forced-choice trials. Stimulus parameters: fundamental spatial frequency, 4 cycles/deg; gratings, horizontal; contrast of fundamental component, 7.5% (N. B.) or 15% (A. F.); presentation time, 250 ms (N. B.) or 150 ms (A. F.).

higher spatial frequency (4 cycles/deg) at 1 deg from the vertical meridian. The results reported in Fig. 4 show that this is not the case.

Indeed, removing the stimuli from the trained to the untrained visual field results in an initial dramatic drop in performance. Then a new learning process starts that brings performance back to a stable level. The final performance levels remain constant thereafter in the two hemifields (Fig. 4, open and filled squares) and different from each other, as expected.

In conclusion, at small distances from the vertical meridian it is possible to have an interhemispheric transfer of learning effects, which is absent at larger eccentricities. However, the transfer occurs only for those stimuli that are equally well discriminated in the two visual hemifields; in a situation where a left field advantage is still present there is a lack of transfer of learning effects.

At this point the question arises as to whether the transfer of learning from the



trained to the untrained region of the visual field, obtained for gratings of 2 cycles/deg or lower at 1 deg eccentricity, is peculiar to regions located on opposite sides of the vertical meridian, or whether it would be a general finding for these spatial frequencies and stimulus interdistance at 1 deg eccentricity. In the latter case a transfer should be found at this eccentricity even when the trained and untrained regions are on the same side of the vertical meridian.

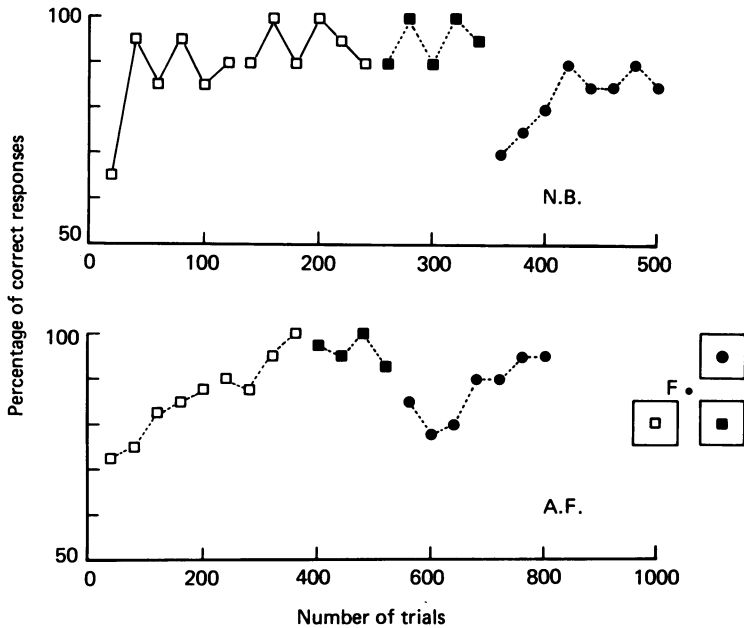


Fig. 5. Learning curves of two subjects for spatial phase discrimination (0 from 75 deg for N. B., 0 from 90 deg for A. F.) at 1 deg from the vertical meridian in the lower (squares) or upper (circles) quadrants of the visual field (see inset). For both subjects the training started in the lower left quadrant (open squares). Each point refers to the percentage of correct responses in a block of twenty (N. B.) or forty (A. F.) forced-choice trials. Stimulus parameters: fundamental spatial frequency, 2 cycles/deg; gratings, vertical; contrast, 3% (N. B.) or 4.5% (A. F.); presentation time, 60 ms (N. B.) or 100 ms (A. F.). The inset shows the position in the visual field of the stimuli to which the different symbols refer. F indicates the fixation point.

To verify this point we have first compared the transfer between regions symmetrical with respect to the vertical or horizontal meridian. The configuration of the regions tested with gratings of 2 cycles/deg is shown in the inset of Fig. 5. We have first confirmed that there is complete transfer between regions symmetrically located with respect to the vertical meridian at 1 deg from it (Fig. 5, open and filled squares). No transfer was found, however, between regions located one above the other (2 deg interdistance) on the same side of the vertical meridian (filled squares, filled circles).

