LATERALITY AND VISUAL PERCEPTION IN MONKEYS

Thesis by

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Abstract

Split-brain rhesus monkeys were tested for differences in the abilities of their two cerebral hemispheres to process visual stimuli. Tests of visual preferences, i.e., what each hemisphere likes to look at, utilized colored photographs as stimuli and in most cases revealed an overall greater preference by the left hemisphere. Furthermore, for some types of stimuli, the hemisphere with the greater preference was correlated with each monkey's handedness; the hemisphere ipsilateral to the preferred hand, possibly equivalent to the human non-dominant hemisphere, showed greater preferences. The monkeys' ability to make same-different judgments about two sequentially-presented visual stimuli was also assessed. The hemisphere contralateral to the preferred hand, possibly equivalent to the human dominant hemisphere, learned this task faster. These results and other examples of left-right differences and of correlations of hemisphericity with handedness in rats, monkeys, and humans reported in the literature suggest that the basis for hemispheric specialization, particularly in infrahuman mammals, may be quantitative asymmetries in emotional and/or attentional processes.

A separate series of experiments investigated the role of selective attention in mirror image discrimination. Normal and partially split-brain monkeys learned both up-down and left-right mirror image discriminations with the place of response in different problems either aligned with the axis of symmetry of the patterns, i.e., close to the salient cues, or 90° orthogonal. The relative ease with which the four possible combinations of mirror image orientation and place of response were learned by the different groups of monkeys, as well as the outcome of tests of interocular transfer and generalization to a new place of response, indicated that restricting attention in various ways can influence the discriminability of mirror images. Theories based on the anatomical connections of the brain are insufficient to account for all of the results of this experiment. Instead, the results support the hypothesis that behavioral asymmetries in attention may account for the difficulties normal animals and people have in telling left from right.

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PART I

INVESTIGATIONS OF HEMISPHERIC SPECIALIZATION IN MONKEYS

INTRODUCTION

The two hemispheres of the human brain have been shown to differ in the way they organize and process information. The left is often described as linguistic, analytical, and sequential, while the right has been characterized as Gestalt, holistic, and spatial (Sperry, 1974). Has this specialization evolved de novo in human beings, or can a similar type of cerebral organization, or its precursors, be found in other animals, specifically man's closest living relatives, the monkeys and apes? If hemispheric specialization is present in infrahuman primates it would indicate that such cerebral organization is not related solely to speech or consciousness as found in man but rather is based on more fundamental types of cerebral mechanisms. Finding hemispheric specialization in nonhuman primates would also be important because these primates could then provide a useful model for studying the development of hemispheric specialization and its modification by environmental, surgical, or chemical methods. Developmental studies of this type are obviously unfeasible with human subjects for ethical reasons; at present disturbances of hemispheric specialization can only be inferred from study of brain-damaged patients receiving insult at different ages. While the great apes would seem to provide the best prospects for finding hemispheric specialization, increasing costs and decreasing availability suggest studying the next best subjects, monkeys.

Evidence in favor of hemispheric specialization in animals comes from three areas. First, anatomical asymmetries between the two hemispheres in the fissure patterns of the cortex such as are found in man (Chi, Dooling and Gilles, 1977; Galaburda, LeMay, Kemper and Geschwind, 1978; Geschwind and Levitsky, 1968; Wada, Clarke and Hamm, 1975) are also present in the great apes (LeMay and Geschwind, 1975; Yeni-Komshian and Benson, 1976) and less reliably in monkeys (Cain and Wada, 1979; Falk, 1978). Second, hemispheric asymmetries in the catecholamine content of the brain are known to exist in rats (Glick, Jerussi and

Zimmerberg, 1977) and man (Oke, Keller, Mefford and Adams, 1978); at least in rats these chemical asymmetries are correlated with paw preferences and turning tendencies (Glick et al., 1977). Associated with this are differences in activity levels following left vs. right hemispheric cortical injury in rats (Denenberg, Garbanati, Sherman, Yutzey and Kaplan, 1978; Robinson, 1979). Finally, the mechanisms for birdsong are lateralized to the left hemisphere of passerine birds (Nottebohm, 1977), showing at the very least that mechanisms for lateralization are not restricted to man.

The split-brain preparation is ideal for testing lateralized functions. Since the optic chiasm has been sectioned in the midline, each eye projects solely to its ipsilateral hemisphere. Additional section of the anterior commissure and corpus callosum restricts input through each eye to only one hemisphere, permitting each hemisphere to be tested in isolation. Split-brain rhesus monkeys have previously been tested in a series of investigations which employed stimuli believed appropriate for testing lateralization and which in addition controlled for variables that could affect the expression of lateralization such as sex, handedness, hemisphere of surgical approach, and order of testing. In these experiments, the left and right hemispheres did not differ in their ability to discriminate stimuli which would favor right hemispheric processing in the human, such as faces and oriented patterns, nor did they differ on tasks requiring sequential comparisons (Hamilton, 1977b,c).

Discrimination learning, however, may be too insensitive to elicit specialized processing. Alternatively, each hemisphere may actually use different strategies but still be equally adept at solving the discriminations. In this thesis visual preferences, i.e., what monkeys like to look at, are examined in the hope of providing a more sensitive test for hemispheric differences. Sequential comparisons, which should elicit lateralized processing in man, were retested with additional subjects to see if they are similarly lateralized in monkeys.

EXPERIMENT 1

VISUAL PREFERENCES OF THE TWO HEMISPHERES OF SPLIT-BRAIN MONKEYS: METHOD 1.

A variety of studies (Butler and Woolpy, 1963; Haude and Detwiler, 1976; Redican, Kellicutt and Mitchell, 1971; Sackett, 1965, 1966; Symmes, 1959) have shown that monkeys will work for the privilege of looking at things. Moreover, the quality of the visual stimulus can determine the rate of work. Butler and Woolpy (1963) and Humphrey (1972; Humphrey and Keeble, 1976) have found that monkeys prefer stimuli which are brighter, colored, in focus, upright, and moving. Humphrey (1972) showed that when intact monkeys were given a choice they displayed a strong initial preference for colored photographs over blank white fields although the preference faded to indifference after about 200 seconds. Differential preferences could be revived by substituting a new photograph which the monkey perceived as different. The magnitude of revival was related to the degree of difference between the old and new pictures. Tested in this way, photographs of different monkeys were always perceived as different individuals but photographs of domestic animals such as horses, sheep, and cats, were classed by species, not individuals, until after much experience had accrued with such photographs (Humphrey, 1974).

If differences exist between the two hemispheres of split-brain monkeys in the way they perceive, recognize, or categorize stimuli, these differences might be revealed through preference testing. For example, the left and right hemispheres might show differences in the magnitude of preference for various categories of stimuli, differences in adaptation to stimuli, or differences in the revival of preference when a new picture is presented. As an extreme example, if one hemisphere were deficient in recognizing individual monkeys as being different, as is the left hemisphere of humans when confronted with human faces (for example: Benton and Van Allen, 1968; De Renzi and Spinnler, 1966; Geffen, Bradshaw and Wallace, 1971; Hecaen and Angelergues, 1962; Leehey, Carey, Diamond and Cahn, 1978; Levy, Trevarthen and Sperry, 1972; Rizzolatti, Umilta and Berlucchi, 1971; Yin, 1970), then a preference that had adapted away should not revive when a photograph of one monkey is substituted for that of another because that hemisphere would fail to recognize the change. The following experiment investigated some of these possibilities.

Methods

Subjects: Eighteen adolescent or subadult split-brain rhesus monkeys (Macaca mulatta), nine males and nine females, were used. However, only seven learned the basic task well enough to be tested. All had received surgical section of the optic chiasm, corpus callosum, and anterior and hippocampal commissures in one or two stages five to thirty-four months prior to testing. During the interim they had received operant behavioral testing on a variety of visual discriminations. The monkeys were housed individually in a colony of about 40 macaques. They were fed monkey chow supplemented with fruit once a day after testing; water was continuously available in the home cage.

Histological verification of the surgery is not yet available. However, each of these monkeys exhibited little or no interocular equivalence on several series of pattern discriminations, thus providing a functional test of the completeness of their brain bisections.

Apparatus: The testing apparatus was a variation of the standard split-brain testing chamber used in this laboratory (Sperry, 1968). Briefly, it consisted of a monkey cage with an attached compartment into which the monkey voluntarily moved when he wished to respond. The split-brain compartment contained eyeholes and armholes with appropriate occluders; adjustable head restraints provided a tailored fit for each monkey and ensured use of the appropriate eye-hand combination.

A translucent white Plexiglas panel situated at arms' length contained an 8" x 8" back-projection screen (56° x 56° of visual angle) centered at eye level upon which photographic slides were shown using a stereo projector with each optical system used independently for presenting two different stimuli. Below the screen was a food well for the delivery of 190 mg banana-flavored food pellets. The food well doubled as a response lever since it was hinged so as to close a microswitch when depressed. The projector fan and a table fan provided masking noise.

Solid-state programming equipment housed in another room controlled stimulus presentation, interval timing, reinforcement, and data printout. The monkeys could be observed during testing by means of a closed-circuit television camera mounted overhead.

Stimuli: The stimuli were 26 mm and 35 mm color photographic slides. They were grouped into four stimulus categories on the basis of picture content.

Picture/white consisted of 24 photographs presented one at a time. Each was paired with a homogenous white field matched in subjective brightness. The subject matter of these photographs varied, but included pictures of people, monkeys, other mammals, birds, flowers, objects, and scenery such as would be found in a personal slide collection. Generally a single object or organism was the focal point of each photograph.

Person/thing consisted of 22 pairs of photographs. One member of each pair was a photograph of one or more persons and the other member was either a scene (N=12), an animal other than a person or monkey (N=6), or a monkey (N=4).

Monkey/monkey consisted of 14 pairs of photographs of the faces of different macaque monkeys and included a variety of facial expressions. Ten pairs consisted of photographs of two different rhesus, three pairs were rhesus/pigtail (M. nemestrina), and one pair was rhesus/cynomolgus macaque (M. fascicularis). When two monkey photographs were paired together, the picture of the monkey preferred by the majority of the subjects was used as the reference for the data of all subjects.

Normal/altered consisted of two copies of each of fourteen photographs of monkeys' faces. For eight of these pairs, one photograph was shown normally and an identical photograph was shown upside-down; for the remaining six pairs, one photograph was shown normally while its counterpart was shown defocused. Three photographs were of pigtail macaques and the rest of rhesus. Picture pairs of this type have previously yielded preferences for the normally-projected picture (Butler and Woolpy, 1963; Humphrey, 1972).

Procedure: The procedure was derived from that used by Humphrey (1972, 1974). Each monkey was trained to hold down the response lever in order to view the photographs and to get food. A picture was available for viewing for as long as the lever was depressed, but could only be seen if the monkey's head was in the correct position behind the eyeholes, interrupting a photocell circuit in series with the projector lamp. One stimulus pair consisting of either a picture and a white field or a pair of pictures was presented in each daily session. The monkey could select which member of the pair he wished to view by releasing the lever and pushing again; the two stimuli for that session alternated on successive pushes. Whichever stimulus was selected remained turned on for as long as the monkey held the lever down. After each 20 seconds of viewing time the monkey was required to release the lever and push again. This ensured that both stimuli were initially presented with equal frequency. After each 80 seconds of observation, five food pellets were dispensed regardless of which slide the monkey had looked at most or how he had divided his time between them. A 20 second time-out period then ensued during which pushes were ineffective. At the end of the time-out the monkey could continue picture-viewing until he had worked 480 seconds (6 bouts of 80 seconds each). The amount of time to the nearest tenth of a second spent viewing one of the pictures and the number of responses made were printed out after every 20 seconds of viewing time. One contralateral eye-hand pair was tested per day, both eyes were tested successively on each stimulus pair, and alternate eyes were tested first on consecutive stimuli.

Data analysis: For each day's data the percent preference shown during the first 40 seconds and during the entire session were calculated. A dominance index, defined as $(\frac{L-R}{L+R})$ 100, where L is the percent preference with the left hemisphere and R is the percent preference with the right hemisphere, was calculated for each stimulus pair. The significance of these measures was determined by appropriate t-tests. The dominance indices were compared with each monkey's hand preference in reaching for food from a tray and bottle (Warren, Abplanalp and Warren, 1967) which had been assessed upon the monkey's arrival into the laboratory and prior to any surgery or formal behavioral testing. Handedness was also expressed as an index, $(\frac{R-L}{R+L})$ 100, where R and L are the percentage of reaches with the right and left hands. These indices are always arranged so that positive scores indicate performance in favor of the left hemisphere and negative scores indicate performance in favor of the right hemisphere. The correlation between dominance and handedness indices was evaluated by testing the significance of the Pearson correlation coefficient, r (Spence, Underwood, Duncan and Cotton, 1968). In addition, the total number of responses for each day's session was noted and the number of responses made by the left and right hemispheres were compared.

Results and Discussion

Left-right differences: The first question to be examined is whether the left and right hemispheres differed in their preferences for visual stimuli. The mean percent preference for each stimulus category is presented separately for the left and right hemispheres of each monkey in Table 1. Across monkeys

TABLE 1

Mean percent preference with each hemisphere based on total time

	Picture/White		Person/Thing		Monkey/Monkey		Normal/Altered	
Subject	LE	RE	LE	RE	LE	RE	LE	RE
MRV	83.37**	54.14**	69.39**	57.55**	61.80**	52.66	50.97	54.72*
IRM	66.49**	52.86**	69.98**	53.22*	65.05**	50.55	49.06	50.82
ZOR	49.49	48.29					49.71	50.78
EDN	49.90	49.06						
ETH	49.76	46.16					50.74	51.65
POT	76.53**	81.67**	51.40+	49.28	51.01	50.36	49.70	48.68
DOE	49.44	50.17	50.35	51.37**	50.85	50.11		
$\bar{x}$	60.71	54.62	60.28	52.86	57.18	50.92	50.04	51.33
SD	±14.64	±12.23	±10.87	±3.52	±7.34	±1.17	±0.80	±2.19
p	$< .10$	$< .20$	$< .10$	$< .20$	$< .10$	$< .20$	ns	$< .20$

**Significantly greater than chance at $p < .01$ or better

*Significantly greater than chance at $p < .05$

+Significantly greater than chance at $p < .10$

Each monkey's name is represented by a three-letter code. Chance is 50% preference.

LE = left eye (hemisphere), RE = right eye (hemisphere).

within each category neither the preference with the left nor right hemisphere differed significantly from chance, which is 50%, although the left hemisphere preference in the categories picture/white, person/thing, and monkey/monkey approached conventional levels of significance. It is interesting to note that the mean left hemisphere preference across monkeys was greater than that for the right in the three experimental categories picture/white, person/ thing, and monkey/ monkey, while preferences were nearly chance for normal/altered. That is, in general monkeys displayed stronger preferences with the left hemisphere than with the right when the available stimuli were of two nominally different kinds, but displayed little preference when the stimuli were both the same photograph of a monkey's face with one shown normally and the other either inverted or defocused. Individual monkeys often had preferences significantly different from chance as indicated in Table 1. This indicates that the monkeys looked longer at one member of the stimulus pair than they did at the other.

Two of the subjects which had preferences near chance performed bizarrely, as discussed later. If the data for DOE and EDN are excluded, the overall left hemisphere preference for picture/white becomes significantly different from chance ($\bar{x}$ = 65.13 ± 15.37, $p < .05$) while the right hemisphere preference, although increased, is still not different from chance ($\bar{x}$ = 56.62 ± 14.38, $p < .20$). The mean preferences of the two hemispheres for person/thing and monkey/monkey also increase when the data for DOE and EDN are dropped, but they still do not reach conventional levels of significance.

To further evaluate possible hemispheric differences in the preferences, a dominance index based on each monkey's preference was calculated for each stimulus pair and the mean dominance index computed for each monkey in each stimulus category. In this way laterality differences in the monkeys' preferences can be compared independent of the particular magnitudes of the preferences.

These dominance indices as well as the means for each stimulus category and the means for each monkey over the three experimental categories are presented in Table 2. For reference, it may be noted that a dominance index of 33% represents a preference by the left hemisphere twice as great as that of the right; a dominance index of -33% represents a right hemisphere preference twice as great as that of the left. The mean dominance index for each category across monkeys was not quite significantly different from zero, although some individual monkeys had significant dominance indices as indicated. When each monkey was given an average dominance index for the three categories in which the subject matter of the two stimuli was intrinsically different, however, the resulting grand mean across monkeys was significantly greater than zero. In other words, when averaged across these three categories the ratio of the preferences of the two hemispheres revealed overall greater preferences by the left hemisphere than by the right.

Dominance–handedness correlations: Handedness relates to laterality in human subjects and therefore may be correlated with hemispheric specialization in the monkey, too. To see whether this is true, the mean dominance index across the three experimental categories was assessed for each monkey as a function of that monkey's handedness index, also listed in Table 2. The scatter plot for that comparison, along with the least squares line of Y on X, is shown in Figure 1. The correlation coefficient was significant ($r = -.827$, $p < .05$), which indicates that there is a correlation between a monkey's handedness and the relative preferences of his two hemispheres for visual stimuli.

Each monkey's dominance and handedness indices were also compared within each stimulus category. These plots, with least squares lines and correlation coefficients, are also presented in Figure 1. There were significant correlations between dominance and handedness for picture/white, person/thing, and normal/altered, while the correlation coefficient for monkey/monkey was not quite significant.

