- C. G. Phillips, Proc. Roy. Soc. London Ser. B 173, 141 (1969); H. G. J. M. Kuypers and J. Brinkman, Brain Res. 24, 29 (1970).
   C. Demanian Computer Science Computer Computer Science Computer Science Scienc
- Brinkman, *Brain*, Nes. 24, 25 (197).
   O. Pompeiano and A. Brodal, *J. Comp. Neurol.* 108, 225 (1957).
   H. G. J. M. Kuypers and D. G. Lawrence,
- Brain Res. 4, 151 (1967).
- R. Nyberg-Hansen, Ergeb. Anat. Entw. Gesch.
   39, 6 (1966); J. M. Petras, Brain Res. 6, 275 (1967)
- (1901).
  8. P. Sterling and H. G. J. M. Kuypers, Brain Res. 7, 419 (1968); A. Rustioni, H. G. J. M. Kuypers, G. Holstege, *ibid.* 34, 255 (1971).
  9. D. G. Lawrence and H. G. J. M. Kuypers, D. G. Lawrence and H. G. J. M. Kuypers,
- Brain 91, 1 (1968); ibid., p. 15. 10. R. W. Sperry, M. S. Gazzaniga, J. E. Bogen, Handbook of Clinical Neurology (North-Holland, Amsterdam, 1968), vol. 4, pp. 273– 291; N. Geschwind, Modern Trends in Neurology (Bu pp. 29-40. (Butterworth, London, 1970), vol. 5,
- J. L. de C. Downer, Brain 82, 251 (1959); M. S. Gazzaniga, Exp. Neurol. 8, 14 (1963). 11. J
- 12. R. E. Myers, R. W. Sperry, N. Miner

McCurdy, Arch. Neurol. 7, 195 (1962); P. McCurdy, Arch. Neurol. 7, 195 (1962); P. Black and R. E. Myers, Functions of the Corpus Callosum (Churchill, London, 1965), pp. 47-59; C. R. Hamilton, J. Comp. Physiol. Psychol. 64, 434 (1968).

- M. S. Gazzaniga, Exp. Neurol. 8, 14 (1963);
   J. S. Lund, J. L. de C. Downer, J. S. P.
- J. Lumley, Cortex 6, 323 (1970).
   R. F. Mark and R. W. Sperry, Exp. Neurol. 21, 92 (1968).
- 15. M. S. Gazzaniga, *ibid.* 23, 11 (1969). 16. ——, *The Bisected Brain* (Apple) (Appleton-Cen-
- ——, The Bisected Brain (Appleton-Cen-tury-Crofts, New York, 1970), p. 58. We thank Prof. D. H. G. Keuskamp and Mr. R. Ducardus, Department of Anaesthesi-ology, Dijkzigt University Hospital, Rotter-dam, for their help with the hypothermic procedure and Dr. R. M. Latto for reading the manuscript. This study was supported in neart he crout 12 at 12 of the Dutch Organiza part by grant 13-31-12 of the Dutch Organiza-tion for Fundamental Research in Medicine (FUNGO) and by a Dutch interdepartmental government grant.

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## Eye and Head Turning Indicates Cerebral Lateralization

Abstract. When solving verbal problems, right-handed people usually turn head and eyes to the right, whereas with numerical and spatial problems, these people look up and left. Left-handed people differ in all these respects. The results suggest that the direction in which people look while thinking reflects the lateralization of the underlying cerebral activity.

In bisymmetrical animals, each side of the central nervous system programs sensory and motor activity for the contralateral side. Man has acquired, in addition, mental processes that are free of specific spatial reference and are distributed asymmetrically between the cerebral hemispheres. An example of symmetrical facilities are the frontal centers for lateral orientation. They control the turning of head and eyes; when the effects of the two centers are equally balanced, attention is directed straight ahead (1). Asymmetry is exemplified by the lateralization of language processes to the left side of the brain and lateralization of spatial and temporal processes to the right side

of the brain (2). When stimulus is to be processed, it is advantageous to present it to the input channel in such a way that it is contralateral to the hemisphere specialized for this process (3). The cerebrum is a highly linked system, and only a few synapses separate any two cortical neurons. This makes the cerebrum vulnerable to interference between two concurrent operations, particularly when both are programmed by the same cerebral hemisphere. Thus, when subjects await a verbal stimulus and must also look centrally, the verbal activation overflows into the left-sided orientation center, driving attentional balance off center and to the right (4). Laterality of thought processes in man might therefore be determined by using the direction of orientation as an indicator (5). When the two hemispheres are equally active, orientation of the subject should be centered on the median plane. When one hemisphere is primarily involved, head and eyes should turn to the opposite side. Those movements would be secondary to the central activity, rather than in direct response to external stimulation.

We predicted that right-handed subjects would orient themselves to the right during verbal activity and to the left during spatial thought. Left-handed subjects could orient themselves either way in either case. The orientation of subjects thinking about numerical problems could not be predicted.