One subject repeated this experiment with gratings of lower spatial frequency (1 cycle/deg) but the same interdistance between the various regions tested (Fig. 6). Even in this case there is no transfer between regions located one above the other, whereas the transfer is complete between regions located on opposite sides of the vertical meridian.

In a second experiment the transfer between two horizontally adjacent regions located on the same side of the vertical meridian was compared with the transfer between two regions located on opposite sides of it. The stimulus configuration was the following. The training stimulus was a grating (1 cycle/deg) 4 deg high and 1 deg wide, extending from 1 to 2 deg from the vertical meridian. The bars of the gratings

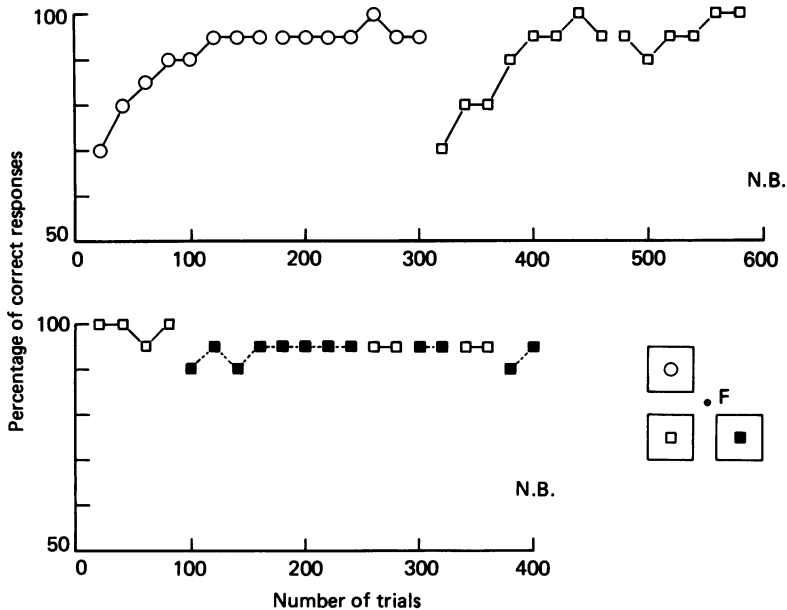


Fig. 6. Learning curves of one subject for spatial phase discrimination (0 from 75 deg) at 1 deg from the vertical meridian in the upper (circles) and lower (squares) quadrants of the visual field (see inset). Data from two consecutive sessions are displayed in the upper and lower graph, respectively. Each point refers to the percentage of correct responses in a block of twenty forced-choice trials. Stimulus parameters: fundamental spatial frequency, 1 cycle/deg; gratings, horizontal; contrast, 4.5%; Presentation time, 60 ms.

were horizontal. No transfer of learning effects was found between this region and the adjacent region extending from 2 to 3 deg from the vertical meridian. On the other hand, complete transfer was found when testing the region extending from 1 to 2 deg on the opposite side of the mid line.

#### *Interocular and interhemispheric transfer*

We know from our previous experiments that there is interocular transfer of learning effects in spatial phase discrimination for stimuli viewed centrally.

We wondered whether the learning effects obtained monocularly in one visual hemifield will show interocular transfer when tested in the other hemifield. We investigated this hypothesis for stimuli presented close (1 deg) to the vertical meridian and of relatively low spatial frequency, i.e. in a situation in which we already know that transfer occurs in binocular viewing. The training stimulus was presented to the right eye in the right visual field and the transfer was tested with a stimulus presented to the left eye in the left visual field. The two stimuli had the same elevation