TABLE 2

Mean dominance indices

Subject	Sex	Handedness Index	Surgical Retraction	Picture/White	Person/Thing	Monkey/Monkey	$\bar{x}_3$	Normal/Altered
MRV	M	-100	RL	20.65**	8.47**	7.96**	12.36	-3.42
IRM	M	-82	RL	11.04**	9.36*	10.39*	10.26	-2.14
ZOR	M	-73	L	1.63			1.63	-1.06
EDN	M	-20	L	0.87			0.87	
ETH	F	-15	L	3.59			3.59	-0.68
POT	F	-5	L	-3.47	1.93+	0.91	-0.21	1.08
DOE	M	32	LR	-1.16	-1.10	0.68	-0.53	
$\bar{x}$				4.74	4.66	4.98	4.00	-1.24
SD				± 8.38	± 5.08	± 4.94	± 5.21	± 1.68
p				$< .10$	$< .10$	$< .10$	$< .05$	$< .10$

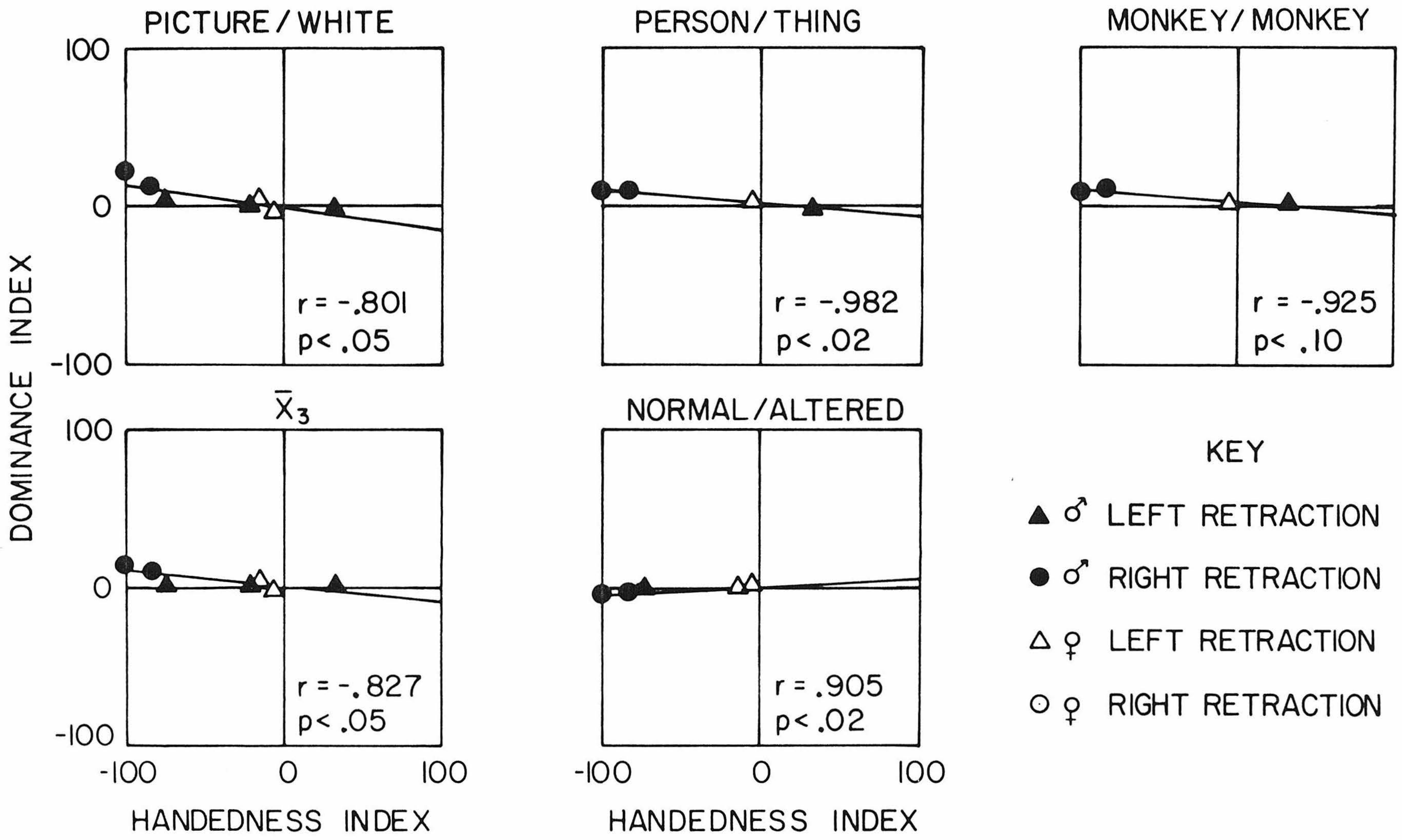
** Significantly greater than zero at $p < .01$ or better

* Significantly greater than zero at $p < .05$

\+ Significantly greater than zero at $p < .10$

Figure 1: The dominance indices for Experiment 1 are plotted as a function of each monkey's handedness index for the three experimental stimulus categories, their mean, and the control category normal/altered. The least squares lines of Y on X have been drawn in.

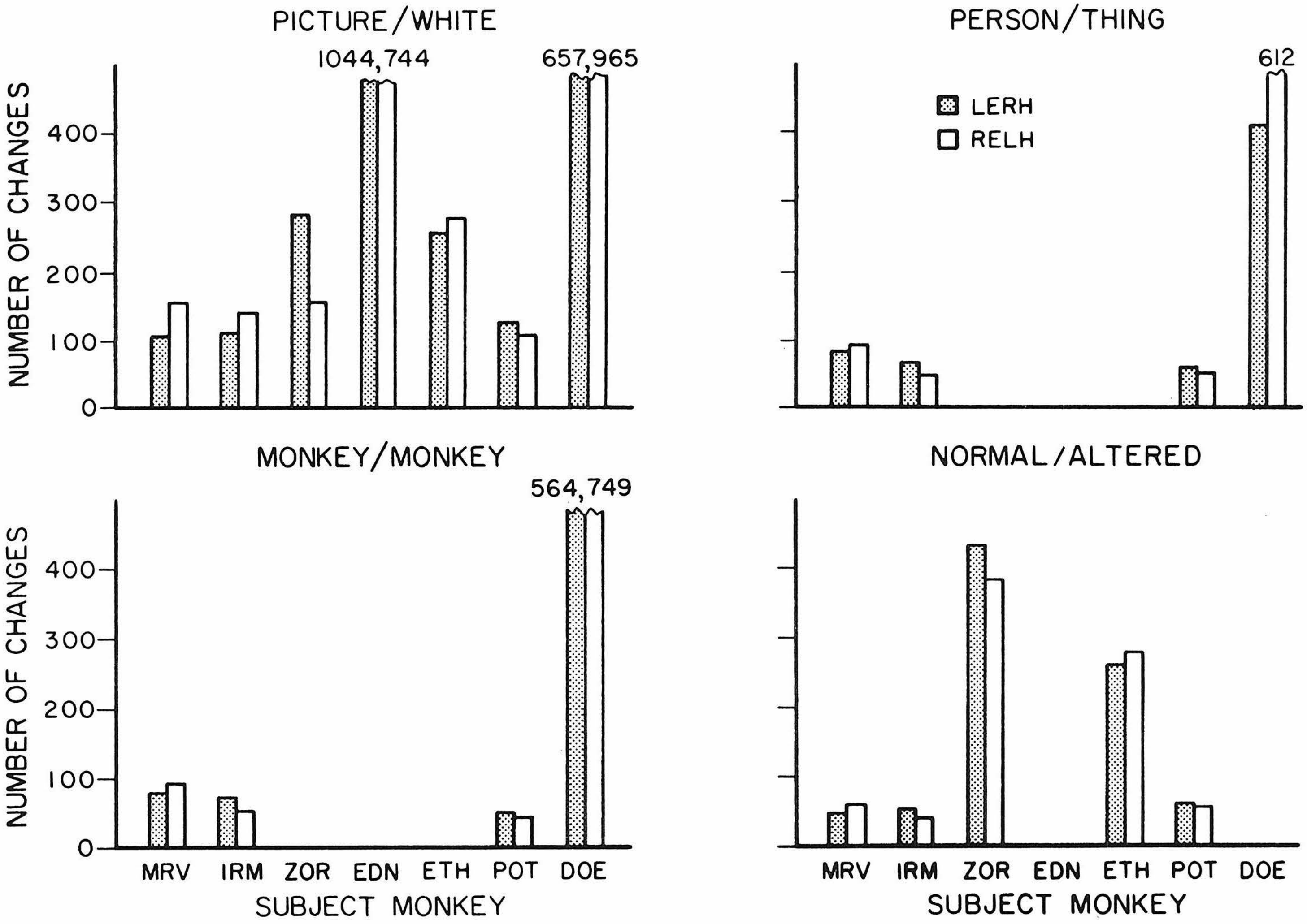
DOMINANCE vs HANDEDNESS, PERCENT PREFERENCE ON TOTAL TIME



The least squares lines for picture/white, person/thing, and monkey/monkey had negative slopes, indicating that the more left-handed a monkey is, the greater the preference with the left hemisphere compared to the right and the more right-handed a monkey is, the greater the right hemisphere preference over the left. Thus there were greater preferences shown by the hemisphere ipsilateral to the preferred hand, the presumed equivalent of the human non-dominant hemisphere. The handedness of monkeys has been reported to be equally distributed from left to right (Lehman, 1978; Warren, 1977) and therefore forms a continuum along which all individuals fall, unlike the skewed bimodal distribution of human handedness. If, as is usually the case with humans, the dominant hemisphere is the one contralateral to the preferred hand then it is reasonable that a continuum in the degree of dominance indices in monkeys would exist. The overall greater left hemisphere preference discussed earlier might result from the excess of left-handed subjects (6 out of 7). Sex of the monkeys and hemisphere of surgical retraction have also been coded in the plots of Figure 1 since these variables might *a priori* influence the expression of hemispheric specialization on a particular task. In fact, no such trends are evident.

Responses: The mean number of picture changes made by each monkey with each hemisphere is shown by stimulus category in Figure 2. The dashed line indicates the minimum possible number of 24 responses; every bar is significantly greater than the minimum. It is apparent that the two hemispheres of each monkey usually made about the same number of responses, yet large individual differences in the overall rate of responding occurred. The three monkeys with the lowest rates, MRV, IRM and POT, when taken together responded an average of 76 times per session, ZOR and ETH, whose rates were moderate, averaged 288 responses per session, while EDN and DOE, the most rapid responders, averaged 777 responses. When these numbers are considered in light of the data in Tables 1 and 2 an inverse

Figure 2: The mean number of picture changes is plotted for the left and right hemispheres of each monkey, segregated by stimulus category. The dashed line indicates the minimum possible number of 24 responses.



MEAN NUMBER OF PICTURE CHANGES MADE BY EACH HEMISPHERE relationship is seen. The monkeys that responded the least had the greatest preferences and those that responded the most had virtually no preferences. EDN and DOE in fact pushed so rapidly that the net result was a virtual flickering from one photograph to the other and back; therefore their data should be viewed with particular caution. In fact, as pointed out earlier, the omission of their data allows the mean left hemisphere preference on picture/white to reach significance. With the exception of EDN and DOE the response rates compared satisfactorily with those obtained by Humphrey (1971, 1972, 1974; Humphrey and Keeble, 1974, 1975, 1976), which ranged from 86 to 192 when adjusted to the same session length as used here.

Even though the two hemispheres of each monkey responded at similar rates, differential behavior was evident in the pattern of responding, and was most evident with those monkeys who responded at the lowest rates. With the exception of EDN and DOE, whose rates were so high as to preclude any pattern, when working with the left hemisphere the monkeys usually sampled both stimuli each time they were required to push and then settled down with one or the other. When working with the right hemisphere, on the other hand, pictures were sampled only at the very beginning of the session. The monkeys then frequently behaved as though they were automatons, pushing only when necessary to accumulate the time necessary to get their food reward. Dominance indices for response rates were calculated for each monkey and plotted as a function of handedness index. None of the least squares lines were significant in contrast to the analogous plots based on percent preference which were significant for three of the categories. This suggests that the response rate is independent of preference and is unlikely to be affected by cerebral asymmetries of the type measured by this experiment.

Idiosyncrasies

Normal/altered: It is worth commenting on the monkeys' performance on normal/altered. Their initial preference was for the inverted or defocused picture, contrary to Butler and Woolpy (1963) and Humphrey (1972, 1974). There is no obvious reason for this difference. This data may be interpreted however, as a reaction to novelty. Faces are more difficult to recognize upside-down than other objects such as houses which are commonly seen in only one orientation, at least for humans (Yin, 1969). Therefore, perhaps the monkeys were more attracted to a picture which was harder to make sense of. Alternatively, given that the monkeys once recognized the photograph as being of a monkey's face, their curiosity was maintained by watching to see what this unusual stranger would do! The dominance indices for each monkey on normal/altered also provide an important control. When they are plotted as a function of handedness the least squares line has a positive slope, whereas in the analogous plots for the other three stimulus categories the least squares lines have negative slopes. This indicates that changing the stimulus material could make the monkeys change their "favored" hemisphere. It argues against these monkeys simply having a "dumb" or surgically damaged hemisphere that mimicked a real hemispheric difference in preferences.

Adaptation: If adaptation had occurred as Humphrey (1972) reported, then the monkeys' preferences would have been stronger at the beginning of the session and waned to chance with time, resulting in overall preferences nearer to chance than the initial ones since the initial strong preference would have been diluted by subsequent chance performance. To see if this were true, the percent preference for the first 40 seconds of stimulus presentation for each hemisphere of each monkey was calculated and compared in a paired difference test to the corresponding preference for each stimulus pair over the total time. In most cases there were no significant differences between the initial and total preferences, indicating that what preferences there were remained constant over the session. The exceptions were significant differences between the initial and total percent preferences considered across monkeys for the left hemisphere on picture/white ($\bar{x} = 3.63 \pm 3.99$, $p < .05$) as found by Humphrey (1972) with intact monkeys viewing binocularly and the left hemisphere on normal/altered ($\bar{x} = -2.59 \pm 2.42$, $p < .05$). Neither person/thing nor monkey/monkey resulted in a significant change between initial and total preferences. Humphrey never reports pairing one photograph against another, so there is no prior evidence for or against adaptation in these cases. As a more stringent test for adaptation MRV, IRM and DOE were run with each eye for an hour a day on five consecutive days on both a picture/white combination and a picture pair on which most monkeys had shown definite and strong preferences. The hope was that after five hours the monkeys would eventually become bored. Instead, the preferences remained relatively constant throughout.

Individual differences. The seven monkeys tested in this experiment showed quite obvious individual differences, unlike Humphrey's (1972) two male rhesus monkeys whose behavior was described as "almost identical in every situation". Humphrey discusses these behavioral similarities at great length and apparently finds them genuine. Had the present study included only monkeys MRV and IRM, who behaved very much the same and who were both subadult males with similar surgical histories and handedness indices, a claim such as Humphrey's might have been made. In subsequent papers (Humphrey, 1974; Humphrey and Keeble, 1974, 1975, 1976) Humphrey reports on more subjects and refrains from comment on the similarities or differences in their behavior.

The present monkeys displayed individual differences in the magnitude of their preferences, from rather definite preferences for one stimulus over another to practically no preference at all in some cases. Even though the left hemisphere did on the average view pictures longer than the right the subject matter in the three principal experiments did not differentially influence the magnitude of preference to any great extent or in any obvious, systematic way. That is, the left hemisphere looked more whether the stimuli were monkey faces, people, or scenery. This lack of stimulus control might suggest that the monkeys were not paying sufficient attention to the stimuli. In fact it sometimes seemed as though they cared more about the small morsel of food than the pictures. Upon occasion some monkeys gave the impression that they had arbitrarily decided upon a "right" and "wrong" photograph and that looking at the "right" one was "good", a philosophy not always shared by the other hemisphere, however. Perhaps these behaviors contributed to the result that the monkeys did not adapt, that is, have an initially high preference which waned to indifference over time. Their initial preferences were usually not as high as those of Humphrey's monkeys and they never dropped as low. In other words when either hemisphere of the split-brain monkeys preferred one stimulus over another the preference was fairly constant over the session. At any rate, it was unfortunate that the monkeys failed to adapt, because since their preferences never declined to indifference, the magnitude of revival of preference in response to a new picture could not be tested as had been hoped. The preferences which were obtained were lower than those of Humphrey (1972, 1974), but are comparable to those obtained with normal monkeys in a variety of other paradigms by Butler and Woolpy (1963), Haude and Detwiler (1976), Redican, Kellicutt and Mitchell (1971), Sackett (1965, 1966), and Symmes (1959).

EXPERIMENT 2

VISUAL PREFERENCES OF THE TWO HEMISPHERES OF SPLIT-BRAIN MONKEYS: METHOD 2.

The seven split-brain monkeys tested in Experiment 1 in several instances showed significant differences in the visual preferences of their two hemispheres when tested in a paradigm similar to that used by Humphrey (1972, 1974). However, the preferences were frequently small in magnitude and individual variability was large. In addition, the paradigm was difficult to teach monkeys to perform and time-consuming to run. These factors preclude testing large numbers of subjects, which is required in order to balance or control variables such as sex, surgery, and pre-operative handedness which could influence the expression of hemispheric lateralization.

In order to overcome some of the difficulties encountered with the Humphrey-type preference testing and investigate further the hemispheric differences that were found a simpler paradigm was tried. It was adapted from that used by Marriott (1978) with squirrel monkeys and involved merely measuring the amount of time monkeys spent looking at stimuli made available to them.

Methods

Subjects: Nineteen adolescent to sub-adult rhesus monkeys (*M. mulatta*) were used. There were ten males and nine females. All had sustained midline section of the corpus callosum, anterior and hippocampal commissures, and optic chiasm in one or two stages one month to five years prior to testing. DPE and IRW had undergone additional midline section of the posterior, habenular, and superior collicular commissures in a third operation. All surgeries were aseptic and were carried out using standard neurosurgical techniques (Sperry, 1968). Housing and feeding of the monkeys were as described in the previous experiment. Between the time of surgery and the present experiment, all monkeys had been tested on a wide variety of operant visual discriminations and were thoroughly familiar with the testing apparatus.

Apparatus: The testing box was the same as that used in the Humphrey-type preference experiment, except that stimuli were presented by means of a Kodak Ektagraphic AF-1 slide projector. Stimulus presentation, delivery of reward pellets, and counting response time were controlled by solid-state programming equipment housed in another room. The monkeys were monitored during testing by means of a closed-circuit television system.

Stimuli were 26 mm and 35 mm colored photographic slides which were grouped on the basis of subject matter into four categories: monkey, person, animal, and scene. Monkey photographs were full face or three-quarter views of faces with various expressions. Pictures of people were of one or more subjects, either head and shoulders or full body in a seated position. Animals were full-body photographs of birds and mammals other than primates. Scenes were outdoor views of fields, lawns, etc., with no animals visible. One control condition was included in which no slides were placed in the projector, but a N.D. 1.0 filter was placed in front of the projector lens.

Eight sets of photographs were compiled, each set consisting of one photograph from each of the four categories. The order in which the categories appeared in each set was determined by a Latin square.

Procedure: The procedure used was modified from that used by Marriott (1978). At the beginning of a testing session a monkey was placed in the testing box and the picture sequence was activated by the experimenter. The availability of each picture for viewing was signalled by the sound of the projector's slide-changing mechanism and the dispensing of one 190 mg banana-flavored reward pellet. A single pellet was given only to bring the monkey forward and was noncontingent on any of the monkey's behavior. The monkey was then free to retrieve the reward pellet and to view the picture through the eyeholes of the split-brain testing front for as long or often as it wished. When the monkey's head was correctly in place behind the eyeholes, it interrupted a photocell beam. This turned on the projector lamp, illuminating the slide and also activating a counter which recorded viewing time to the nearest tenth of a second. After three minutes of slide availability regardless of how much the monkey looked, a new slide was made available, signalled as before by the sound of the projector mechanism and the dispensing of one pellet.

Each monkey was adapted to the testing situation by binocular training on four picture sets, each comprised of four pictures, one from each category, presented one set per day on consecutive testing days. For the main experiment four new picture sets were used and the monkeys were tested monocularly. Alternate contralateral eye-hand pairs were tested on successive days with the eye tested first balanced across monkeys. The order of testing eyes for a particular monkey was balanced across sets of pictures so that, for example, the left eye-right hand pair was tested first on the first and third sets and the right eye-left hand was tested first on the second and fourth sets, or vice versa.

Each monkey was also tested for one day with each eye on a control white condition in which only a plain white field was available for viewing. Five monkeys received the control condition between the binocular and monocular testing, six monkeys received the control condition between the second and third monocular picture sets, and eight monkeys received the control following four monocular sets.

Data analysis: The total amount of time out of a maximum of three minutes which was spent viewing each slide was recorded to the nearest tenth of a second. From this, the percentage of the total available time spent viewing each picture was calculated and averaged for each monkey across the four exemplars of each category. In addition, the total amount of time out of the possible 12 minutes that each monkey could spend viewing the four stimuli in a day's session was set equal to 100% and the portion of that time spent with each picture was computed. Again, these scores were averaged within each stimulus category for each individual subject.

Dominance indices, calculated as $\frac{(L-R)}{(L+R)}100$, where L is the score obtained by the left eye and R is the score obtained by the right eye, were computed for each of the two performance measures. An index of 33% equals a performance by the left hemisphere that was twice as great as the performance by the right and a 50% index indicated a three-times advantage of the left hemisphere over the right. Negative indices show a right hemisphere advantage, with -33% equal to a factor of two and -50% equal to a factor of three right hemisphere advantage over the left. The dominance indices for each category were compared to each individual's handedness index, which is defined as $\frac{(R-L)}{(R+L)}100$, with R equal to the percentage of reaches for food made by the right hand and L equal the analogous score for the left hand. Handedness testing (Warren et al., 1967) was done upon the monkey's arrival in the laboratory and prior to any behavioral testing or surgery.

Percent looking behavior and dominance indices were statistically evaluated when appropriate by t-tests or Pearson correlation coefficients (Spence et al., 1968).

