verbal activity is lateralized to the left but spatial representation is more diffusely distributed, although emphasized in the right hemisphere.

In LH's, there were more horizontal than vertical movements in all conditions. The few vertical movements were indifferently up or down. During verbal and spatial tests, the right and left head movements were about equally frequent.

Thus, LH's have a roughly equal incidence of representation of both verbal and spatial function, in the right and left hemispheres, and in most cases (16 of the 20) both activities appeared to be represented in the same hemisphere.

In summary, the results closely reproduced the known circumstances, that is, lateralization to the left for RH's, and lateralization to the left or right, in roughly equal amounts, for LH's. In RH's there was bilateral spatial representation, with some emphasis on the right hemisphere. In LH's there was (i) higher relative incidence of horizontal deviations than in RH's and (ii) consistent gaze direction irrespective of cognitive set. The findings with numerical problems are harder to interpret as the questions asked may have involved several processes differing in lateralization. Thus, in LH's one or the other hemisphere seems to be in control at a given time. The dearth of vertical deviations indicates infrequent simultaneous activation of the hemispheres; the consistency of lateral gaze suggests that the same hemisphere that processes verbal information also processes spatial information. This could indicate either that both functions are lateralized in a given individual in a stable manner in the same hemisphere, or that while both hemispheres have language and spatial potential, only one hemisphere operates at a given time. In either case, a certain inefficiency could be generated by this type of cerebral representation.

Previous studies of "lateral gaze behavior" (5) have looked for differences between rather than within individuals. Some problems can be solved in more than one way (for instance, by verbalization or by visualization). Different subjects might elect different strategies and might then show different patterns of gaze and head deviation when confronted with the same problem.

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10. I thank Gale McCarty for testing subjects, and Merrill Elias for statistical advice.

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Color Adaptation of Spatial Frequency Detectors in the Human Visual System

Abstract. *Observers exposed alternately to a vertical grating of one spatial frequency in red light and a vertical grating of different spatial frequency in green light subsequently report frequency-specific color aftereffects when shown gratings in white light. Aftereffects occur, however, only when inspection gratings differ in spatial frequency by one octave or more and the frequency of at least one grating is above 3 cycles per degree. This spatial selectivity of the aftereffect is considered in terms of a neural adaptation model incorporating evidence on the tuning of spatial frequency detectors in the human visual system.*

McCollough (*1*) found that orientation-specific aftereffects can be induced by displaying alternately a horizontal grating in blue light and a vertical grating in orange light. When the gratings were subsequently viewed in white light, observers reported that horizontal lines appeared orange and vertical lines blue. In explaining this aftereffect, McCollough proposed that during exposure to vertical lines in orange light only neural detectors tuned to both the specific orientation and wavelength are excited. Because these analyzers are suppressed for a period of time after inspection, the white vertical lines presented as the test stimulus are signaled via vertical edge-detectors sensitive normally to the complementary color. Hepler (*2*) has offered a similar explanation of color aftereffects which are specific to the direction of motion.

McCollough's explanation implies that the ease with which the aftereffect can be induced is dependent on the extent to which spatial values associated with different colors during inspection are signaled via nonoverlapping neural channels. Microelectrode recording has shown that tilt detectors in the infrahuman visual system are each tuned 20 deg or so on either side of a preferred orientation (*3*). Psychophysical studies in which masking paradigms were used suggested that similar selectivity in input processing occurs in the human visual system (*4*). McCollough's account, therefore, supposes it is difficult to induce orientation-specific color aftereffects unless inspection gratings differ by 40 deg or more; this expectation has been confirmed experimentally (*5*).