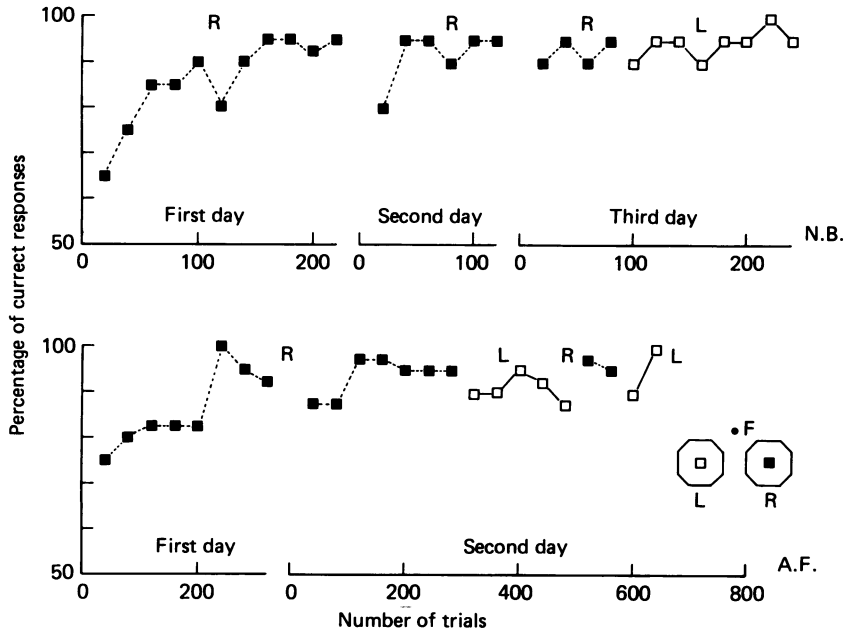


Fig. 7. Learning curves of two subjects for monocular spatial phase discrimination (0 from 90 deg) in the lower left (open squares) or lower right (filled squares) quadrants of the visual field. R, right eye; L, left eye. Each point refers to the percentage of correct responses in a block of twenty (N.B.) or forty (A.F.) forced-choice trials. Stimulus parameters: fundamental spatial frequency, 1 cycle/deg; gratings, oblique (45 deg); contrast, 3%; presentation time, 100 ms (N.B.) or 200 ms (A.F.).

(1 deg below the horizontal meridian, see inset in Fig. 7) and both projected in the nasal retina. The results shown in Fig. 7 indicate a complete interocular transfer in both subjects.

#### DISCUSSION

The findings of the present experiments can be summarized as follows. The left field advantage in the discrimination of complex gratings, present for stimuli separated by 5 deg or more from the vertical meridian, is absent for stimuli extending 1 to 5 deg on either side of the meridian if their fundamental spatial frequency is 2 cycles/deg or less. At higher spatial frequencies the left field advantage is present even close to the meridian, unless the contrast is very high. A similar dependence upon the eccentricity and the spatial frequency of the stimulus is found for the transfer of learning effects between regions located symmetrically with respect to the vertical meridian. Indeed, there is no transfer for stimuli separated 5 deg or more from the vertical meridian. For stimuli extending 1 to 5 deg there is transfer, provided their fundamental spatial frequency is 2 cycles/deg or less.

Most of these results have been obtained for two subjects, although crucial findings have been confirmed in two other subjects. Moreover, that a left field advantage in spatial phase discrimination is present at 5 deg eccentricities had already been assessed in a larger number of subjects (Fiorentini & Berardi, 1984). Since in this work

we were only concerned with changes in this left field advantage as a function of eccentricity and stimulus parameters, we feel confident that the small number of subjects does not call into question the general validity of the results obtained.

The lack of lateralization (and the transfer of learning) found at small distances from the vertical meridian could result from a direct bilateral representation of a strip of the visual field near the vertical mid line (due to the naso-temporal overlap of the retino-cortical projections), from an interhemispheric transfer of information, or both.

Let us first discuss the first possibility. Anatomical data for the cat and the monkey indicate the presence in the retina of a vertical strip (1 deg wide in the monkey) in which ganglion cells that project contralaterally are intermingled with ganglion cells that project ipsilaterally (Stone, Leicester & Sherman, 1973; Bunt, Minckler & Johanson, 1977). The resulting functional overlap at the level of the visual cortex (17/18 border) has been investigated in the cat. It has been found that the receptive field centres of cells recorded in one hemisphere extend in the ipsilateral visual field not further than 1 deg from the mid line (Leicester, 1968).

Whether an anatomical naso-temporal overlap is present in the human visual system is not known. The animal data would suggest that, if present, the resulting bilateral representation should be limited to a vertical strip approximately 1 deg wide, i.e. less than the horizontal separation of our stimuli. In addition, a possible naso-temporal overlap may fail to have a functional role in visual tasks similar to ours. That this is indeed the case is suggested by previous psychophysical experiments on humans in which differences in reaction times for visual stimuli presented at 4 deg either on the left or right of the mid line were shown to remain practically unvaried when the stimuli were as close to the vertical meridian as  $\pm 15$  min of arc (Harvey, 1978; Haun, 1978). Differences in reaction times such as those observed in these experiments are attributed to an interhemispheric transfer and should not be present near the vertical mid line if information from this portion of the visual field was available to both hemispheres.