Results and Discussion

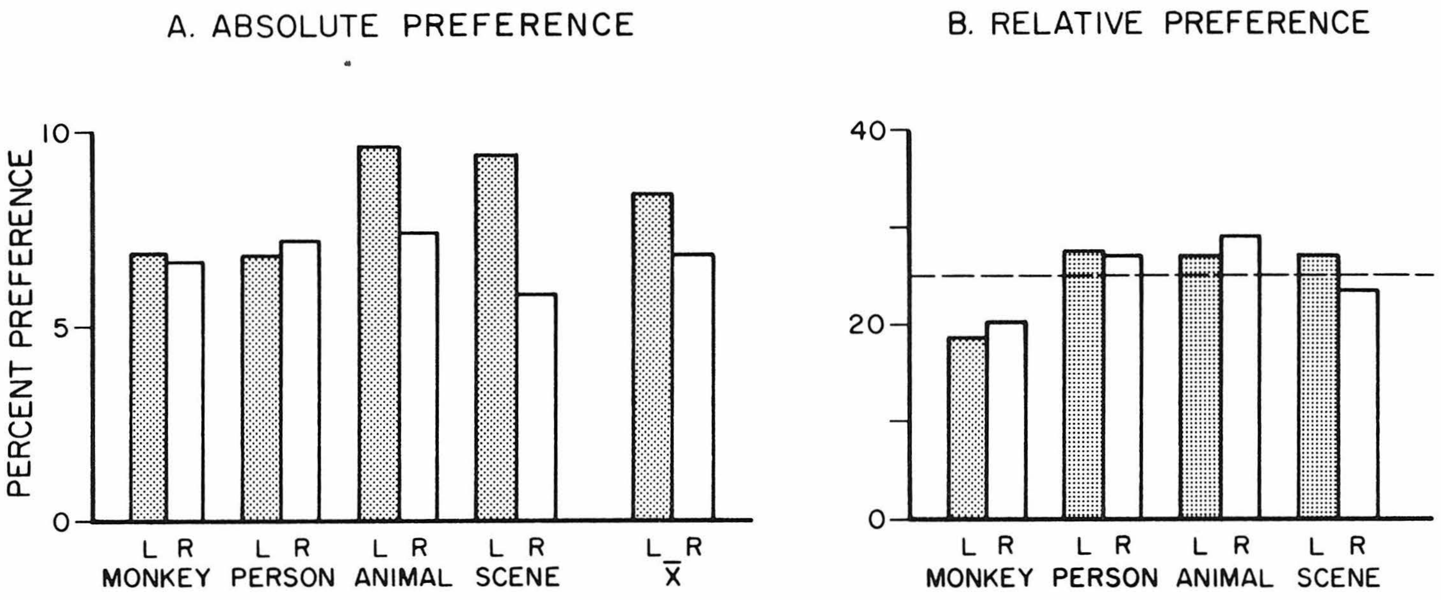
Absolute preferences: Table 3 presents the mean percent of the available time spent looking monocularly by each monkey. Looking time has been segregated into stimulus categories and the data for the two eyes have been presented separately. The means across monkeys for the left and right eyes in each category are diagrammed in Figure 3a. Looking times for the left and right eyes are significantly different

TABLE 3

Mean percent of absolute preference with each hemisphere

Subject	Monkey		Person		Animal		Scene		$\bar{x}$	
	LE	RE	LE	RE	LE	RE	LE	RE	LE	RE
MRV	34.89	16.21	6.99	16.68	39.28	11.60	17.07	2.14	24.56	11.66
TEA	2.56	2.44	1.96	0.94	2.44	2.08	2.97	2.79	2.48	2.06
DPE	2.04	3.86	5.74	7.19	4.81	8.00	8.11	3.07	5.17	5.53
IRM	6.40	31.71	19.82	29.69	42.08	44.50	36.44	29.60	26.19	33.88
BRN	3.90	7.19	5.11	6.57	4.15	4.28	3.15	4.47	4.08	5.63
ZOR	4.08	3.49	6.67	3.49	8.03	6.29	11.32	2.29	7.52	3.89
EDN	3.43	1.24	12.44	3.61	5.18	2.36	13.01	5.75	8.52	3.24
ETH	5.26	1.56	3.97	3.56	14.18	2.62	11.32	3.06	8.76	2.62
IRW	0.86	0.10	1.01	0.20	0.79	0.21	0.66	0.12	1.32	0.28
POT	49.22	33.36	30.47	36.65	38.19	32.89	46.64	28.56	41.13	32.86
CRN	5.85	7.61	5.33	4.69	4.01	5.58	4.35	5.12	5.98	4.65
MNX	0.33	0.50	4.33	5.85	3.17	3.93	5.49	4.46	3.33	3.68
RYE	1.39	2.32	1.94	2.62	1.90	3.51	2.32	1.64	3.40	4.54
CSM	3.33	3.03	7.12	3.21	3.82	3.25	4.25	2.32	4.64	2.94
DOE	1.64	1.07	1.78	1.03	0.94	1.50	0.34	1.56	1.24	1.29
BOO	2.93	6.51	5.99	5.75	5.74	4.75	4.90	6.46	4.89	5.87
EDG	1.56	4.11	4.24	3.94	3.06	1.88	1.15	3.88	2.50	3.45
HSH	0.93	0.18	3.17	1.04	1.67	1.61	3.94	2.58	2.43	1.35
LMN	0.35	0	0.62	0.06	0.60	0.10	0.74	0	0.58	0.04
$\bar{x}$	6.89	6.66	6.77	7.20	9.69	7.42	9.38	5.78	8.38	6.81
SD	±12.74	±9.89	±7.25	±9.93	±13.78	±11.52	±12.36	±8.39	±10.62	±9.70

Figure 3: A. The mean absolute preference across monkeys for each of the four stimulus categories is presented separately for the left and right hemispheres. B. The mean relative preferences for each category are presented as in A. The dashed line represents 25% preference.


A. ABSOLUTE PREFERENCE
PERCENT PREFERENCE
10
5
0
L R
MONKEY
L R
PERSON
L R
ANIMAL
L R
SCENE
L R
X̄
B. RELATIVE PREFERENCE
40
20
0
L R
MONKEY
L R
PERSON
L R
ANIMAL
L R
SCENE

from each other only for the category scene ($\bar{x} = 3.60 + 5.78$, $p < .01$) but are nearly so for the category animal ($\bar{x} = 2.27 \pm 6.94$, $p < .10$) and the mean of all categories ($\bar{x} = 1.49 \pm 4.39$, $p < .10$). The number of seconds out of the total available time that the monkeys actually looked was rather low but even so was comparable to the amount of time monkeys spent viewing stationary photographs reported by others (Butler and Woolpy, 1963; Redican *et al.*, 1971; Sackett, 1965, 1966).

The amount of time spent looking was affected by the photographs, because when the monkeys were given only a plain white field to view in one daily session (12 minutes) to each eye looking time was significantly lower than when photographs were given. Overall the pictures were viewed about twice as long as the blank screen. Therefore, the time spent looking at photographs was more than just the minimum time necessary to retrieve the food pellet that was dispensed whenever a new photograph was made available for viewing. It can also be shown that looking behavior was not simply a function of food motivation. Two of the monkeys were retested subsequent to the main experiment after receiving their day's ration of food one hour prior to testing. Looking times were slightly lower, but the satiated monkeys still looked at the photographs more than at the blank screen.

Left-right differences were also examined by analyzing the dominance indices calculated for each monkey from the absolute preferences averaged over all picture categories. The mean dominance index across monkeys was positive and significantly different from zero (Table 4). An overall left hemisphere preference for observing was again found, confirming the results of Experiment 1. In order to see whether the various stimulus categories contributed differentially to this result, a dominance index was calculated for each monkey's absolute looking time for each picture and a mean dominance index over four exemplars was obtained for each category; they are also listed in Table 4. For every category except monkey, the mean dominance index averaged across subjects was positive and

TABLE 4

Dominance indices for absolute preferences

Subject	Sex	Retraction	Handedness Index	Dominance Index				
				Monkey	Person	Animal	Scene	$\bar{x}$
MRV	M	RL	-100	40.26	-6.80	42.68	43.81	29.99
TEA	M	R	-97	0.04	37.58	13.60	-8.93	10.56
DPE	F	LRL	-87	-29.26	-12.86	-18.38	31.28	-7.30
IRM	M	RL	-82	-31.22	-23.51	6.31	2.40	-11.50
BRN	F	RL	-77	-20.16	-6.62	-0.76	-19.02	-11.64
ZOR	M	L	-73	7.00	30.34	14.70	42.42	23.62
EDN	M	L	-20	42.48	51.82	30.92	54.36	44.90
ETH	F	L	-15	54.32	6.66	30.42	34.87	31.57
IRW	M	RLR	-9	64.76	75.93	38.07	68.90	61.92
POT	F	L	-5	23.36	-11.66	16.48	33.93	15.53
CRN	M	LR	3	1.19	17.61	-6.52	-2.65	2.41
MNX	F	L	6	-32.45	-3.82	-1.07	11.50	-6.46
RYE	F	R	26	3.09	-8.59	-19.02	23.02	-0.38
CSM	M	R	27	-32.38	32.67	9.04	32.90	10.56
DOE	M	LR	32	11.99	23.74	-16.09	-35.01	-3.84
BOO	F	R	35	-26.44	10.91	4.22	4.20	-1.78
EDG	M	L	52	-51.90	21.74	23.48	-11.33	-4.50
HSH	F	LR	84	35.42	47.77	4.88	20.00	27.02
LMN	F	R	93	100.00	83.88	89.68	100.00	93.39
$\bar{x}$				8.43	19.30	13.82	22.46	16.00
SD				±40.11	±30.40	±25.78	±32.62	±27.65
p				< .20	< .01	<.02	< .005	< .02

All t-tests are for difference from zero.

significantly different from zero. This indicates that overall monkeys looked at photographs longer with their left hemispheres than with their right hemispheres. This finding is in accord with the findings of the previous experiment on preferences.

Each monkey's dominance indices were assessed as a function of that monkey's handedness index because, as discussed under the previous experiment, lateralization of brain function and handedness are related in the human being and furthermore, such comparisons showed significant relationships in the previous experiment on visual preferences. Figure 4 illustrates these comparisons. The slopes of the least squares lines are positive, in contrast to those of Experiment 1. That is, in general right-handed monkeys spent more time looking with their left hemispheres than with their right, while left-handed monkeys spent more time looking with their right hemispheres than with their left. The correlation coefficient was significant for only one category, person ($r = 0.467$, $p < .05$). It appears doubtful that a meaningful relationship between dominance and handedness exists in this experiment for which there is more variability due to fewer observations per subject.

Relative preferences: To see how the monkeys divided up their total looking time among the four categories the absolute looking time in each session was set equal to 100% and the percentage of that time spent with each picture was calculated. For each monkey, a mean was taken over the four exemplars of each picture category, keeping the data for left and right eyes separate within a category. These are presented in Table 5. Figure 3b shows the means across monkeys plotted by eyes and categories. The means for left and right eyes are not significantly different from each other in any category, which means that the two hemispheres divided up their relative looking time in about the same way.

If each monkey were to divide his looking time equally among the four pictures presented in each session, it would be expected that one quarter, or 25%, of the time looked would be spent with each category. In two categories, person

Figure 4: Each monkey's dominance indices based on absolute preferences are plotted as a function of that monkey's handedness index. Each stimulus category is represented separately as well as the mean across categories. The least squares line of Y on X has been drawn in for each plot.

DOMINANCE vs HANDEDNESS FOR ABSOLUTE PREFERENCE

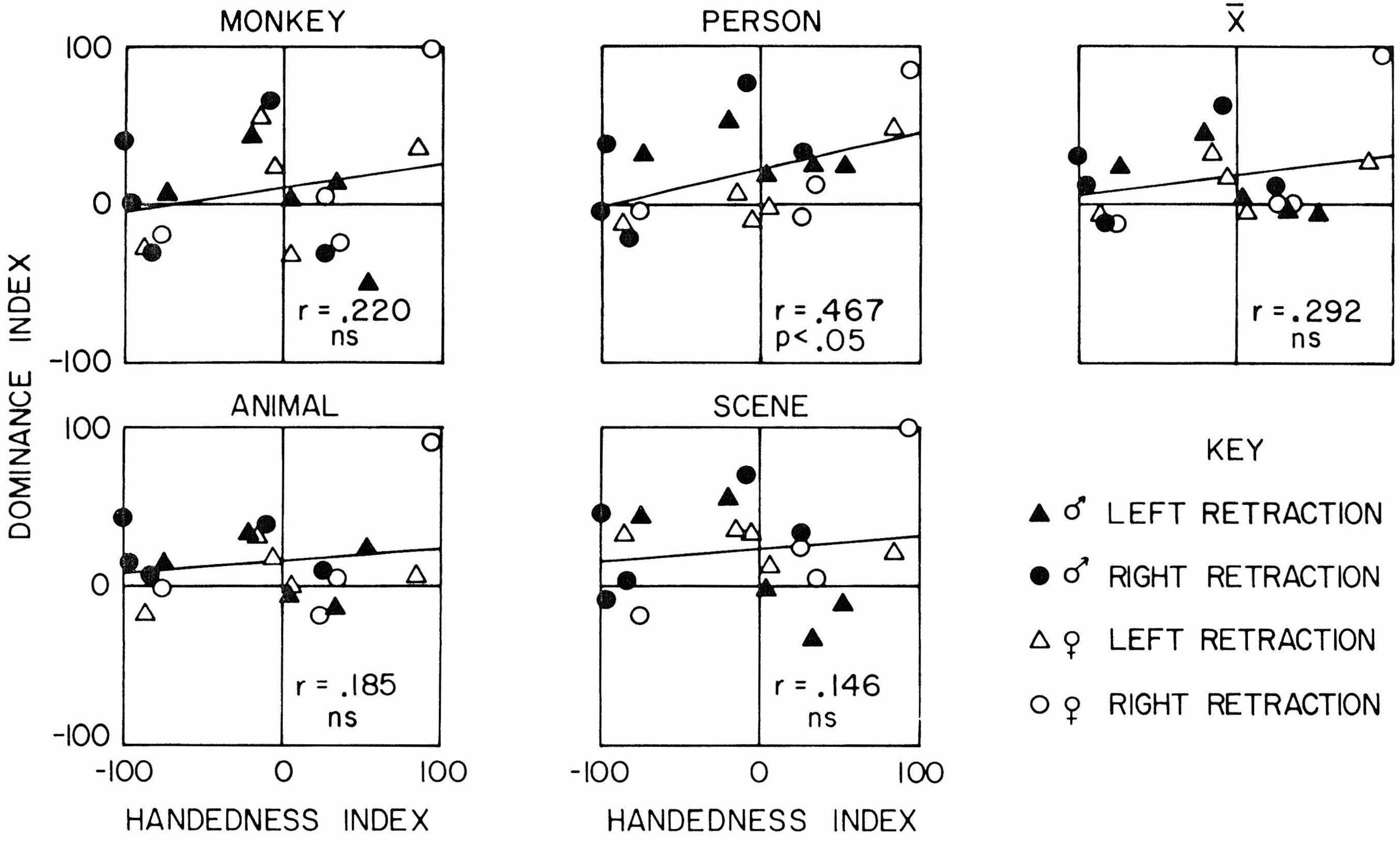


TABLE 5

Percent relative preference for each picture

	Monkey		Person		Animal		Scene	
Subject	LE	RE	LE	RE	LE	RE	LE	RE
MRV	35.51	32.82	13.78	25.70	36.47	33.71	14.24	7.77
TEA	25.53	30.04	20.36	11.60	25.42	23.21	28.82	35.16
DPE	10.30	16.88	27.60	35.14	26.58	34.03	35.52	13.96
IRM	5.94	26.26	19.72	21.49	39.56	33.36	34.78	18.90
BRN	26.37	29.47	29.25	26.26	24.93	22.17	19.45	22.10
ZOR	17.96	26.92	26.31	20.60	26.88	36.52	28.85	15.96
EDN	10.82	11.59	41.88	29.60	13.89	16.91	33.41	42.14
ETH	20.37	13.00	20.36	36.34	30.87	22.73	28.40	27.94
IRW	17.06	13.71	27.54	23.31	26.37	39.18	29.03	23.80
POT	29.50	26.72	18.48	29.16	22.94	23.56	29.08	20.56
CRN	31.92	32.50	27.50	19.73	19.21	22.74	21.36	25.03
MNX	2.58	7.50	30.94	34.83	23.10	26.74	43.37	30.94
RYE	18.49	21.62	22.54	20.66	32.29	44.81	26.67	12.91
CSM	17.08	20.58	35.04	28.36	21.77	29.51	26.11	21.55
DOE	29.03	20.62	35.60	19.74	21.19	30.07	14.18	29.57
BOO	16.17	28.12	29.68	21.26	28.36	25.14	25.78	25.50
EDG	13.72	33.15	41.56	24.22	32.82	19.59	11.89	23.04
HSH	9.81	3.10	31.45	20.63	16.62	27.10	42.13	49.17
LMN	10.44	0	20.25	65.00	45.95	35.00	23.36	0
$\bar{x}$	18.35	20.77	27.36	27.03	27.12	28.74	27.18	23.47
SD	±9.21	±10.23	±7.72	±10.60	±7.91	±7.30	±8.65	±11.44
p	< .005	< .05	< .10	< .30	< .20	< .025	< .20	< .30

and scene, the relative preference for that particular category did not differ significantly from 25%. However, for the monkey category the relative preference was significantly *less* than 25%, for both the left eye ($\bar{x} = -6.65 + 9.21$, $p < .005$) and the right eye ($\bar{x} = -4.23 + 10.23$, $p < .05$) while for the category animal it was significantly *greater* than 25% for the right eye only ($\bar{x} = 3.74 \pm 7.30$, $p < .025$). That is, monkey photographs significantly inhibited viewing by each hemisphere of split-brain subjects, but animal photographs caused the right hemisphere to look more, showing that the monkeys' performance was affected by picture content. This is not surprising. It is known that monkeys can discriminate photographs of one monkey from photographs of another monkey and can generalize well to new exemplars of the same animals (Hamilton, 1977b; Hamilton, Tieman and Farrell, 1974; Rosenfeld and Van Hoesen, 1979). Unpublished observations from this laboratory on the same subjects used in this experiment have shown that when confronted with large photographs of other monkeys in free vision, subject monkeys made socially-appropriate responses such as lip-smacking, presenting, threatening, fear-grimacing, and looking away. These responses were not made to other categories of photographs. Therefore the suppression of viewing in response to monkey photographs is interesting, especially since when rhesus monkeys are confronted with stressful situations, even mildly stressful ones, they will respond by looking at everything *but* the threatening object or individual, making occasional quick glances in the direction of the stressful stimulus (Hinde and Rowell, 1962; Redican, 1975). Redican *et al*. (1971) and Sackett (1966) reported suppression of looking by monkey photographs, but specifically when the photographed animal was displaying either a grimace (Redican *et al*., 1971) or an open-mouth threat (Redican *et al*., 1971; Sackett, 1966) and especially when the monkey being tested was an infant or juvenile.

Dominance indices for the individual monkeys on the relative time spent with each category were also computed for each photograph and averaged over the four exemplars in each category and are listed in Table 6. Plots of these dominance indices as a function of each monkey's handedness are found in Figure 5 along with their least squares fits and correlation coefficients. All of the slopes of the least squares lines for these plots were positive. However, none of the correlation coefficients was significant, although the one for the category person nearly reached significance. The coefficients for the categories monkey, animal, and scene, although not significant, were higher than those for the absolute preferences.

This experiment, then, suggests that overall the left hemisphere of split-brain monkeys likes to look more at photographic slides than does the right hemisphere, confirming the results of Experiment 1. This effect, however, in most cases is not reliably related to the individual monkey's handedness preferences.