We show that color aftereffects similar to the McCollough effect can be generated by exposing alternately a vertical grating of one spatial frequency in red light and a vertical grating of different spatial frequency in green light. Masking and aftereffect experiments (*6*) employing achromatic stimuli have indicated that there are specialized detectors within the human visual system similar to periodicity analyzers demonstrated in the cat and monkey cortex by microelectrode recording (*7*). The masking data have further suggested that in human vision a single class of detector is involved in signaling all frequency values below 3 cycle/deg, and analyzers responsive at greater periodicity values are each maximally excited at a specific frequency and tuned within the range of one octave in spatial frequency on either side of the preferred value. By incorporating evidence on the tuning of spatial frequency detectors into McCollough's selective adaptation model, we predicted fre-

quency-specific color aftereffects would be found only when the inspection gratings displayed in different colored light differed from each other in spatial frequency by one octave or more, and the frequency of at least one grating was above 3 cycle/deg.

Six pairs of square-wave gratings were used as inspection stimuli in the experiment, namely, 0.5, 0.75; 0.5, 1.0; 0.5, 1.5; 5.0, 7.5; 5.0, 10.0; and 5.0, 15.0 cycle/deg. In each testing session one grating within a pair was displayed in red light (Wratten filter 26, with a dominant wavelength of 620.6 nm in illuminant A) and the other grating was shown in green light (Wratten filter 55, with a dominant wavelength of 524.1 nm in illuminant A). The two gratings were matched in space-average luminance at 39.53 cd/m^2. Pairings of color and spatial frequency were counterbalanced between observers and over sessions. The gratings were presented alternately by back-projection onto a translucent screen subtending 12 by 9 deg. Each presentation was for 5 seconds, and there was a dark interval of 1.5 seconds between successive displays. The observers were not required to maintain fixation, and the phase relation between the gratings was not controlled. Neither of these variables critically affects adaptation in the perception of spatial frequency (*6*).

Viewing of the inspection gratings was interrupted by a test probe after 5, 10, 13, 16, 19, 22, 25, 28, and 31 minutes. Five stimuli, consisting of two vertical gratings arranged laterally, were shown without color filters during a probe; each stimulus was exposed for 5 seconds followed by a dark interval of 1.5 seconds. Fifteen probe stimuli, representing the two inspection frequencies paired with each of the eight spatial frequency values studied in the experiment, were presented on three occasions in a session in an order randomized across observers and sessions. Therefore, within a single session an observer was shown each inspection frequency on 27 occasions and the other six gratings on six occasions each. The observer's task on probe trials was to report whether either of the displayed gratings appeared colored, and if so, whether the color most resembled red or green.

Eight observers, four of whom had no prior knowledge of the McCollough effect, were tested individually over six sessions separated by periods of between 1 day and several weeks (*8*). In each session measures were obtained with a single pair of inspection gratings. The order of testing with the six pairs of gratings was randomized between observers.

The results shown in Fig. 1, A, B, and C, indicate the percentage of occasions an appropriate color response (red or green) was given when a grating of specific spatial frequency was displayed as a probe stimulus. There were almost no occasions on which observers gave other than the anticipated color response. Values are plotted separately for cases where the inspection gratings differed in spatial frequency by half an octave (Fig. 1A), one octave (Fig. 1B), and one and a half octaves (Fig. 1C). Similar functions were obtained for "red" and "green" reports, and the measures were therefore pooled. The results confirm the predictions that were outlined earlier. It was relatively easy to induce a frequency-specific color aftereffect when the inspection gratings differed from each other by an octave or more and exceeded 3 cycle/deg. Color aftereffects were either difficult or impossible to induce when the inspection gratings differed in spatial frequency by half an octave (irrespective of absolute periodicity values) or displayed lines at 1.5 cycle/deg or less (irrespective of relative spatial frequency) (*9*).