Forty undergraduate subjects participated, 20 right-handed (RH) and 20 left-handed (LH) as ascertained by questionnaire (6). Each subject was seated in a desk chair in a lighted, soundproof room, facing a wall covered by a floor-length black cloth. A camera (Sony Videocorder) was focused on him through a small opening in the cloth. The experimenter sat behind the subject, and the recording apparatus was behind the experimenter.

Three sets of 20 questions each were prepared. A "verbal" set was derived from scales 1 to 3 of the Proverbs Test. A "numerical" set consisted of simple calculations and problems based on the quantitative ability section of the Medical College Admissions Test Study Book and the Graduate Record Examination Study Book. Spatial questions required the subject to visualize and specify spatial relationships of familiar local landmarks and visual arrangements.

The subject was told to concentrate

Table 1. Means and summary of analysis of variance for experiment 1; V, verbal; N, numerical; S, spatial; ns, nonsignificant. Specific contrasts were done following a significant interaction.

	Horizontal			Up			Right		
	v	N	S	v	N	S	v	N	S
				Eye		×.		- *,	
RH means	13.4	7.8	8.0	4.4	10.2	9.4	11.5	3.7	1.8
LH means	13.9	13.2	13.3	3.4	4.4	3.7	5.5	6.4	6.0
Hand preference $\times$									0.0
problem-solving mode		P < .0001			<b>P</b> < .0001			P < 0.001	
Specific contrasts	V vs. N	N vs. S	V vs. S	V vs. N	N vs. S	V vs. S	V vs. N	N vs. S	V vs. S
RH: <i>P</i>	<.0001	ns	<.0001	<.0001	ns	< .0001	< 0001	ns	< 0001
LH: <b>P</b>	ns	ns	ns	ns	ns	ns	ns	ns	ns
				Head					
RH means	8.2	4.0	4.0	5.8	8.6	9.9	72	26	17
LH means	13.0	11.8	11.8	3.6	5.3	40	5.8	4.6	60
Hand preference $\times$					015	1.0	5.0	4.0	0.0
problem-solving mode		P < .02			<b>P</b> < .01			P< 0001	
Specific contrasts	V vs. N	N vs. S	V vs. S	V vs. N	N vs. S	V vs S	V vs N	N vs S	V vs S
RH: <i>P</i>	<.0001	ns	<.0001	< .001	ns	< 0001	< 0001	ns	< 0001
LH: P	ns	ns	ns	<.05	ns	ns	ns	<.03	< .0001 ns

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Table 2. Means and summary of analysis of variance for experiment 2; V, verbal; N, numerical; S, spatial; ns, nonsignificant. Specific contrasts were done following a significant interaction.

	Horizontal		Up		Right		
	v	S	v	S	v	S	
		Eye					
RH means	8.4	5.7	2.4	5.6	7.3	1.8	
LH means	10.0	8.8	1.2	1.8	5.2	5.2	
Hand preference $\times$							
problem-solving mode	n	s	P<.	001	P < .0001		
Specific contrasts	V vs	s. S	V	vs. S	V v	V vs. S	
RH: <i>P</i>			<.0001		<.	< .0001	
LH: P			n	s	n	ns	
		Head					
RH means	8.0	3.6	2.8	7.6	7.0	1.0	
LH means	8.6	8.2	1.4	1.6	3.8	3.4	
Hand preference $\times$							
problem-solving mode	P < .0	P < .0001		<b>P</b> < .0001		P < .0001	
Specific contrasts	V vs. S		V vs. S		V vs. S		
RH: P <.0001		0001	<.0001		<.	< .0001	
LH: <b>P</b>	ns		n	s	n	ns	

on answering each of a series of questions within 30 seconds, to remain seated, and not to look behind him. The three sets of 20 questions were read to each subject in a counterbalanced repeated measurements design. Each trial was concluded either when the subject had answered or after 30 seconds. The audiovisual readings were subsequently played back and scored for accuracy of response as well as for the direction of the first gaze deviation and the first head movement after the end of each spoken question. Each was classified in terms of the direction (up, down, right, or left) that best described it. Resolving power for gaze and for head displacement was 5° (7). Two judges were available for scoring, but it was found that movements were gross and unequivocal, giving no scope for dispute.

Mean number of gaze and of head deviations in the various directions are separately presented in Table 1; the variance for eye and head movements was analyzed by use of a multivariate program for repeated measurements designs (8). Gaze deviation occurred on every trial. Head movements were absent on nearly 14 percent of trials.

Subjects who were RH's made horizontal eye movements more frequently than vertical ones under the verbal condition; vertical eye movements were mostly upward. The horizontal eye movements were generally to the right under verbal interrogation, showed no difference with numerical questioning, and were generally to the left during spatial problems. Head movements in RH's gave similar results. Vertical movements prevailed under numerical and spatial conditions, and under all three conditions upward movements outnumbered downward ones. Horizontal movements did not exceed vertical ones in the verbal condition, but among horizontal movements those to the right were far more prevalent. There was no lateral bias among horizontal movements while the subjects solved numerical and spatial problems.