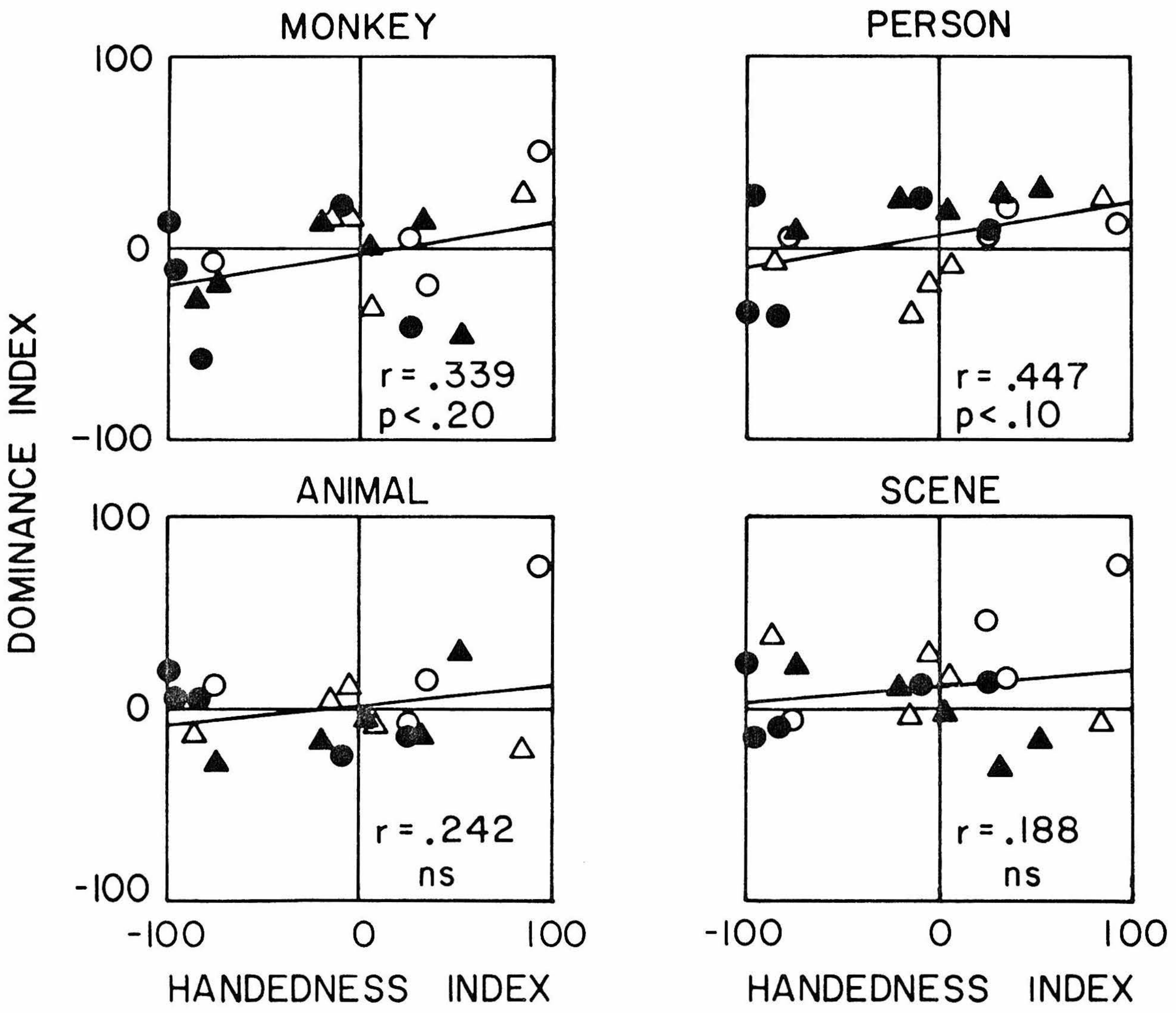
TABLE 6

Dominance indices for relative preferences for each picture

	Dominance Index			
Subject	Monkey	Person	Animal	Scene
MRV	12.70	-33.02	19.33	12.18
TEA	-10.80	28.06	4.85	-16.54
DPE	-25.98	-8.43	-12.97	37.92
IRM	-58.11	-36.64	3.84	-9.90
BRN	-8.31	6.65	11.66	-7.04
ZOR	-20.00	7.36	-30.40	21.01
EDN	11.75	23.41	-18.06	9.47
ETH	15.80	-35.37	3.78	-3.26
IRW	20.82	25.46	-25.56	11.34
POT	16.15	-20.05	10.47	27.92
CRN	0.38	18.96	-7.34	-3.44
MNX	-31.58	-9.29	-9.50	17.18
RYE	4.74	3.41	-7.76	45.33
CSM	-41.56	8.45	-13.89	11.90
DOE	13.83	27.44	-13.43	-31.44
BOO	-19.53	20.60	14.95	15.51
EDG	-46.58	29.36	28.17	-17.44
HSH	27.97	26.52	-21.56	-7.86
LMN	50.00	11.32	73.64	75.00
$\bar{x}$	-4.65	4.96	0.54	9.89
SD	±28.13	±22.57	±23.83	±25.08
p	< .30	< .20	ns	< .10

Figure 5: The dominance indices for relative preferences are plotted as a function of handedness index.

DOMINANCE vs HANDEDNESS FOR RELATIVE PREFERENCE



EXPERIMENT 3

HEMISPHERIC DIFFERENCES IN PROCESSING SEQUENTIAL COMPARISONS

Investigations designed to determine the existence of hemispheric specialization in split-brain monkeys have employed not only tests of visual preferences, but also tests of learning ability using stimuli of types which should elicit lateralized processing by the human brain (Hamilton, 1977b). Most of these experiments used stimuli that would involve right hemispheric processing in human subjects. In general no differences were found between the two hemispheres in their abilities to learn these tasks. In contrast, the results of an experiment using a task designed to favor left hemisphere processing are presented here.

The human left hemisphere has been described as being linguistic, analytical, sequential and temporal (Sperry, 1974). Rhesus monkeys are not capable of learning language in the human sense even though they do possess a wide range of species-specific vocalizations. In fact, a related species, the Japanese macaque (*M. fuscata*), has been reported to show differential hemispheric processing of species-specific vocalizations (Beecher, Petersen, Zoloth, Moody and Stebbins, 1979; Petersen, Beecher, Zoloth, Moody and Stebbins, 1978). However, the analysis of the hemisphericity of human-type linguistic processing is probably best deferred to those who study the great apes which have learned sign language and other symbolic languages (Gardner and Gardner, 1971; Patterson, 1978; Premack, 1971; Rumbaugh, 1977).

It has been suggested that the capacity to produce and perceive language is based on a more fundamental process, the analysis of the sequential and temporal order of stimuli (Hirsh, 1967; Lashley, 1951; Neff, 1964). A variety of studies on normal and brain-damaged human subjects have determined that temporal perception is mediated by the left hemisphere. Efron (1963a,b) reported that the left hemisphere of normal right-handed subjects is the locus for the temporal discrimination of simultaneity and order tested with both light flashes and finger shocks; that is, a temporal discrimination is not performed until the two stimuli to be compared have been transferred into the dominant (left) hemisphere. Furthermore, patients with left hemisphere damage were much worse at determining the order or simultaneity of auditory or visual stimuli than right brain-damaged patients, and, of the patients with left hemisphere lesions, those who were also aphasic showed the worst performance of all (Efron, 1963c). Other tasks in which the left hemisphere of man is superior to the right involve determining the temporal order or sequence of auditory and visual stimuli (Albert, 1972; Carmon and Nachshon, 1971; Halperin, Nachshon and Carmon, 1973), processing stimulus duration (Gordon, 1967; Mills and Rollman, 1979), identifying rhythmic elements in music (Gordon, 1978), and analyzing Morse code (Papcun, Krashen, Terbeek, Remington, and Harshman, 1974).

Konorski's (1959) successive same-different task was chosen as a type of sequential task that was not only within the capabilities of the rhesus monkey, but could also be modified, if necessary, into other related tasks such as a delayed sequential comparison, cross-modal comparison, or reporting the order of the stimuli, which are more demanding on the subjects and which could possibly tap other lateralized mechanisms. Only the performance of the two separated hemispheres of split-brain monkeys on the basic task will be reported here.

Methods

Subjects: Twelve split-brain rhesus monkeys (M. mulatta), six males and six females, were used. All monkeys had sustained surgical section of the optic chiasm, corpus callosum, and anterior and hippocampal commissures in one or two stages. Four monkeys, DPE, IRW, MNX and RYE, had also undergone midline section of the posterior, habenular, and superior collicular commissures in a second (MNX, RYE) or third (DPE, IRW) operation. All monkeys had been trained on a variety of visual discrimination tasks since their surgeries and before the present experiment. Housing and feeding of the monkeys were as described in previous chapters.

Apparatus: As in the previous experiments, the monkeys were trained in a split-brain testing apparatus similar to that described by Sperry (1968). For this experiment, though, the monkeys were trained in a room together with up to six other monkeys in individual training boxes.

The response panel was made of anodized black aluminum and was situated at arms' length in front of the split-brain compartment. It contained a single circular stimulus and response screen 1-1/2 inches in diameter located at eye level. Below the screen was a food cup for delivery of 190 mg banana-flavored Noyes reward pellets. Stimuli were presented by means of a miniature in-line projector (IEE, Inc., Van Nuys, California); presentation followed Gellerman (1933) sequences. Digital logic modules (BRS-LVE) controlled stimulus presentation, delivery of reward pellets, timing, and tabulation of correct trials. The monkeys could be monitored during training via an overhead closed-circuit television camera.

Procedure: A symmetrically rewarded Go/No-Go paradigm was used. A white light illuminated the response screen when the monkey could respond. A push initiated the presentation of the first stimulus (S_1), followed by an interstimulus interval (ISI) during which the screen was dark, followed by the second stimulus (S_2). The length of each stimulus and the interstimulus interval was half a second. Following the second stimulus, the white light returned for up to five seconds to signal the response interval. The monkey's task was to push again during the response interval if S_1 and S_2 were different (Go response) and to withhold a response if S_1 and S_2 were the same (No-Go response). Either of these correct responses was rewarded with one banana pellet. Either of the other two possible responses, a Go response when S_1 and S_2 were the same, or a No-Go response when S_1 and S_2 were different, was incorrect and led directly to the ten second intertrial interval without food reinforcement.

The stimuli used consisted of a pair of colors, red and green, and three pairs of symmetrical patterns, white on a black background. They were learned in the same order by all subjects, with the colors presented first.

Each monkey was trained on one pair of stimuli using one contralateral eye-hand pair until the criterion of 36 correct responses in four consecutive blocks of ten trials was reached and was overtrained to the criterion of 108 correct responses in 12 consecutive blocks of ten trials. The monkey was then trained on the same pair of stimuli with the opposite eye-hand pair to the same criteria, before proceeding on to a new stimulus pair. Contralateral eye-hand pairs were used because in the split-brain monkey, each eye is connected only to the hemisphere ipsilateral to it and each hand is run primarily from the hemisphere contralateral to it; thus, training the left eye-right hand, for example, is equivalent to training the left hemisphere. The eye initially trained was balanced across monkeys. Alternate stimulus pairs were learned first by opposite eyes.

Data analysis: The number of errors through the criterion of 36/40 on each problem was assessed for each eye of each subject. From the errors a dominance index was calculated as $(\frac{R-L}{R+L})\ 100$, where R and L are equal to the errors made by the right and left eyes (hemispheres), respectively. Hand preferences in reaching for food (Warren <u>et</u> <u>al</u>., 1967) were assessed upon each monkey's arrival into the laboratory and before any surgery or formal testing. For each monkey a handedness index was computed as $(\frac{R-L}{R+L})\ 100$, with R and L equal to the percentage of reaches with the right and left hands. Both of these indices are arranged so that predominant performance by the left hemisphere is indicated by a positive index and predominant performance by the right hemisphere is indicated by a negative index. The data were statistically evaluated by t-tests and Pearson (r) correlation coefficients when appropriate.

Results and Discussion

Each monkey's errors through criterion with each eye are presented in Table 7. The dominance indices calculated on errors with the left and right eyes on each problem are presented in Table 8 along with each monkey's vital statistics. KIP's data are included in the tables but are omitted from statistical analysis because of failure to complete the fourth pair of patterns which leaves her data unbalanced; the overall results are even more significant if KIP's data are included. A mean dominance index was calculated for each monkey. The grand mean assessed over eleven monkeys was not significantly different from zero ($\bar{x} = 5.03 \pm 26.10$, ns) which indicates that overall neither hemisphere excelled in learning the task. This is in keeping with the results of other experiments investigating the learning abilities of the two hemispheres of split-brain monkeys on tasks employing stimuli which should favor lateralized processing in man (Hamilton, 1977b,c).

As pointed out in Experiment 1, unlike man, the handedness preferences of monkeys are equally distributed from left to right (Lehman, 1978; Warren, 1977). It is reasonable, then, that if hemispheric specialization does exist, it might also occur on a continuum from left to right and averaging all monkeys together would yield a net dominance near zero. Figure 6 shows the mean dominance index for each monkey plotted as a function of that monkey's handedness with the least squares line of Y on X drawn in. The correlation coefficient is significant ($r = 0.718$, $p < .02$) which indicates that the hemisphere which learned the task significantly faster was correlated with the monkey's handedness. That is, a left-handed monkey learned faster with its right hemisphere and a right-handed

TABLE 7

Errors through criterion with each eye on the sequential task

	Problem 1		Problem 2		Problem 3		Problem 4	
Subject	LE	RE	LE	RE	LE	RE	LE	RE
TEA	231	69	155	90	59	13	4	71
DPE	662	580	135	291	122	54	11	2
KIP	694	589	981	1013	1874	422	>337	-*
BRN	338	344	139	51	202	67	68	102
ZOR	451	4390	115	68	34	86	562	100
IRW	303	195	119	169	27	103	5	8
CHT	230	107	166	64	21	292	123	12
MNX	929	627	113	132	391	3	5	35
RYE	427	1300	394	175	69	15	35	40
DOE	412	354	135	420	198	276	61	457
EDG	235	474	548	643	99	131	41	210
LMN	322	840	65	295	29	40	3	179

*KIP failed to learn the fourth problem with either eye.

TABLE 8

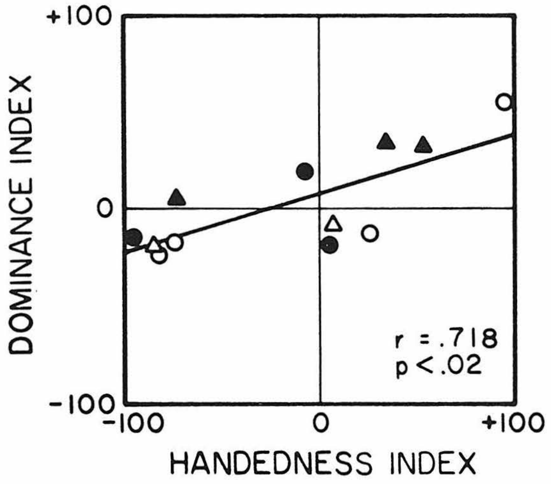
Dominance indices for each monkey on the sequential task

Subject	Sex	Surgical Retraction	Handedness Index	Problem 1	Problem 2	Problem 3	Problem 4	$\bar{x}$
TEA	M	R	-97	-54.00	-26.53	-63.89	89.33	-13.77
DPE	F	LRL	-87	-6.60	36.62	-38.64	-69.23	-19.46
KIP	F	R	-83	-8.18	1.60	-63.24	-	-23.27*
BRN	F	RL	-77	0.88	-46.32	-50.19	20.00	-18.91
ZOR	M	L	-73	81.37	-25.68	43.33	-69.79	7.31
IRW	M	RLR	-9	-21.69	17.36	58.46	23.08	19.30
CHT	M	R	4	-36.50	-44.35	86.58	-82.22	-19.12
MNX	F	LR	6	-19.41	7.76	-98.48	75.00	-8.78
RYE	F	RL	26	50.55	-38.49	-64.29	6.67	-11.39
DOE	M	LR	32	-7.57	51.35	16.46	76.45	34.17
EDG	M	L	52	33.71	7.98	13.91	67.33	30.73
LMN	F	R	93	44.58	63.89	15.94	96.70	55.28

*KIP's data are included in the table but are excluded from statistical analysis.

Figure 6: Dominance indices have been graphed as a function of handedness index for each monkey and a line representing the least squares fit of Y on X has been drawn in. Closed symbols represent male monkeys and open symbols represent female monkeys. Triangles denote a left hemisphere approach during surgery, circles denote right hemisphere retraction.

DOMINANCE vs. HANDEDNESS
SEQUENTIAL TASK



monkey learned faster with its left hemisphere. Two other factors which might possibly influence the expression of hemispheric specialization, sex of the subject and side of surgical approach, have also been coded in Figure 6. Any effect of these factors would appear as a clustering of the appropriate symbols. As can be seen, no such effect is evident.

These differences in performance as a function of handedness can be related to human studies. Most of the relevant studies in the literature report only data from right-handed subjects; an extrapolation must be made to predict the performance of left-handed subjects. Efron (1963a), though, does report both right and left-handed subjects and in fact finds a significant difference between them in their judgment of the simultaneity of two stimuli. In the normal right-handed subject, when a comparison must be made between two stimuli, one presented to each hemisphere, the stimulus entering the right hemisphere must be transferred to the left in order for the comparison to be made. Efron states that the data from approximately 26% of the left-handed subjects differed by more than one standard deviation from the data of the rest of the group. When the performance of these subjects was analyzed separately, it differed significantly from that of the rest of the left-handed subjects and also from that of the right-handed subjects, showing in fact, the opposite effect; that is, a change in which of the two stimuli must actually occur before the other for them to be perceived as simultaneous. Efron hypothesized that these subjects were "true" sinistrals with a dominant right hemisphere, and that the rest of the left-handed group had mixed dominance. Therefore, Efron's data are consistent with the monkey data reported here, in that right- and "true" left-handed subjects showed opposite hemispheric superiorities for processing a sequential comparison between two stimuli. If the dominant hemisphere of a monkey is the one contralateral to its preferred hand, then the hemispheric superiority of these monkeys for the sequential same-different judgment is as would be expected in human subjects.

GENERAL DISCUSSION

Three main questions were asked in these experiments on hemispheric specialization. First, is the left hemisphere specialized differently from the right? Second, are hemispheric differences, if found, correlated with other factors indigenous to the subjects such as handedness? These two questions could be related, or they could both be independently true or false. Third, are hemispheric differences, if present, related to either the general nature of the stimuli employed or to the specific meaning or interest evoked by the content of the stimuli?

Overview of Results

Left-Right Differences: Dominance indices as defined in the Methods are a meaningful way of assessing hemispheric differences because they allow comparisons to be made between monkeys while normalizing for individual differences in response levels. For the three experiments reported here, the mean dominance indices for the various stimuli were positive, indicating a left hemisphere superiority, in eleven out of thirteen cases, the exceptions being the category normal/altered in the first preference experiment (Table 2) and the relative preference for the category monkey in the second preference experiment (Table 6). The mean dominance indices were significantly different from zero in three out of these thirteen cases, namely, the preferences in the second experiment for the categories person, animal, scene (Table 5). Therefore, the left hemisphere's overall performance was frequently different from that of the right, but not always significantly so, in showing greater tendencies to look at visual stimuli and to learn sequential comparisons. In general, this result is not as robust as the correlation of dominance with handedness indices discussed next, and in Experiment 1 may be at least partially attributable to the excess of left-handed monkeys in that experiment.