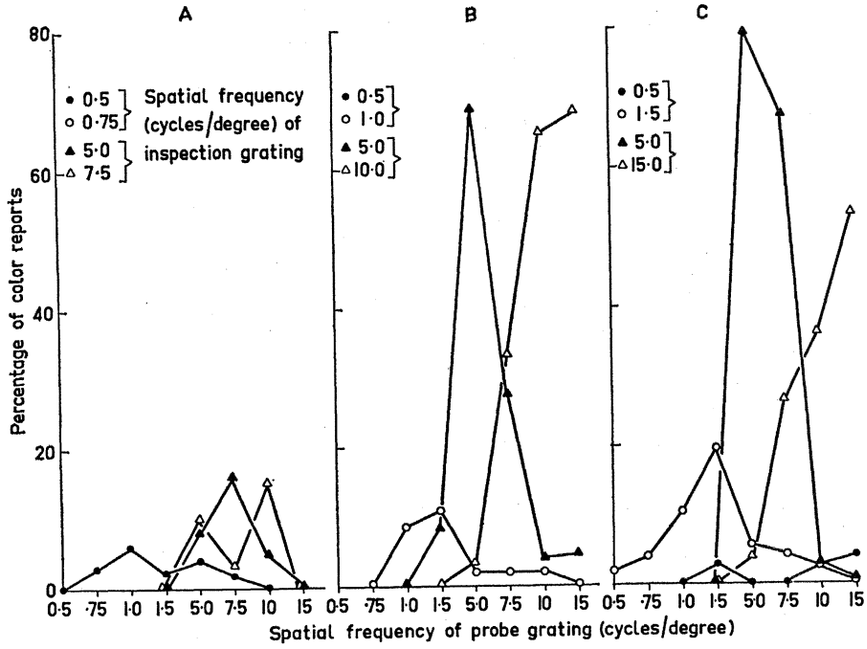

Fig. 1. The percentage of occasions a color response was given when a square-wave grating of specific spatial frequency was displayed in white light as a probe stimulus. In (A) the inspection gratings (one of which was viewed in red light and the other in green light) differed in spatial frequency by half an octave, in (B) by one octave, and in (C) by one and a half octaves. For each octave value the graphs also show the proportion of probe trials on which color afteraffects were induced when inspecting gratings in the ranges of 0.5 to 1.5 cycle/deg (symbols ● and ○) and 5.0 to 15.0 cycle/deg (▲ and △) were used. Points typically have not been plotted in cases where no color responses were given.

At least three mechanisms have been proposed for the orientation-specific color aftereffects first reported by McCollough: negative afterimages, selective adaptation of relatively unspecialized neural units, and selective adaptation of edge-detectors tuned to contour orientation. The afterimage explanation has been shown to be incorrect (*10*). In outlining a model postulating sensory units ("dipoles") less specialized than feature-detectors, Gibson and Harris (*10*) argued it should be possible to induce color aftereffects comparable to the McCollough effect for spatial properties such as length of line, curvature, periodicity, and movement if selective suppression of feature-detectors is involved. They report that aftereffects cannot be induced for length of line or curvature. The results of the present experiment support the feature-analyzer explanation and indicate that careful attention must be given to the response characteristics (including tuning) of a given type of

detector in generating predictions as to whether color aftereffects will be produced. We have shown that frequency-specific color aftereffects occur only when the inspection gratings presented with the different colors are signaled via relatively nonoverlapping neural channels. The tuning characteristics of length of line and curvature detectors must be considered in examining whether color aftereffects can be induced with these spatial properties. Unfortunately, information of this nature is not at present available from either microelectrode or masking studies.

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8. Because McCollough (*1*) had shown that orientation-specific color aftereffects can persist for a week or longer, each observer viewed the test stimuli in white light at the start of a session to establish whether there was carry-over of aftereffect from the preceding induction period. Intervals of 1 to 3 days were generally sufficient for complete decay to have occurred, but one observer regularly reported a color aftereffect a week or more after induction.
9. In terms of the model developed earlier it should be possible to induce color aftereffects with the use of one grating in the lower periodicity range and the other in the higher range. The same eight observers were tested with gratings of 0.5 cycle/deg displayed in red (green) light and 10 cycle/deg in green (red) light. Test measures were obtained with gratings ranging from 0.5 to 15 cycle/deg shown in white light. The appropriate color response was obtained on 77 percent of trials with the probe stimulus of 0.5 cycle/deg and on 80 percent of trials with the probe grating of 10 cycle/deg. The rate of appropriate color reports diminished as the periodicity of the test grating differed from that of the inducing grating. In addition, judgments were obtained when the inducing gratings displayed vertical lines and test gratings horizontal lines. Color aftereffects could not be generated under these conditions, and this demonstration of orientation-specificity in periodicity processing is in accord with masking and aftereffect measures obtained by Blakemore and Nachmias (*6*) with achromatic stimuli.
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Role of Heterochromatin in Homologous Chromosome Pairing: Evaluation of Evidence