Assuming that the direction of orientation indicates the laterality of cerebral representation, we confirm that, in RH's, language processes are lateralized to the left side, while spatial skills are more evenly distributed but are emphasized in the right hemisphere. Numerical thought is evenly distributed between the hemispheres. Among LH's, horizontal movements outnumber vertical ones under all conditions. The prevalent direction of the vertical movements was upward. In the verbal questioning, upward gaze barely outweighed the downward, and right and left head turns did not differ in frequency of occurrence. During spatial and numerical problem solving, movements to the right and left did not differ in frequency except for an excess of head movements to the left during numerical thought.

Among LH's, therefore, dominance of right and left hemispheres for verbal activity occur with roughly equal frequency (9). The same seems to apply to numerical and spatial functions. The lateral orientation for the verbal and the spatial condition was congruent in 18 of 20 LH's. This suggests that functions that are widely distributed across the cerebrum in RH's are more closely packed in one hemisphere (sometimes the right and sometimes the left) in LH's, or at least are performed by the same hemisphere during the period of the experiment.

The lack of a difference in the success rate in answering the three types of questions indicates that task difficulty was not a factor in the differences in responses obtained.

A further test of the validity of the verbal-spatial dichotomy was performed under the stringent condition that the task be held constant with respect to input and be varied only with respect to the mode of response, either verbally or by transcription onto a matrix.

Forty undergraduates, 20 right- and 20 left-handed, as established by questionnaire (6), participated. Twelve statements were prepared, each specifying a particular arbitrary relationship between a circle, a square, and a cross. Each statement took the form "Theis above the -----, and to the left/right of the ----." The series of statements were presented twice, in different random sequence, to each subject. As soon as the sentence was over, the subject counted backward, from five to one, at a rate of one number per second. The interval was interpolated in order to have subjects rehearse the sentence that they had to repeat or to give them time to visualize the specified spatial relationships before looking down at the sheet on which they entered their responses. For the verbal tests, the subject then repeated verbatim the statement he had heard. For the spatial tests, he inscribed the designated spatial arrangement onto a sheet of paper with a grid.

As in the first experiment, audiovisual recordings were made, were played back, and were scored for the first eye and head movement after the end of each stimulus.

Gaze deviations occurred on every trial. Head movements were absent in over 6 percent of the trials. Mean number of eye and head movements under each condition are presented in Table 2, as well as analyses of variance that were performed as described for the first experiment.

Horizontal head and eye movements outnumbered vertical movements for the verbal tests in RH's. In the spatial tests, this discrepancy was absent for gaze and reversed for head movement. Upward deviations outnumbered downward ones in all conditions. Head and eye deviations to the right predominated over movements to the left in the verbal tests, while there was no difference for head movements during the spatial tests; the relation was reversed for gaze, which was more often to the left. This supports the inference that, in RH's, 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.

MARCEL KINSBOURNE Departments of Pediatrics and Neurology, Duke University Medical Center, Durham, North Carolina 27710

## **References and Notes**

- 1. C. S. Sherrington, Integrative Action of the Nervous System (Yale Univ. Press, New Haven, Conn., 1906); E. C. Crosby, J. Comp. Neurol. 99, 437 (1953).
- 2. O. L. Zangwill, Cerebral Dominance and Its Relation to Psychological Function (Oliver and Boyd, Edinburgh, 1960); V. B. Mount-castle, Ed., Interhemispheric Relations and Cerebral Dominance (Johns Hopkins Press, Baltimore, 1962).
- 3. D. Kimura, Neuropsychologia 4, 275 (1966); M. J. White, Psychol. Bull. 72, 387 (1969).
- 4. M. Kinsbourne, Acta Psychol. 33, 193 (1970); R. Bruce and M. Kinsbourne, in preparation.
- 5. M. E. Day, Percept. Mot. Skills 19, 443 (1964); J. D. Duke, J. Gen. Psychol. 78, 189 (1968); P. Bakan, Percept. Mot. Skills 28, 927 (1969)
- 6. M. Annett, Brit. J. Psychol. 61, 545 (1970).

D. C. Edwards, J. R. Antes, R. W. Adams, G. A. Truman, *Percept. Mot. Skills* 32, 435 (1971).
 J. W. Cole and J. E. Grizzle, *Biometrics* 22, March 2010, 2010.

- 810 (1966); C. F. Starmer, Proceedings of the 6th Annual Southeastern Meeting of the Assooin Annual Southeastern Meeting of the Association for Computing Machinery and National Meeting of Biomedical Computing, Durham, N.C., June 1967.
  9. R. Conrad, Brit. J. Psychol. 55, 75 (1964);
- A. Subirana, in Handbook of Jeurology, P. J. Vinken and G. V Clinical W. Bruyn, Neurology, P. J. Vinken and G. W. Bruyn, Eds. (North-Holland, Amsterdam, 1969), vol. 4, pp. 248–272; M. E. Humphrey and O. L. Zangwill, J. Neurol. Neurosurg. Psychiat. 15, 184 (1952); B. Milner, in Interhemispheric Relations and Cerebral Dominance, V. B. Mountcastle, Ed. (Johns Hopkins Press, Baltimore, 1962), pp. 177–195. I thank Gale McCarty for testing subjects, and Mertill Elias for statistical advice 10.
- 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 edgedetectors 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-