Correlation with Handedness: Significant correlations were found between the monkeys' dominance indices and their handedness indices for visual preferences as measured by the Humphrey-type technique (Experiment 1) and for the sequential task (Experiment 3). It is unfortunate that so few monkeys completed testing on Experiment 1 and that those which did were predominantly left-handed. The paradigm was so difficult to teach the monkeys (eleven of the original eighteen refused to perform) and so time-consuming to run that it was not feasible to test additional subjects. Nevertheless, the data for percent preferences were consistent and the correlations with handedness were high. The second preference experiment, which was intended to allow larger numbers of monkeys to be tested more easily, only produced a significant dominance/handedness correlation for one category, the absolute preference for photographs of people, and it was in the reversed direction from those in Experiment 1. Considering the general unreliability of the correlations in Experiment 2 this aberrant result with photographs of people will not be considered further, although post hoc interpretations for this result could be formulated. As indicated before, however, Experiment 2 did show a significant general preference for looking with the left hemisphere.

The sequential task analyzed the monkeys' abilities to make same-different judgments about two sequentially presented stimuli. Unlike the preference experiments, it measured learning ability to a criterion of 90% correct responding. The task also revealed a significant correlation between dominance and handedness with a slope opposite to that of Experiment 1.

In terms of the brain of most human subjects, then, the pictures of Experiment 1 were viewed more by the monkey's equivalent of the human non-dominant hemisphere and the sequential comparisons were learned more readily by the monkey's equivalent of the human dominant hemisphere. Thus, these results with split-brain monkeys parallel those frequently reported for human subjects.

Relationship to Stimuli: Hemispheric differences were only related to the type of stimuli in a gross way. Preferences for the pictorial stimuli in Experiment 1 produced negative correlations with handedness, that is, these stimuli were preferred more strongly by the hemisphere ipsilateral to the preferred hand. Conversely, processing sequentially-presented stimuli produced positive correlations with handedness and therefore the discrimination was learned faster with the hemisphere contralateral to the preferred hand.

There was very little difference between the two hemispheres in their preferences for photographs of different subject matter, which is disappointing. Although some categories of photographs were differentially viewed as discussed earlier, the monkeys' behavior with regard to stimulus content was generally very similar for the two hemispheres. Thus, no evidence was found for differential stimulus control in the two hemispheres.

Explanations and Interpretations

The results of the studies reported here showed in several cases differential behaviors by the two hemispheres of split-brain rhesus monkeys. For some tasks the differences may be attributed to a general superiority of the left hemisphere over the right, while for others the hemisphere which performs better is related to the individual monkey's handedness preferences. Other evidence of functional asymmetries in rats, monkeys, and humans suggests the possibility that differential cerebral processing may be a common feature of mammalian brains. Some of these studies favor general left-right differences while others favor hemispheric differences related to the handedness of the subjects.

Left-Right Differences: Comparing left-right differences suggested that there was a general preference by the left hemisphere for viewing pictorial material, although this preference was generally not stimulus-related. Therefore, it is less like the qualitative difference in cognitive processing often attributed to hemispheric specialization in man, but rather, may represent a difference in the emotional/attentional levels of the two hemispheres and may therefore reflect a quantitative difference in hemispheric activity. Other recent experiments reporting left-right differences may be similarly interpreted as evidence for the differential lateralization of emotion, attention, or affect.

Changes in activity levels as measured by running-wheel or open-field tests have been reported in rats following ablations of the right, but not left, cerebral cortex. Robinson (1979) reported that following right cerebral infarctions caused by ligation of the right middle cerebral artery, rats became significantly more active than they were preoperatively, while rats with left hemisphere infarctions and sham operates showed no activity increases over baseline. Left hemisphere lesions also had no effects on catecholamine concentrations while right lesions resulted in ipsilateral depletion of norepinephrine in the cortex and locus coeruleus and dopamine in the substantia nigra.

Denenberg, et al. (1978) also found changes in activity levels tested by open-field behavior with right, but not left neocortical ablations in rats who had been handled in infancy. A further effect of lateralization was also shown: rats handled in infancy who had also lived in an enriched environment reduced their activity to nearly zero in the open field while handled rats without enrichment experience were significantly more active than any others. Both handling in infancy and enrichment experience traditionally reduce emotionality and increase exploratory behavior in adulthood.

Both of these experiments with rats can be interpreted as evidence for hemispheric differences in emotionality, activation, or attention. Since both left- and right-handed rats were almost certainly included as subjects (Collins, 1968, 1977) the results seem to represent a true difference between left and right hemispheres.

Two recent reports have claimed to have found a left hemispheric superiority for processing auditory stimuli in monkeys. Five Japanese macaques each showed a statistically significant right ear advantage for discriminating species-specific vocalizations, whereas only one of four control monkeys of other species did (Beecher, et al., 1979; Petersen, et al., 1970). Dewson (1977) found that lesions of the left but not right superior temporal gyrus of cynomolgus macaques disrupted the performance of an audiovisual conditional comparison when delays of more than a few seconds were interposed between the auditory and visual elements. The left hemisphere deficit was ameliorated if the delays were incremented by very small amounts.

Certainly these experiments can be interpreted in the traditional way as involving differences in the cognitive abilities of the two hemispheres. However, each might also result from the lateralization of emotional or attentional mechanisms. The Japanese macaques were required to operantly discriminate between two subclasses of the "coo" vocalization, a naturally-occurring part of the vocal repertoire of all macaques which is used primarily during affinitive, contact-seeking behavior. Of the two types of coo vocalizations used for the study, one is given by calm but isolated animals seeking social contact and the other is produced primarily by estrous females soliciting male consorts (Beecher, et al., 1979; Petersen et al., 1970). Both seem likely to have high emotional significance to monkeys, and therefore the reported right ear advantage might be attributable to emotional or affective hemispheric asymmetries. Dewson's (1977) results may also be interpreted as differences in activity or arousal between the two hemispheres. For example, lesioning the left hemisphere may have disturbed the monkey's attentional mechanisms, so that it was unable to perform the task at delays longer than a few seconds when the delay was incremented in one-second jumps. The deficit was ameliorated when the delay was incremented in 0.2 second steps, presumably below the monkey's "jnd" for detecting a delay interval increase. Dewson himself suggests self-generated interference as the basis for the deficit.

Human subjects have also shown hemispheric differences that reflect general emotional and attentional asymmetries. Work with both normal and brain-damaged subjects and the results of sodium amytal tests have shown that the right hemisphere reacts in a more depressive and catastrophic fashion and perceives emotional stimuli as more unpleasant and horrible, while the left hemisphere is comparatively indifferent (Dimond, Farrington, and Johnson, 1976; Gainotti, 1973; Gardner, Ling, Flamm, and Silverman, 1975; Perria, Rosadini, and Rossi, 1961; Rossi and Rosadini, 1967). Sperry, Zaidel, and Zaidel (1979) reported that when testing separately the hemispheres of two right-handed split-brain patients the responses from the right hemisphere to emotionally-laden pictures were somewhat more intense and less restrained and qualified than those from the left hemisphere, although on a general level the two hemispheres reacted similarly. Sperry *et al.* (1979) suggest that perhaps more subtle tests than those they employed would better differentiate shades of laterality differences in emotional responses. Recent vigilance studies of Dimond (1976) have implied that the capacity for sustained attention was the property of the human right hemisphere, while the left was susceptible to lapses of attention which Dimond termed "black holes of consciousness". Ellenberg and Sperry (1980) confirmed this finding with a passive, signal detection task similar to Dimond's, but went on to say that for an active bimanual sorting task both hemispheres of split-brain patients were able to simultaneously sustain concentration and alertness for prolonged periods of up to one hour. Thus human subjects show left-right asymmetries in emotion and attention in situations which may be similar to those experienced by the monkeys during preference testing.

Unpublished work from this laboratory has shown that normal monkeys and split-brain monkeys viewing binocularly react to photographs like those used in the preference tests in socially appropriate ways. Preference testing, in which monkeys view photographs, may for them be an affective situation. For a monkey the appropriate reaction in an affective situation such as viewing a more dominant monkey is to look away, to avoid eye contact, and to look primarily at anything and everything else, while stealing quick glances back at the intrusion (Hinde and Rowell, 1962; Redican, 1975). Monkeys had greater preferences with the hemisphere ipsilateral to their preferred hand, or the nondominant hemisphere with respect to handedness. If monkeys are comparable to human beings, then these results are compatible with the body of evidence cited above.

Thus the results of several experiments support the premise that left-right differences in performance may be evidence of hemispheric asymmetries in emotional and/or attentional levels in mammals.

Correlation with Handedness: The behavioral and neurochemical asymmetries found in rats may also relate to the lateral asymmetries correlated with handedness displayed by the monkeys in the present experiments. Rats have been found to have strong side preferences in a variety of "spatial" tasks, for example, turning tendencies in both nocturnal activity and after administration of d-amphetamine, side preferences in a T-maze, paw preferences in a two-bar lever pressing situation, and side of bar preference in a two-bar situation. All of these behavioral measures correlate with the dopamine asymmetry found in the striatum of the forebrain; specifically, the hemisphere with the higher dopamine content (higher by 10-15%) is contralateral to the side of preference. Approximately equal numbers of rats have this type of asymmetry on the left or right (Glick et al., 1977), which is similar to the distribution of handedness in mice (Collins, 1968; 1977). Therefore several behavioral asymmetries may be related to paw preferences in rats.

Glick, Weaver, and Meibach (1980) reported that the threshold for electrical self-stimulation of the lateral hypothalamus is lower on the side contralateral to the preferred direction of rotation, i.e., lower thresholds for self-stimulation occur on the same side of the brain as the higher dopamine concentration. Glick et al. (1980) stated that self-stimulation thresholds might be correlated with pleasure and affect and hypothesized that the side of the brain with the lower reward threshold would also have a higher aversion threshold. With regard to the present preference experiments the hemisphere with the lower reward threshold and higher aversion threshold could logically be the one with greater preferences.

The overwhelming majority of experiments in the tremendous volume of literature on hemispheric specialization in man has involved mostly right-handed subjects. Therefore, it is hard to tell absolute left-right differences from hemispheric specialization correlated with handedness in human subjects. Those investigators who have included left-handed subjects generally term them an inhomogeneous group. One of the few experiments applicable here which has not only included left-handed subjects but has also attempted to make sense of their data with respect to right-handers is the work by Efron (1963a) discussed in Experiment 3. Briefly, the judgment of which of two stimuli must actually occur first for the perception of simultaneity was completely reversed for a small subset of the left-handed subjects as compared to the right-handed and the rest of the left-handed subjects. Efron hypothesized that those subjects displaying reversed performance were "true" left-handers whose cerebral dominance was completely reversed from that of true right-handed subjects. The remainder of the left-handed group had mixed dominance. Thus his results correlate with handedness of the subjects better than with simple left and right hemisphere differences. Thus there is evidence from rodents and humans, at least, that behavioral or perceptual asymmetries are correlated with handedness and that all of these are correlated with brain asymmetries.

It may be possible to interpret much of the evidence for hemispheric specialization usually attributed to differences in cognitive processing as differences in affective mechanisms instead. Perhaps such general left-right differences in emotionality and arousal play a much more important role in hemisphericity than is usually assumed, and may even be correlated with handedness, as are many behavioral and perceptual asymmetries. Perhaps this affective asymmetry is basic to most mammals with an additional asymmetry in cognitive processing added in man.

PART II

DIRECTED ATTENTION IN MIRROR IMAGE DISCRIMINATION BY SPLIT-CHIASM AND NORMAL MONKEYS

Many normal animals have more difficulty discriminating patterns which are left-right mirror images of each other than they do discriminating up-down mirror images (Figure 7). These animals include octopuses (Sutherland, 1957, 1960), goldfish (Campbell, 1971; Mackintosh and Sutherland, 1963), rats (Kinsbourne, 1971; Lashley, 1938; Tee and Riesen, 1974), cats (Parriss, 1964; Warren, 1969), monkeys (Bossom, 1960; Riopelle, Rahm, Itoigawa and Draper, 1964), chimpanzees (Nissen and McCulloch, 1937), human children (Clark and Whitehurst, 1974; Huttenlocher, 1967; Over and Over, 1967; Rudel and Teuber, 1963; Serpell, 1971), and human adults (Farrell, 1979).

To explain these findings many people from the time of Mach to the present have suggested that the preponderance of symmetry in the nervous system may underlie left-right confusion (see Corballis and Beale, 1976). For example, Noble (1966, 1968) has suggested that the topographic representation of visual information in the cerebral cortex of the monkey is reversed left for right when it is transferred across the homotopically organized interhemispheric commissures. Thus the cortical representation of the positive stimulus seen through one eye resembles the cortical representation of the negative stimulus seen through the other eye, as diagrammed in Figure 8. According to this interpretation normal monkeys experience difficulty in learning left-right mirror images because in addition to the veridical representation of a stimulus in each hemisphere there is also a mirror image "ghost" representation resulting from commissural input. Since the veridical and mirror image representations provide conflicting information the monkey succumbs to some confusion and takes longer to learn a left-right discrimination. Learning eventually occurs because Noble postulates that the direct input is stronger and wins out over the callosal "ghost". Up-down mirror images are not similarly affected because for them a left-right reversal looks the same as the original.

Figure 7: Left and right are frequently confusing.

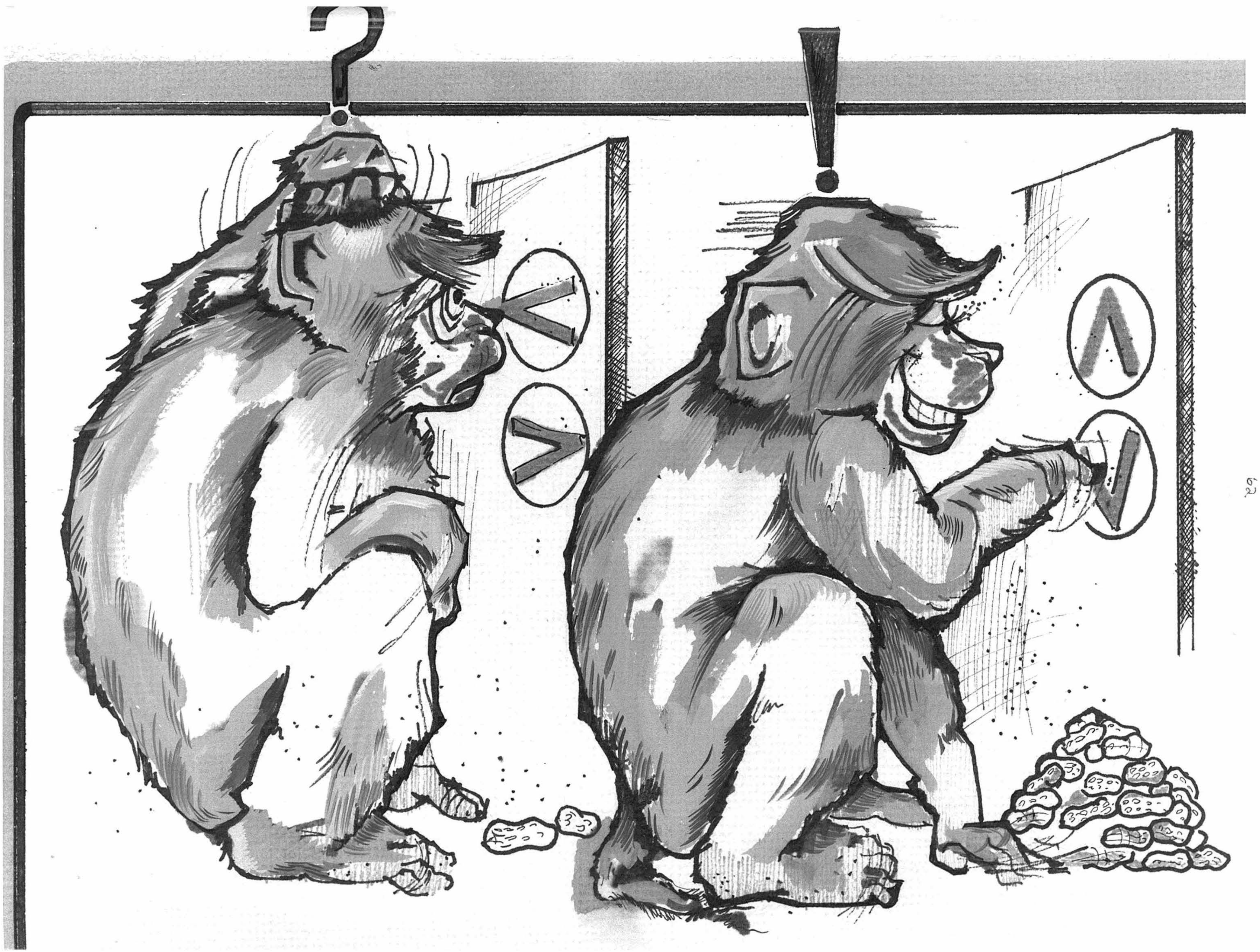
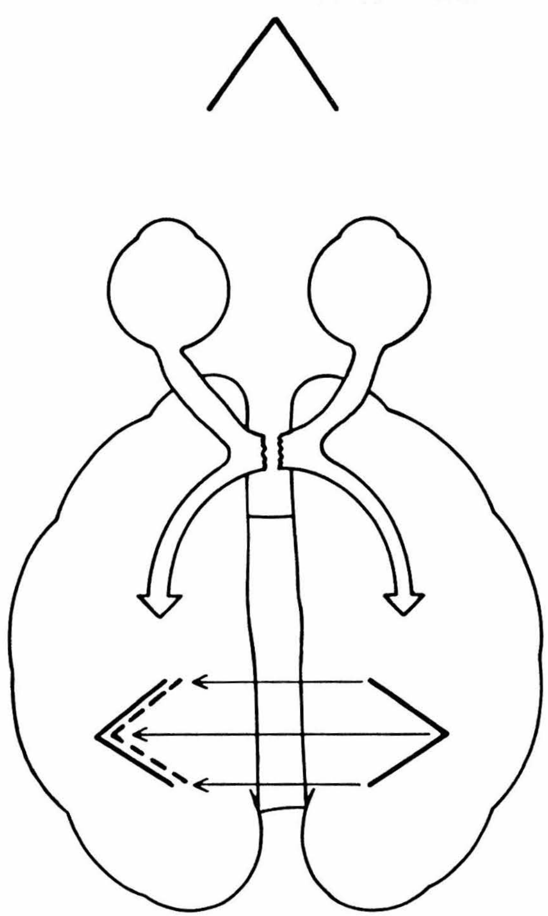
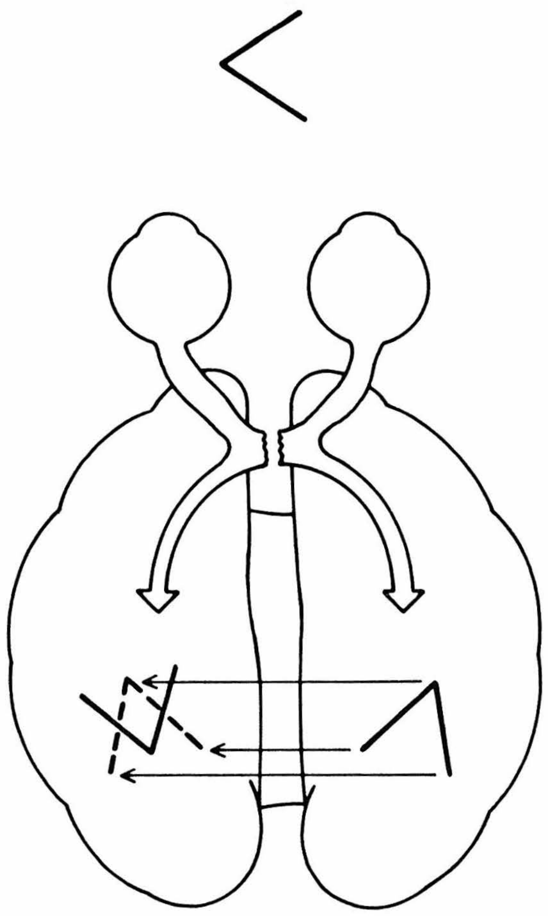


Figure 8: Noble's hypothesis. The solid V's on the cortex represent the direct projection of what the chiasm-sectioned monkey sees. The dotted V's represent the callosal "ghost" representation of the stimulus projected across the interhemispheric commissures (from Hamilton, Tieman and Brody, 1973).