Yunis and Yasmineh in their article (*1*) stated: "A careful appraisal of the information that has accumulated about heterochromatin . . . and on satellite DNA . . . suggests that these entities have vital structural functions: they maintain nuclear organization, protect vital regions of the genome, serve as an early pairing mechanism in meiosis, and aid in speciation." These are interesting ideas worth study, but it can be questioned whether current evidence in support of any of them is compelling. Many references seem to me to have been misinterpreted, mistakenly cited, or not critically evaluated. In particular this comment urges inspection of the evidence that heterochromatin serves a role in chromosome pairing.

Yunis and Yasmineh reported that in certain plants aggregations of heterochromatic regions "result in the grouping of centromeres near one pole of the nucleus and telomeres near the other" [with references to Levan (*2*), Vanderlyn (*3*), and Wagenaar (*4*)] and that in premeiotic interphase or early meiotic prophase such nonhomologous aggregation is exemplified by bouquet formation [references to Swanson (*5*) and White (*6*)]. Further, they considered such aggregations to be universal in germ cells, the aggregations "having been observed even in fungi" [references to Shaw (*7*), White (*6*), Ohno *et al.* (*8*), although not one of these references mentions heterochromatic aggregations in fungi]. Of Levan, Vanderlyn, Wagenaar, Swanson, and White, none directly attributes polar aggregations of centromeres to a tendency for heterochromatin to aggregate, and only White supports such a mechanism at telomeres.

Many organisms show no tendency for polar heterochromatic aggregations in any striking way. The activity of the spindle mechanism at the previous anaphase is generally considered to be related to the collection of centromeres at the pole, and in some organisms also to the appearance of telomeres at the opposite pole at interphase and early prophase, since little rearrangement of chromosomes seems to occur during interphase.

Evidence for initiation of pairing of homologous chromosomes through heterochromatin was seen by Yunis and Yasmineh in reports of pairing of heterochromatic regions at interphase and early meiotic prophase. The references cited in support of this idea should be surveyed. LaCour and Wells (*9*) found homologs paired at zygotene in *Fritillaria lanceolata* plants that had conspicuous proximal heterochromatin and found homologs not obviously paired at leptotene in plants lacking such heterochromatin. But comparisons were not made at the same stage, and in any case pairing at leptotene would be more difficult to identify in chromosomes lacking conspicuous heterochromatin. Further, in the material with conspicuous heterochromatin (the only material where appropriate observations could be made), homologs were thought to be aligned throughout their length, and synaptonemal complex formation was seen earlier in euchromatic than in heterochromatic regions. Maguire (*10*) noted only that homologous heterochromatic regions in *Zea mays* appeared closer together than random expectation predicts at a stage when other regions of the chromosomes could not be meaningfully traced (and therefore might have been more or less closely paired than the heterochromatic portions). Chauhan and Abel (*11*) reported close pairing of heterochromatic regions under similar conditions in *Impatiens balsamina* and *Salvia nemorosa.* Yunis and Yasmineh cited Hyde's work (*12*) as another example of pairing of heterochromatic regions [the text reference (p. 1206, column 1, line 19) was to Shaw (*7*) due to an error by *Science*]. Hyde reported pairing of homologous heterochromatic regions in *Plantago ovata* at a stage he interpreted to be early zygotene where, again, the remainder of the chromosomes could not be traced. Stack and Brown (*13*) (not cited by Yunis and Yasmineh) have reported close pairing of heterochromatic regions at premeiotic interphase in *Plantago ovata,* but did not infer from this that pairing is initiated at these regions. In fact they thought it likely that pairing is initiated in this organism at the chromosome ends, which appear euchromatic, whereas the heterochromatic regions are centric.

The point that should be noted is