Given the similarity of the visual tasks (particularly in Haun, 1978), we think that the conclusion derived from those findings should apply to ours, and therefore rule out an explanation of our results purely in terms of a naso-temporal overlap. That such an explanation is indeed rather unlikely is also suggested by the following arguments.

The first is based on the property of perceptual learning in complex grating discrimination being limited to the visual area stimulated. The only exception is found for regions symmetrically placed with respect to the vertical meridian (1 deg from it) and gratings of low spatial frequency. If this exception has to be ascribed to an incomplete naso-temporal division, one has to assume a substantial overlap of receptive fields of retinal cells projecting ipsilaterally and contralaterally within a portion of the visual field up to at least  $\pm 2$  deg from the mid line. This, however, is difficult to reconcile with the fact that no transfer is obtained either between two horizontally contiguous regions contained within this strip and lying on the same side of the mid line, or between two regions located one above the other with a 2 deg interdistance.

The second argument is related to the findings obtained with gratings of higher spatial frequency (i.e. the lack of transfer of learning effects (Fig. 4) and the presence

of left field advantage for spatial phase discrimination at all but the highest contrast (Fig. 2)). An explanation in terms of a dual representation of a medial strip would require the further assumption that retinal cells projecting to the 'wrong' hemisphere are much less sensitive to contrast than neighbouring cells projecting to the 'right' hemisphere. This assumption does not find any support from the available animal data.

In conclusion, we think that on the basis of the previous psychophysical findings and in view of the arguments presented above, an explanation of the present results purely in terms of a direct bilateral representation of the vertical mid line is unlikely.

This does not exclude the possibility that a dual representation of the vertical mid line is present in man and plays a role in other visual functions (like, for instance, stereopsis), possibly in parallel with interhemispheric commissures (Blakemore, 1970; Mitchell & Blakemore, 1970; Bishop, 1973; Lassonde, Paquette, Cavanagh & Eizner-Favreau, 1986).

Let us now discuss the other possible explanation, the interhemispheric transfer of visual information.

The findings that seem to us most relevant to the discussion of this interpretation are the following.

(1) The transfer of learning effects between two non-overlapping areas of the visual field is peculiar to areas on opposite sides of the vertical meridian. There is no transfer between two non-overlapping areas lying on the same side of the vertical meridian.

(2) The lateralization which is absent close to the vertical meridian gradually reappears further away from the mid line up to 5 deg eccentricity. At this eccentricity (distance from the vertical meridian) there is no interhemispheric transfer of learning.

(3) The interhemispheric transfer of learning is selective for the orientation of the stimuli to be discriminated.

(4) The interhemispheric transfer of learning also occurs interocularly.

These findings are consistent with an interhemispheric transfer of information between regions symmetrically located with respect to the vertical meridian and limited to a strip of a few degrees on either side of it. Within these regions, the transfer seems to occur between structures not only orientation selective, but also tuned to the same stimulus orientation and receiving inputs from both eyes.

This is reminiscent of the properties of callosal connexions between visual cortical areas, as described for the cat (Berlucchi & Rizzolatti, 1968).

Binocular callosal neurones with receptive fields extending for a few degrees on either side of the vertical meridian, and with the same stimulus specificity throughout their receptive field, could be involved in the learning process and in the transfer of visual information implied by our findings. Evidence for a specific role for callosal connexions in the interhemispheric transfer in form discriminations also comes from clinical findings indicating that in man anterior commissures are incapable of transferring information for spatial analysis (Martin, 1985). It also has to be remembered that in the monkey, anterior commissures interconnect areas where neurones are insensitive to changes in stimulus orientation (Gross, Rocha-Miranda & Bender, 1972). The selectivity for the stimulus orientation of the learning process itself indicates that the neurones of the cortical areas involved in this interhemispheric transfer are orientation selective.

If the interpretation in terms of callosal interhemispheric transfer is correct, then

our findings are in very good agreement with the limitations in the callosal transfer of spatial frequency information demonstrated for the cat (Berardi *et al.* 1987).

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