Callosal Projection
Agrees
With Direct Projection



Callosal Projection
Disagrees
With Direct Projection

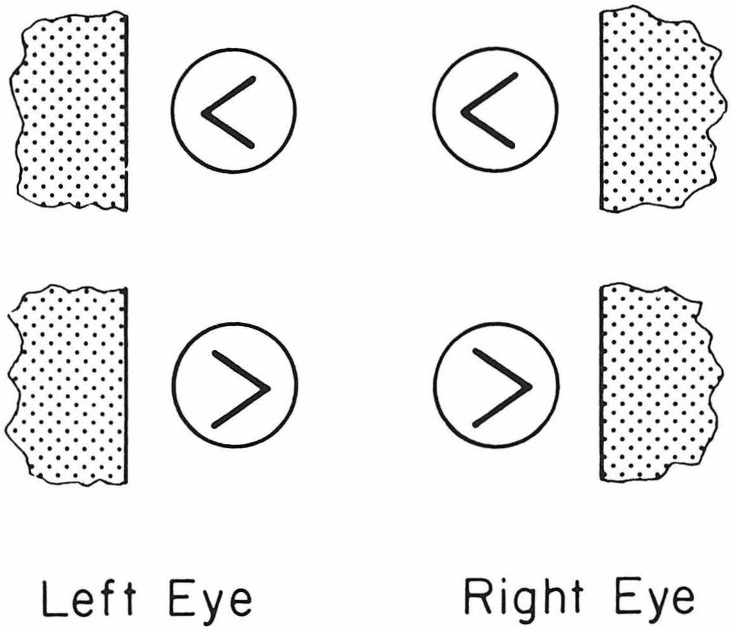
In the monocularly trained chiasm-sectioned monkey, each eye projects only to the ipsilateral hemisphere. As a test of his hypothesis Noble (1966, 1968) postulated that interocular transfer of left-right mirror images is paradoxical in chiasm-sectioned monkeys because the topographic cortical representation of the negative stimulus received through the untrained eye resembles the callosal projection of the positive stimulus from the other hemisphere. Corballis and Beale (1970a, 1976) have elaborated upon this theory and have proposed that it is the memories of visual information which are reversed left for right rather than the perceptual traces.

Monocularly trained split-chiasm monkeys (Hamilton and Tieman, 1973; Lehman, 1973; Lehman and Spencer, 1973; Noble, 1966, 1968; Starr, 1971) do demonstrate paradoxical interocular transfer, that is, unlike normal animals, they prefer the previously unrewarded stimulus when tested through the untrained eye. Interocular transfer of up-down mirror images and symmetrical patterns, on the other hand, remains veridical. In the goldfish and pigeon, each eye projects directly to the contralateral optic tectum. These animals, like monkeys, display paradoxical interocular transfer of left-right but not up-down mirror images (goldfish: Campbell, 1971; Ingle, 1967; pigeons: Beale and Corballis, 1968; Beale and Williams, 1971; Clarke and Beale, 1972; Corballis and Beale, 1967, 1970b; Mello, 1965, 1966a,b). Mello suggested that, like Noble's case for the monkey, commissural inversion of left-right positional information may account for paradoxical interocular transfer of lateral mirror image discriminations in the pigeon (Mello, 1965; 1968).

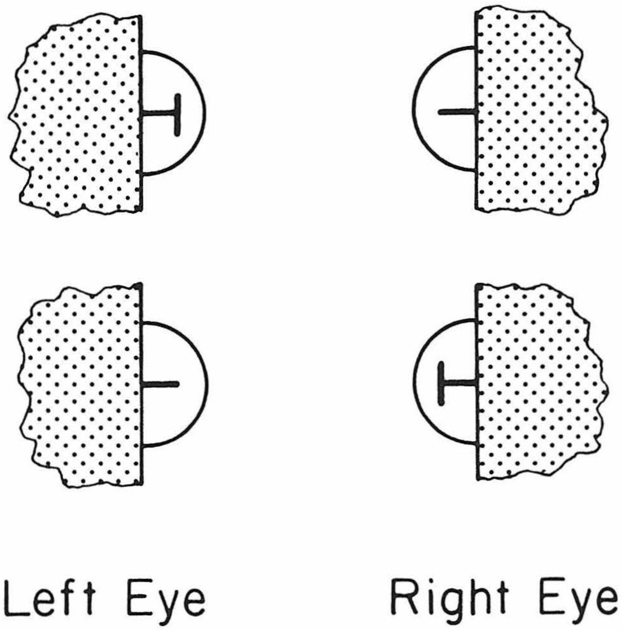
Several investigators have suggested an alternative to Noble's explanation for the paradoxical interocular transfer of left-right mirror images in the chiasm-sectioned monkey which is based on behavioral attentional mechanisms. In the monkey midline section of the optic chiasm produces a temporal hemianopia in each eye. When the animal views stimuli monocularly the blind visual field may provide a mnemonic with which to code orientation as illustrated in Figure 9A. Alternatively, assuming on the average fairly accurate central fixation of the stimuli, the hemianopia present within each eye may mask part of the pattern from view (Hamilton, Tieman and Winter, 1973), so that a monkey viewing with one eye will selectively attend to only the contralateral halves of the stimuli as diagrammed in Figure 9B. Upon testing for interocular transfer the hemianopia changes sides. Since one half of a given laterally asymmetric pattern looks like the opposite half of the pattern's mirror image, the monkey selects the negative stimulus as looking more like the positive training stimulus and paradoxical transfer results (Hamilton and Tieman, 1973; Hamilton, Tieman and Brody, 1973). Similar interpretations were suggested by Lehman (1973).

The hypothesis of selective attention to stimuli because of the hemianopia has been confirmed behaviorally. Lehman (1973) trained split-chiasm monkeys binocularly to discriminate between a square and a diamond. Testing each eye alone with novel composite stimuli revealed preferences for the composite whose side contralateral to the seeing eye was most like the originally trained positive stimulus, the square; these preferences were opposite for the left and right eyes. In other experiments normal and split-chiasm monkeys demonstrated veridical interocular transfer of up-down mirror images in a two-choice paradigm, but while transfer of left-right mirror images was veridical for the normal subjects split-chiasm monkeys performed near chance with the second eye (Hamilton and Tieman, 1973). Furthermore, when other chiasm-sectioned monkeys were tested for interocular transfer definite reversals of left-right discriminations occurred in some cases while in others veridical transfer was found (Hamilton, unpublished). This variable paradoxical interocular transfer of left-right discriminations can result from selective attention to stimulus cues depending on how well each individual attends. Anatomical theories based on commissural inversion are insufficient

Figure 9: An illustration of two possible ways in which the blind visual fields might contribute to paradoxical transfer of lateral mirror images (from Hamilton, Tieman and Brody, 1973).



a. Coding of Stimulus Orientation Relative to Blind Visual Field



b. Masking of Stimuli by Blind Visual Field to account for these results since variable performance, presumably resulting from the conflict of reversed information favoring the negative stimulus received though the second eye and veridical information favoring the positive stimulus received via the commissures, would not be predicted since anatomical connections are the same for all subjects.

Beale and Corballis (1968) proposed a similar behavioral attentional mechanism to explain the paradoxical interocular transfer of left-right mirror images in pigeons. Monocularly viewing pigeons tend to displace their pecking laterally toward the side of the seeing eye and therefore attend selectively to cues on that side of the response key. With the opposite eye open pecking is displaced to the opposite side and cues on that side of the key are seen (Beale and Corballis, 1967). This has been termed "beak shift" (Beale and Corballis, 1968). There is a good correlation between the extent of beak shift and the degree of paradoxical transfer for any particular bird, although paradoxical transfer does not necessarily depend on beak shift (Beale and Corballis, 1968; Beale and Williams, 1971). Experiments investigating displaced pecking have further implicated selective stimulus control and beak shift as factors in discrimination and interocular transfer of lateral mirror images in pigeons (Beale and Williams, 1971; Clarke and Beale, 1972; Corballis and Beale, 1970b).

Noble's (1966, 1968) commissural inversion theory postulates that the learning rates for lateral and vertical mirror image discriminations by split-chiasm monkeys would be similar. However, in fact split-chiasm monkeys find discriminations of left-right mirror images easier to learn than those of up-down mirror images (Hamilton, unpublished; Hamilton and Tieman, 1973). Masking or coding lateral mirror images by the bitemporal hemianopia can account for these results while Noble's theory does not. Since opposite sides of the positive and negative stimuli are identical, masking a lateral mirror image changes it from a left-right discrimination into a simple, easy to learn pattern discrimination (Figure 9B). Masking has no differential effect on up-down mirror images, since both sides of each pattern are the same. Masking likewise has no effect on bilaterally symmetrical pattern discriminations.

Explanations such as those of Hamilton and Lehman involving restricted attention contingent on the bitemporal hemianopia interpret more satisfactorily the results obtained on learning rates and paradoxical interocular transfer of left-right mirror images with split-chiasm monkeys, but unlike Noble's explanation they do not immediately explain the difficulties normal monkeys have discriminating left-right mirror images, since attention restricted by a blind hemifield involves an artificially contrived situation.

Can the concept of selective attention be reasonably extended to interpret the left-right difficulties of normal animals? This experiment tests whether or not it can. The prominent up-down asymmetries in the environment such as gravity, floors, ceilings, and the sky may provide a natural reference for coding up and down, while differential left-right cues are more ambiguous. In the laboratory, several investigators have demonstrated the importance of spatial stimulus-response contiguity in the performance of visual discriminations by monkeys. That is, the prepotent sample of cues utilized by monkeys is limited to the highly restricted region surrounding the place where the monkey touches the stimuli in responding. Visual sampling falls off with respect to a spatial gradient as the distance from the monkey's fingers increases (Horel, Schuck, and Meyer, 1961; Meyer, Polidora and McConnell, 1961; Schuck, 1960; Schuck, Polidora, McConnell and Meyer, 1961). Selective attention in association with stimulus-response contiguity could explain the left-right mirror image confusion experienced by normal subjects. In all cases where left-right difficulties were experienced in discrimination learning the nature of the training apparatus was such that the animals responded to the tops or bottoms of the stimuli (rats: Tee and Riesen, 1974; cats: Parriss, 1964; Warren, 1969; monkeys: Noble, 1966, 1968; Riopelle *et al.*, 1964; chimpanzees: Nissen and McCulloch, 1937). In the few studies where the place of response was ambiguous or to the center of the stimuli no left-right difficulties were experienced (rabbits: Van Hof, 1966; cats: Sutherland, 1963; normal monkeys: Hamilton and Tieman, 1973; Hamilton, Tieman and Brody, 1973).

The upper and lower edges of left-right mirror image stimuli are quite similar while the lateral edges are quite different; the opposite is true for up-down mirror images. As Riopelle *et al.* (1964) have pointed out, if the place of response to stimuli in a left-right mirror image discrimination task were located asymmetrically to one side of the discriminanda so that the salient cues were near the monkey's fingers perhaps left-right mirror image discriminations would become easier than if the place of response were 90° removed from the salient cues, as is the case in most training apparatus such as the Wisconsin General Test Apparatus and Grice box. Up-down mirror images should also be easy to discriminate with the place of response located near the salient cues, that is, at the top or bottom of the stimuli. Locating the place of response to the left or right should make up-down mirror image discriminations harder to learn.

The present experiment was designed to test the effects of asymmetric response on the discrimination of left-right and up-down mirror images. Split-chiasm monkeys were trained monocularly in order to compare directly the predicted effects of restricted attention induced by place of response with the known effect of restricted attention caused by the bitemporal hemianopia. Because of the asymmetry in reaching all problems should be learned faster with aligned responses than with orthogonal ones and because of the scotomata lateral mirror images should be learned faster than vertical ones. In addition, interhemispheric transfer was assessed with the place of response changed 180° from that trained to see if cues near the place of response were in fact used during learning. Selective attention due to the place of response predicts paradoxical transfer of discriminations learned with aligned responses and veridical transfer of discriminations with orthogonal responses. Selective attention due to the hemianopia predicts paradoxical transfer of left-right mirror images and veridical transfer of vertical mirror images.

In addition, the generality of the effects of restricted attention induced by means of asymmetric response was tested in normal monkeys to see how restricting attention by manipulating the place of response might influence learning and thereby explain left-right confusion in normal subjects. Transfer tests with the place of response changed 180° were also run to evaluate the extent to which asymmetric responding actively restricted attention to cues near the place of response.

Methods

Subjects: Sixteen adolescent macaque monkeys of closely related species were tested. There were ten rhesus monkeys (Macaca mulatta), four pigtail macaques (M. nemestrina), and two cynomolgus monkeys (M. fascicularis). All were wild-born. Three species were used because India's ban on the exportation of rhesus monkeys has made them difficult to obtain. Pigtail macaques have performed comparably to rhesus previously in this laboratory. Cynomolgus monkeys have been reported to take slightly, but not significantly, longer to learn visual discriminations than rhesus (Leiby, Campbell and Butter, 1978; Schrier, 1966). In the present experiments comparisons of learning rates will be made primarily within each subject so species differences, if they exist, should not be a major hindrance.

The monkeys were housed individually in standard primate cages in a colony of about forty macaques. Water was continually available in the home cage. The monkeys were fed their ration of monkey chow supplemented with half an apple once a day following testing.

Eight of the rhesus monkeys had received extensive training on a wide variety of visual discrimination problems in the automated testing boxes used at Caltech which are similar to those described by Sperry (1968). The other eight monkeys were experimentally naive at the start of the experiment but were given extra practice on visual discrimination problems before training on mirror images. Eight of the monkeys were partially split-brain subjects and the other eight were normal monkeys. In each group half were experienced, half naive. The four pigtails were partial splits; the two cynomolgus were normal. The exact parcellation of surgery, species, and educational history is given in Table 9.

All split-brain surgery was performed in one operation per monkey under sodium pentobarbital anesthesia using standard aseptic technique and a dorsal approach. Special retractors and a Zeiss operating microscope facilitated visualization of the midline structures being sectioned. Each partial split sustained midline section of the optic chiasm and front and body of the corpus callosum. Four monkeys had additional section of the anterior commissure, leaving only the posterior centimeter of the splenium of the corpus callosum intact (intact splenium monkeys = IS). The other four had the entire corpus callosum and underlying hippocampal commissure split, leaving intact the anterior commissure (IAC). Both the splenium and the anterior commissure are capable of mediating interocular equivalence for visual pattern discriminations (for review see Hamilton, 1980). The side of surgical approach was balanced across monkeys. Antibiotics were administered post-operatively and the one-week recovery period was uneventful.

Apparatus: A Wisconsin General Test Apparatus (WGTA) modified for use with split-brain monkeys was used. It consisted of a monkey cage 24" x 24" x 18" wide with an attached split-brain testing compartment (Sperry, 1968). In responding a monkey voluntarily placed its head between a set of adjustable wedges, looked out through a pair of eyeholes, and reached through the armholes to respond and retrieve the reward. The eyeholes and armholes could be occluded as desired to

TABLE 9

Subjects in mirror image experiment

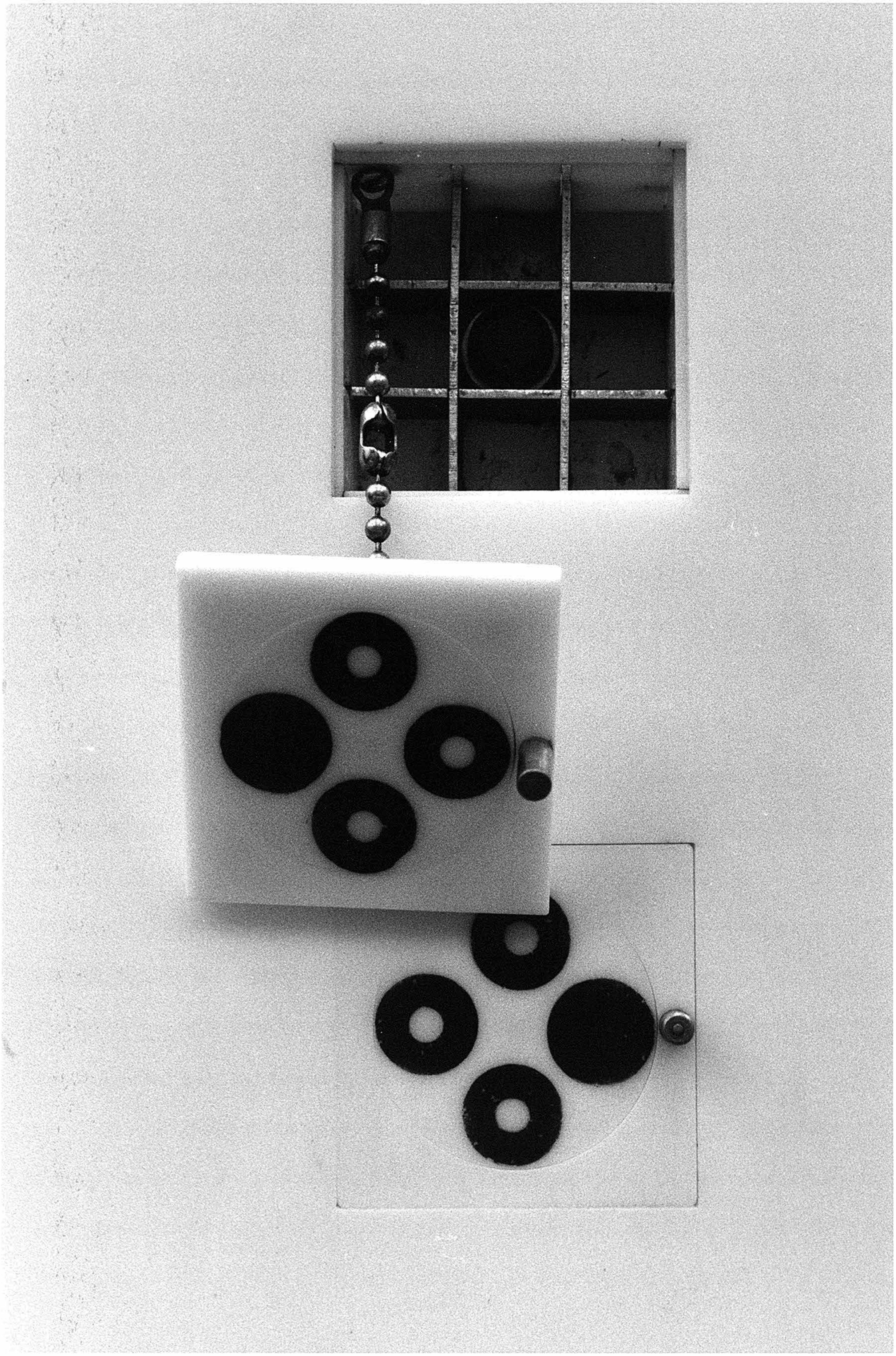
Surgery	Subject	Sex	Species	Schooling
Intact Splenium	BUD	M	Rhesus	Trained extensively in automated boxes
	GGI	F	Rhesus	Trained extensively in automated boxes
	GWE	F	Pigtail	Naive
	OWN	M	Pigtail	Naive
Intact Anterior Commissure	QID	M	Rhesus	Trained extensively in automated boxes
	VIM	M	Rhesus	Trained extensively in automated boxes
	HGH	M	Pigtail	Naive
	JLL	F	Pigtail	Naive
Normal	AMY	F	Rhesus	Naive
	FRE	M	Cynomolgus	Naive
	KEF	M	Rhesus	Naive
	NKE	F	Cynomolgus	Naive
	DSH	M	Rhesus	Trained extensively in automated boxes
	LDD	F	Rhesus	Trained extensively in automated boxes
	LME	M	Rhesus	Trained extensively in automated boxes
	STN	F	Rhesus	Trained extensively in automated boxes

restrict eye and hand usage. For some of the experiments with normal monkeys, the split-brain testing front was replaced by a set of bars so that the monkeys could be trained in free vision.

For all experiments the discrimination panel, 21 3/4" wide x 32" high, was made of white Plexiglas and stood vertically in front of the monkey's compartment. It could be slid forward to within arm's length of the monkey or backward for baiting foodwells and setting up the trials. The panel contained two foodwells situated one above the other with the top of the upper one at eye level of the split-brain front. A vertical arrangement was selected to ensure that split-chiasm monkeys would see both stimuli equally well. Each foodwell was normally covered by a square door 2-1/2" on a side which was recessed so that its front surface was flush with the panel. The doors were connected to the panel by short chains which fitted neatly inside the foodwells when the doors were in place. Stimuli appeared on 2" diameter white Plexiglas disks which fitted into the square doors. From the back of the door a screw fitted through the door into the back of the disk, securing it to the door but allowing the disk to turn freely. Thus a pattern could be rotated to any orientation. A stop could be tightened to hold the disk and its pattern in a particular orientation. The head of the screw contacted a small magnet in the foodwell which helped to hold the door in place. Each door had a brass peg 7/32" in diameter and 1/2" long centered along one edge of the door perpendicular to the plane of the door and disk. When the doors were in place on the panel only the pegs protruded. The doors could be placed in the panel so that the pegs were to the top, bottom, right, or left of the stimulus disks. In order to respond the monkeys either grasped the peg and pulled the door out or pushed sideways on the peg to knock the door out. The panel, doors, and foodwells are illustrated in Figure 10.

An opaque Masonite guillotine barrier was lowered between the monkey's cage and the panel between trials to prevent the monkey from seeing the baiting.

Figure 10: The WGTA panel is pictured, as set up for discriminating lateral mirror image stimuli with an aligned response. The negative stimulus has been displaced in order to reveal the foodwell behind it.



The WGTA panel itself served to shield the experimenter from the monkey's view during trials. The panel was moderately illuminated by two Tensor lights alongside the monkey's cage.

The stimulus patterns were cut from adhesive-backed Letraset and pasted onto the white Plexiglas disks. The four mirror image stimuli used (Figure 11) were black shapes identical on three sides and different on the fourth. They subtended 14-19 degrees of visual angle, depending on the length of the individual monkey's arms. The axis of symmetry of a pattern was defined as a line passing through the middle of the odd side and the center of the pattern. Pairs of identical patterns could be oriented either as left-right or up-down mirror images.

Procedure: All problems were trained as simultaneous two-choice discriminations. For each trial the experimenter baited the proper foodwell, oriented the stimuli appropriately and set the doors in place, pushed the WGTA panel forward, and raised the opaque barrier. The sound cues generated by the sliding panel and barrier signalled the monkey that a trial was available. After the monkey had removed one stimulus door and retrieved the reward if the choice were correct, the panel was withdrawn and the opaque barrier lowered. The experimenter recorded the outcome of the trial and prepared the next. Correct trials were rewarded with a raisin (N = 10), piece of apple (N = 5), or piece of sugar-coated breakfast cereal (N = 1), according to each monkey's preference. Incorrect trials went unrewarded. The intertrial interval was the time necessary for the experimenter to record one trial and prepare the next, about 8-10 seconds.

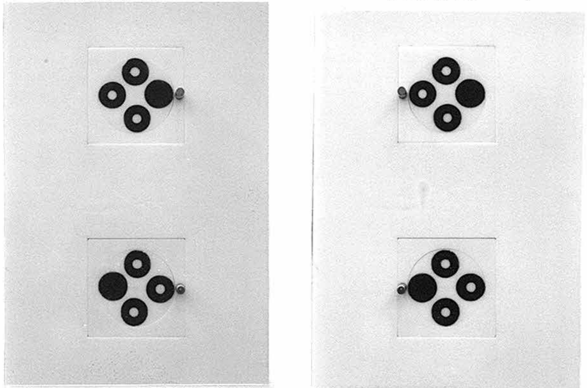
Generally each monkey was trained fifty trials a day, five to seven days a week using a noncorrection procedure. The position of the rewarded stimulus was varied according to Gellerman (1933) sequences. Ten fifty-trial sequences were prepared and the entire set of 500 trials was used before any were repeated.

Figure 11: Each of the patterns used is illustrated as a mirror image pair. They have been shown in the sequence of orientation/response configurations learned by monkeys BUD, JLL, and NKE. The monkey responds by using the peg to pull the door out. The rewarded stimulus is illustrated on top in each case, but during testing it alternated position according to Gellerman (1933) sequences.

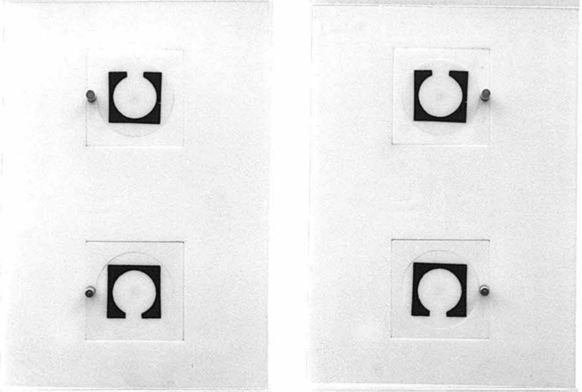
MIRROR IMAGE STIMULI

Trained Tested

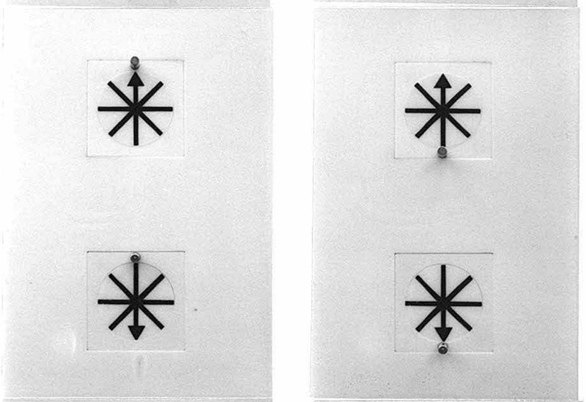
1. Lateral Aligned
   Pattern R+/L
   Response R
   RELH → LERH



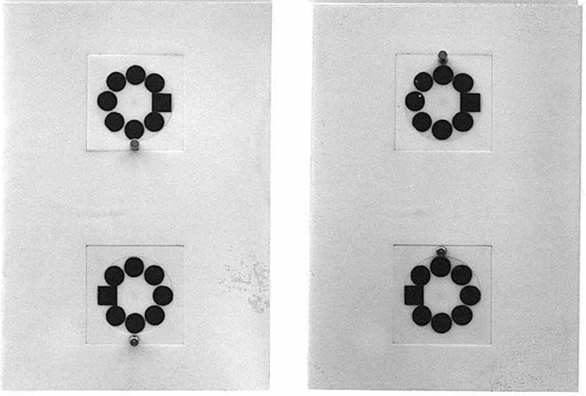
2. Vertical Orthogonal
   Pattern U+/D
   Response L
   LERH → RELH



3. Vertical Aligned
   Pattern U+/D
   Response U
   RELH → LERH



4. Lateral Orthogonal
   Pattern R+/L
   Response D
   LERH → RELH



Each monkey was taught by successive approximations to remove plain white doors and retrieve the reward. Prior to training on mirror image discriminations, each monkey was trained monocularly one to four symmetrical pattern discriminations to familiarize it with the training procedure and each of the four possible peg positions. Interocular transfer of these discriminations was tested with the peg position changed 180°.

Each partially split-brain monkey then learned monocularly four mirror image discriminations to a criterion of 36 correct responses in four consecutive blocks of ten trials (36/40) and was overtrained to a criterion of 90 correct responses in ten consecutive blocks of ten trials (90/100). Two of the discriminations were of lateral mirror images and the other two were of vertical mirror images. One each of the lateral and vertical mirror image discriminations was learned with the peg position aligned with the axis of symmetry of the patterns, the other with the peg position orthogonal by 90°. Thus a 2 x 2 design resulted with pattern, lateral or vertical, as one factor, and response, aligned or orthogonal, as the other. Examples of each of the four conditions are presented in Figure 11. Following attainment of criterion each monkey was tested for interocular transfer to the opposite contralateral eye-hand pair with the peg position changed 180° from that trained. Training continued until the criteria 36/40 and 90/100 were attained. All monkeys learned problems 1 and 3 with their right eye-left hand first and problems 2 and 4 with their left eye-right hand first. The actual patterns were always presented in the same order, but the type of mirror image, lateral or vertical, and the response position were counterbalanced across monkeys, as given in Table 10.

The training protocol for the normal monkeys is also given in Table 10. Training for the four naive normal monkeys was identical to that used for the partially split-brain monkeys. Each monkey learned four mirror image discriminations monocularly and was tested for interocular transfer with the place of response changed 180°. The four experienced normal monkeys, who were trained before

TABLE 10

Order of training mirror image problems

Monkey		Problem 1	Problem 2	Problem 3	Problem 4
Partially Split-Brain Monkeys Trained in Split-Brain Apparatus and Tested for Interocular Transfer with Place of Response Changed 180°					
BUD	Pattern	R+/L	U+/D	U+/D	R+/L
	Response	R	L	U	D
GGI	Pattern	U+/D	L+/R	R+/L	D+/U
	Response	R	L	U	D
GWE	Pattern	L+/R	D+/U	U+/D	L+/R
	Response	U	D	R	L
OWN	Pattern	U+/D	R+/L	R+/L	D+/U
	Response	U	D	R	L
QID	Pattern	L+/R	D+/U	U+/D*	L+/R
	Response	U	D	R	L
VIM	Pattern	U+/D	R+/L	R+/L	D+/U
	Response	U	D	R	L
HGH	Pattern	U+/D	L+/R	L+/R	D+/U
	Response	R	L	U	D
JLL	Pattern	R+/L	D+/U	U+/D	R+/L
	Response	R	L	U	D
Normal Monkeys Trained in Split-Brain Apparatus and Tested for Interocular Transfer with Place of Response Changed 180°					
AMY	Pattern	U+/D	R+/L	R+/L	D+/U
	Response	U	D	R	L
FRE	Pattern	L+/R	D+/U	U+/D	L+/R
	Response	U	D	R	L
KEF	Pattern	U+/D	L+/R	L+/R	D+/U
	Response	R	L	U	D
NKE	Pattern	R+/L	D+/U	U+/D	R+/L
	Response	R	L	U	D

TABLE 10 (continued)

Normal Monkeys Trained in Free Vision and Given Only 50 Generalization Trials with Place of Response Changed 180°

DSH	Pattern	R+/L	R+/L	D+/U	D+/U
	Response	R	U	L	D
LDD	Pattern	U+/D	U+/D	L+/R	L+/R
	Response	U	R	D	L
LME	Pattern	U+/D	U+/D	L+/R	L+/R
	Response	R	U	L	D
STN	Pattern	R+/L	R+/L	D+/U	D+/U
	Response	U	R	D	L

*An alternate pattern was substituted.

U = up, D = down, L = left, R = right. The plus (+) indicates the rewarded orientation; thus R+/L means that the monkey was rewarded for choosing the stimulus with its odd side to the right, while the stimulus with its odd side to the left was unrewarded.

the experimental design had been established for the other subjects, learned four mirror image discriminations in free vision using the bar front for the testing cage. Thus they learned binocularly and with free choice of hand usage. Instead of being tested for interocular transfer following the original learning of each discrimination these normal monkeys were given 50 trials of generalization testing on each problem with the peg position changed 180°. Retraining did not continue to criterion unless criterion was reached within the 50 allotted trials.

Data analysis: Because of missing data analyses of variance will be delayed until the remaining monkeys have completed their training. The results available so far will be evaluated by means of multiple t-tests on the main effects. Where appropriate, averaged differences were calculated, using every monkey whose data were complete. For this comparison the two conditions of one experimental variable were differenced while keeping the other variable constant and the resulting differences between the two conditions in question were averaged for each subject. Thus for each subject the effect of pattern was assessed by $\frac{(VA-LA)+(VO-LO)}{2}$ and the effect of response was evaluated by $\frac{(VO-VA)+(LO-LA)}{2}$, where VA is the score obtained on vertical mirror images with aligned responses and LA, VO, and LO are the analogous scores for the lateral aligned, vertical orthogonal, and lateral orthogonal conditions, respectively. These averaged differences were then assessed across monkeys for their difference from zero. Positive values indicate that the scotoma and the response position, respectively, had the predicted effect in restricting attention.

Two measures of interocular transfer were used. The first was the change in initial performance (ΔI), calculated as the percent correct in the first twenty trials with the second eye minus the percent correct in the first twenty trials with the first eye. Thus positive values represent veridical transfer and negative values represent paradoxical transfer. The second measure was the percent savings on errors in relearning through criterion, calculated as $(\frac{A-B}{A+B})\,100$, where A and B are equal to the errors through the criterion 36/40 with the first and second eyes, respectively. Again, positive values represent veridical transfer and negative values indicate paradoxical transfer. However, whether paradoxical transfer actually produces negative savings or simply reduced savings cannot be decided theoretically. Data from all monkeys are used for evaluating transfer because individual differences are normalized by the measures used.

Results and Discussion

Acquisition: The errors through the criterion 36/40 made by each monkey with the eye trained first on each mirror image discrimination are presented in Table 11 under the columns headed "first eye". Blanks indicate data which are not yet complete and dashes indicate tests which were not run. The scores from all monkeys are presented in Table 11 but for statistical purposes only the data from the monkeys who have completed testing in the balanced design will be considered. For easy reference, the means for this subset of subjects have been placed in 2 x 2 matrices of the main effects as Table 12.

Partially split-brain monkeys. Inspection of the means shows that partially split-brain monkeys learned lateral mirror images faster than vertical ones, irrespective of the place of response (lateral $\bar{x} = 170$, vertical $\bar{x} = 359$). This is the anticipated result due to selective attention caused by the scotoma which each of these monkeys has because of its optic chiasm section. However, this difference presently is not significant across the four completed monkeys (df = 3, $p < .20$) when assessed by the averaged differences between conditions described under Methods.

The means also show that when the place of response was aligned with the axis of symmetry of the mirror image patterns partially split-brain monkeys

TABLE 11

Errors through criterion with each eye on the mirror image discriminations

	Vertical Aligned		Lateral Aligned		Vertical Orthogonal		Lateral Orthogonal	
Eye	1st	2nd	1st	2nd	1st	2nd	1st	2nd
Partially Split-Brain Monkeys								
BUD	74	78	230	1771	226	20	151	753
GGI	131	86	38	131	117	21	472	444
GWE	261	58			139	9		
OWN	1284	155					100	670
QID	770	129	38	29	864	108	202	198
VIM	187	322	80	101	502	220	150	110
HGH			53	129	338	164	9	143
JLL			945					
$\bar{x}$	451		231		364		181	
SD	±479		±357		±283		±157	
Normal Monkeys								
AMY	561	270	173	14	246	2	319	45
FRE	241	13	29	304	144	52	2476	
KEF	452	63	1508	67	298	46	68	0
NKE	476	237	437	355	450	70		
DSH	25	-	82	-	34	6	118	5
LDD	706	-	204	-	152	4	32	4
LME	271	4	2	-	114	2	206	-
STN	80	-	120	-	103	-	167	-
$\bar{x}$	352		319		193		484	
SD	±237		±499		±133		±884	

TABLE 12

2 x 2 matrix of errors through criterion

Partially Split-Brain Monkeys (N=4)

		Pattern		
		Vertical	Lateral	$\bar{x}$
Response	Aligned	291	97	194
	Orthogonal	427	244	336
	$\bar{x}$	359	170	

Normal Monkeys (N=7)

		Pattern		
		Vertical	Lateral	$\bar{x}$
Response	Aligned	334	303	318
	Orthogonal	156	484	320
	$\bar{x}$	245	393	

learned faster than when the place of response was orthogonal by 90° (aligned $\overline{x} = 194$, orthogonal $\overline{x} = 336$). Averaged differences across the four monkeys who have finished testing show that this result is significant (df = 3, $p < .01$). This was the predicted result if monkeys pay attention to local cues near their place of response and supports the main hypothesis of the experiment, namely, that responding near the salient cues of a mirror image pattern facilitates its discriminability.

Normal monkeys. Inspection of the means in Table 12 for the normal monkeys' data shows that they found lateral mirror images harder to learn than vertical ones (lateral $\overline{x} = 393$, vertical $\overline{x} = 245$), a result which, however, was not significant when analyzed by averaged differences (df = 6, $p < .30$). This result is in the expected direction, namely, that for normal monkeys vertical mirror images should be easier to learn than lateral ones, and agrees with the results of many previous experiments. Normal monkeys found mirror images with an aligned response slightly, but not significantly, easier to learn than those with an orthogonal response (aligned $\overline{x} = 318$, orthogonal $\overline{x} = 320$).

In summary, the means of the acquisition data indicate that partially split-brain monkeys found lateral mirror images easier to learn than vertical mirror images, in accord with selective attention due to the scotoma. Normal monkeys, on the other hand, found vertical mirror images easier than laterals. Partially split-brain and, to a lesser extent, normal monkeys found mirror images easier to learn when the response was aligned, supporting the hypothesis that selective attention due to place response may be a way of accounting for mirror image difficulties in general.

Interocular Transfer and Generalization to a New Place of Response: The percent correct on the first twenty trials of each problem with each eye and the difference between eyes (ΔI) are presented for each monkey in Table 13.

TABLE 13

Initial Performance - Percent Correct on First Twenty Trials with Each Eye

	Vertical			Lateral			Vertical			Lateral		
	Aligned			Aligned			Orthogonal			Orthogonal		
	1st	2nd	Δ	1st	2nd	Δ	1st	2nd	Δ	1st	2nd	Δ
Partially Split-Brain Monkeys												
BUD	45	50	5	45	25	-20	55	50	-5	75	25	-50
GGI	65	70	5	50	25	-25	50	90	40	40	45	5
GWE	65	70	5	40			60	70	10	55		
OWN	50	65	15	35						55	35	-20
QID	55	60	5	60	55	-5	50	45	-5	60	45	-15
VIM	30	35	5	55	20	-35	40	60	20	50	65	15
HGH	35			60	0	-60	60	70	10	85	25	-60
JLL				45	35	-10						
$\bar{x}$			6.67			-25.83			11.67			-20.83
SD			±4.08			±19.85			±16.93			±29.57
p			<.01			<.025			<.10			<.10
Normal Monkeys												
AMY	60	50	-10	55	55	0	65	95	30	50	80	30
FRE	45	80	35	60	70	10	60	70	10	55	30	-25
KEF	30	50	20	45	55	10	50	65	15	50	100	50
NKE	35	55	20	50	45	-5	35	60	25			
DSH	50	25	-25	40	35	-5	50	85	35	55	75	20
LDD	70	20	-50	35	30	-5	40	90	50	60	80	20
LME	60	95	35	90	70	-20	55	100	45	60	85	25
STN	55	40	-15	45	45	0	55	50	-5	55	60	5
$\bar{x}$			1.25			-1.88			25.63			17.86
SD			±30.91			±9.61			±18.41			±23.25
p			ns			<.30			<.005			<.05

The difference scores have been plotted in Figure 12. The originally trained places of response, aligned and orthogonal, have been segregated and within each response category the data for vertical and lateral mirror image patterns are presented separately for each monkey.

Partially split-brain monkeys. In Figure 12, it can be seen that for every partially split-brain monkey, the ΔI score for lateral mirror images is lower than the corresponding score for vertical mirror images. The ΔI scores for lateral patterns are in fact negative for all but two cases, and those exceptions involved orthogonal responses. For easy comparison across monkeys the average ΔI scores have been placed in a 2 x 2 matrix in Table 14. The mean ΔI for lateral patterns is negative (-23.33) indicating paradoxical interocular transfer, while the mean ΔI for vertical mirror images is slightly positive (9.17) indicating veridical transfer. Averaged differences indicate that the difference in ΔI between lateral and vertical patterns is significant (df = 3, $p < .025$). The paradoxical interocular transfer of lateral, but not vertical, mirror images is the expected result because if the scotoma resulting from chiasm section permitted the monkey to attend to only half of the pattern during acquisition of the discrimination, the scotoma and the side of the pattern seen would reverse when the seeing eye was changed.

Table 14 also shows that although all of the mean ΔI scores for the response condition are negative due to the lateral mirror image effect, the scores for the aligned response condition ($\bar{x} = -9.58$) are more negative than those for the orthogonal condition ($\bar{x} = -4.58$). Although the averaged differences are not significant, the general effect of paradoxical transfer indicates that the monkeys probably learned the discriminations in the aligned condition on the basis of local cues near their place of response. When the place of response was shifted 180° for interocular transfer, the meaning of the local cues was reversed and paradoxical transfer resulted. With orthogonal responses, local cues were not very useful in solving

Figure 12: The percent difference in initial performance on the first twenty trials (second eye score—first eye score) is presented for each monkey. Vertical shading represents vertical mirror image patterns, horizontal shading represents lateral mirror image patterns. * indicates that the mean was significantly different from chance at $p < .05$ or better.

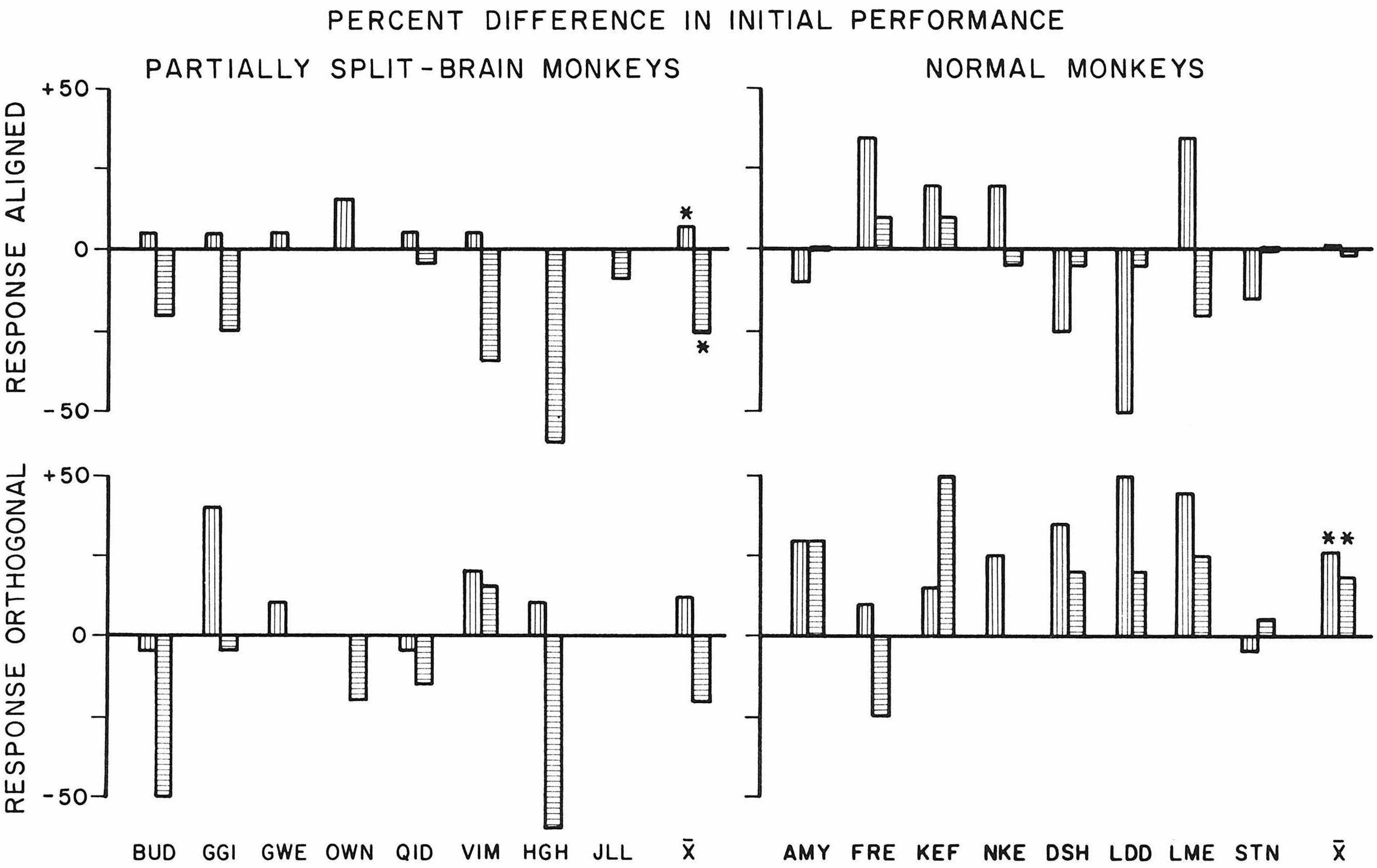

PERCENT DIFFERENCE IN INITIAL PERFORMANCE
PARTIALLY SPLIT-BRAIN MONKEYS
NORMAL MONKEYS
RESPONSE ALIGNED
RESPONSE ORTHOGONAL
+50
0
-50
+50
0
-50
*
*
**
BUD
GGI
GWE
OWN
QID
VIM
HGH
JLL
X̄
AMY
FRE
KEF
NKE
DSH
LDD
LME
STN
X̄

TABLE 14

2 x 2 matrix of ΔI

Partially Split-Brain Monkeys

		Pattern		
		Vertical	Lateral	$\bar{x}$
Response	Aligned	6.67	-25.83	-9.58
	Orthogonal	11.67	-20.83	-4.58
	$\bar{x}$	9.17	-23.33	

Normal Monkeys

		Pattern		
		Vertical	Lateral	$\bar{x}$
Response	Aligned	1.25	-1.88	-0.32
	Orthogonal	25.63	17.86	21.75
	$\bar{x}$	13.44	7.99	

the discrimination, so transfer was not as affected by the change of response position.

The percent savings scores in relearning the discriminations to criterion with the second eye, presented in Table 15 and Figure 13, yield results similar to the ΔI scores. As can be more easily seen in the appropriate 2 x 2 matrix of Table 16, the partially split-brain monkeys again showed paradoxical interocular transfer of lateral, but not vertical, mirror image discriminations (lateral $\bar{x} = -34.64$, vertical mean = 49.80). This was significant when evaluated by averaged differences (df = 3, $p < .05$) and illustrates once again the effectiveness of the scotoma in restricting attention to part of the stimuli.

Similarly, there were negative savings in relearning discriminations with aligned responses ($\bar{x} = -0.12$) and positive savings in relearning for orthogonal responses ($\bar{x} = 15.28$). The averaged differences across monkeys between response conditions were significant (df = 3, $p < .05$).

Normal monkeys. The ΔI scores for the normal subjects are also presented in Tables 13 and 14 and Figure 12. Although the mean ΔI scores were somewhat lower for lateral ($\bar{x} = 7.99$) than for vertical ($\bar{x} = 13.44$) mirror images, the averaged differences between the conditions were not statistically significant (df = 6, $p < .40$). Because normal monkeys do not have a sectioned optic chiasm, restricted attention due to a scotoma is not a factor. The result indicates that the monkeys on the average generalized about equally well with regard to pattern orientation, but the ΔI scores for lateral patterns may be slightly lower because these discriminations were more difficult to learn originally and therefore may be more susceptible to disruption.

With respect to place of response, however, normal monkeys showed veridical transfer when the response was orthogonal ($\bar{x} = 21.75$) but paradoxical transfer when the response was aligned ($\bar{x} = -0.32$). The averaged differences

TABLE 15

Percent Savings in Relearning Mirror Image Discriminations

	Vertical Aligned	Lateral Aligned	Vertical Orthogonal	Lateral Orthogonal
Partially Split-Brain Monkeys				
BUD	-2.63	-77.01	83.74	-66.59
GGI	20.74	-55.03	69.57	3.06
GWE	63.64		87.84	
OWN	78.46			-74.03
QID	71.30	13.43	77.78	1.00
VIM	-26.52	-11.60	39.06	15.39
HGH		-41.76	34.66	-88.16
JLL				
$\bar{x}$	34.16	-34.39	65.44	-34.89
SD	±43.42	±35.72	±23.02	±46.11
p	<.10	<.05	<.005	<.10
Normal Monkeys				
AMY	35.02	85.03	98.39	75.28
FRE	89.76	-82.58	46.94	
KEF	75.53	91.49	73.26	100.00
NKE	33.52	10.35	73.08	
DSH	-	-	70.00	91.87
LDD	-	-	94.87	77.78
LME	97.09	-	96.55	-
STN	-	-	-	-
$\bar{x}$	66.18	26.07	79.01	86.23
SD	±30.15	±81.26	±18.77	±11.73
p	<.01	<.30	<.005	<.005

Figure 13: Identical to Figure 12 except that the percent savings in relearning the criterion, calculated as $(\frac{A-B}{A+B})\ 100$ as described in text, are plotted.

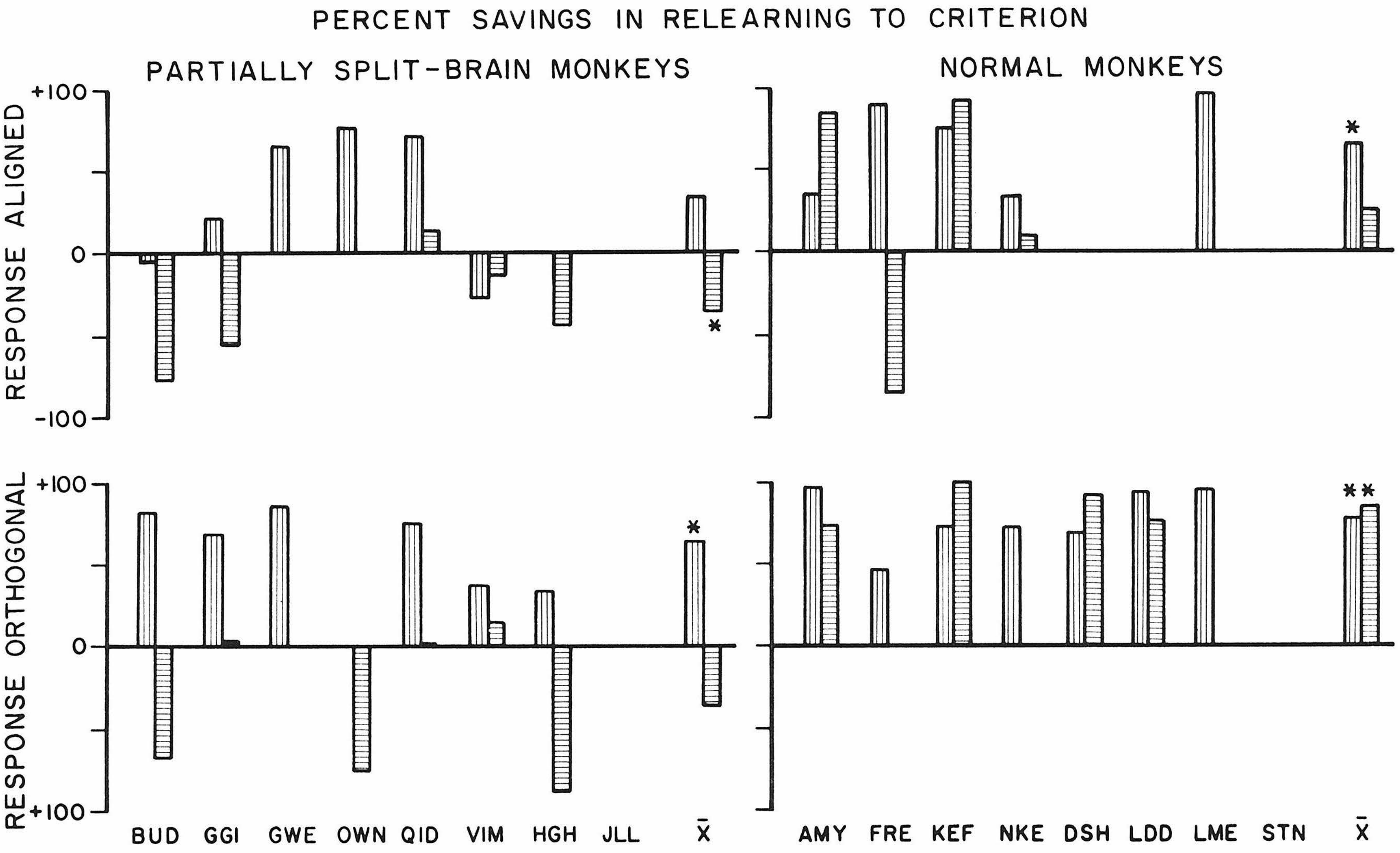

PERCENT SAVINGS IN RELEARNING TO CRITERION
PARTIALLY SPLIT-BRAIN MONKEYS
NORMAL MONKEYS
RESPONSE ALIGNED
RESPONSE ORTHOGONAL
+100
0
-100
+100
0
+100
BUD
GGI
GWE
OWN
QID
VIM
HGH
JLL
X̄
AMY
FRE
KEF
NKE
DSH
LDD
LME
STN
X̄
*
*
*
**

TABLE 16

2 x 2 matrix of percent savings

Partially Split-Brain Monkeys

		Pattern		
		Vertical	Lateral	$\bar{x}$
Response	Aligned	34.16	-34.39	-0.12
	Orthogonal	65.44	-34.89	15.28
	$\bar{x}$	49.80	-34.64	

Normal Monkeys

		Pattern		
		Vertical	Lateral	$\bar{x}$
Response	Aligned	66.18	26.07	46.13
	Orthogonal	79.01	86.23	82.62
	$\bar{x}$	72.60	56.15	

across monkeys were statistically significant (df = 6, $p < .05$). This result is in accord with the expectations of this experiment. Paradoxical generalization by normal monkeys has never before (to the author's knowledge) been predicted with respect to mirror image discriminations.

Percent savings (Table 15, Figure 13), which could not be calculated in every case because four monkeys, DSH, LDD, LME, and STN, were not always retrained to criterion following the change of place of response, gave similar, but not identical results. The overall mean savings shown in the lower matrix of Table 16 were lower for lateral mirror images than for vertical ones (lateral $\bar{x} = 56.15$, vertical $\bar{x} = 72.60$) with most of the effect due to the lateral aligned condition. This result was not quite statistically significant (df = 1, $p < .10$), however, probably because only two subjects could contribute completed data for averaged differences, but, like the I scores, indicates that lateral mirror image discriminations were more easily disruptable. Savings were better with orthogonal responses than with aligned responses, but in this case savings for both conditions were veridical (orthogonal $\bar{x} = 82.62$, aligned $\bar{x} = 46.13$) and not significantly different. Considering the results of the generalization tests with respect to both pattern and response suggests that, in line with the rationale for the experiment, the monkeys may have learned the discriminations by using the place of response as a mnemonic to code orientation or alternatively, attended selectively to cues near their place of response. Changing the place of response reverses the mnemonic or the cues which results in reduced transfer. Individual variability occurs depending on how well the monkeys used place of response as a mnemonic and how facile they were at switching their strategies in generalization testing.

To summarize, partially split-brain monkeys learned to discriminate lateral mirror images faster than vertical ones whereas conversely, normal monkeys found vertical mirror images easier to discriminate than lateral ones. This is consistent with previous experiments. Both partially split-brain and normal monkeys found discriminations of either orientation easier when the place of response was aligned, that is, close to the salient cues of the stimuli, than when it was orthogonal by 90°. This result, presently significant only for the partially split-brain monkeys, is in the predicted direction according to the hypothesis that responding directly to the salient cues of a mirror image pattern facilitates its discriminability and in addition provides a mnemonic for coding orientation.

More convincing evidence supporting the hypothesis that restricted attention to stimulus cues may play a role in mirror image discrimination comes from tests of interocular transfer and generalization to a new place of response. When tested for interocular transfer with the place of response changed 180° partially split-brain monkeys showed paradoxical interocular transfer of lateral mirror images and veridical interocular transfer of vertical mirror images. Partially split-brain monkeys also displayed paradoxical transfer of all mirror images learned with aligned responses. Transfer of patterns with orthogonal responses was low, although usually veridical. Normal monkeys showed veridical generalization of both lateral and vertical mirror images when, following acquisition, the place of response was changed 180°. Generalization was poorer if the discrimination had originally been learned with an aligned response than if the original response had been orthogonal. This suggests that both partially split and normal monkeys utilized the cues near their place of response in originally learning the discrimination and continued to pay attention to the cues near the place of response when its position was reversed by 180°.

Commissural inversion versus attentional theories: The results of this experiment help to shed some light on which of these two theories may be more appropriate for explaining the difficulties many animals experience with left-right discriminations.

Partially split-brain monkeys found discriminations of lateral mirror images easier to learn than those of vertical mirror images. This result is counter to the commissural inversion hypothesis which predicts that lateral and vertical mirror images should be equally easy to learn (Noble, 1968). However, it is in keeping with other experimental results (Hamilton and Tieman, 1973; Hamilton, unpublished) and also with the predictions from attentional theories. In the chiasm-sectioned monkey the scotoma present in each eye may mask part of the pattern from view if the monkey fixates accurately. As a result, confusing lateral mirror images are transformed into simple pattern discriminations that are easier to learn. Alternatively the scotoma may provide a mnemonic with which to code orientation. The left and right sides of vertical mirror images are similar so masking or coding would not have a noticible effect on them.

Partially split-brain and normal monkeys found mirror image discriminations easier when the place of response was aligned with the axis of symmetry of the patterns than when the response was orthogonal. Anatomically based theories cannot account for this result, since they do not take into account the place of response. Attentional theories, however, predict the result obtained. Schuck and others (Horel et al., 1961; Meyer et al., 1961; Schuck, 1960; Schuck et al., 1961) have reported that monkeys attend selectively to local cues near their place of response. With regard to mirror image discriminations, Riopelle et al. (1964) made the prediction that monkeys would find left-right discriminations easier if they responded to the lateral edges of the patterns and furthermore, that up-down discriminations would become more difficult if the monkeys responded to the lateral edges rather than the tops or bottoms of the stimuli. The present results bear this out.

The interocular transfer of left-right mirror images was paradoxical in partially split-brain monkeys but the transfer of up-down mirror images was veridical.

Both theories predict this result. Commissural inversion claims that since information is reversed left for right as it crosses through the interhemispheric commissures the representation of the rewarded stimulus delivered by the commissures is equivalent to the negative, unrewarded stimulus as seen through the untrained eye. Attentional mechanisms state that as the side which the scotoma is on switches with change of eye the opposite halves of the stimuli are seen. Since the monkey then perceives the negative stimulus as being most similar to the previously rewarded one paradoxical transfer occurs.

Partially split-brain and normal monkeys had worse and often even paradoxical interocular transfer (or generalization) of the aligned condition when the place of response was changed 180°; transfer of the orthogonal condition was veridical. Again anatomical theories ignore the possibility of this result. Attentional theories, though, predict it since in the aligned condition the cues near the place of response are the ones necessary to learn the discrimination. When the place of response is changed 180° the local cues near the response are exactly reversed from what they had been with regard to the rewarded stimulus. If the monkey were attending only to local cues, generalization of both lateral and vertical mirror images should be paradoxical.

There was individual variability in the results of the present experiment. Because commissural inversion should be present equally for every subject there would be no variability by that mechanism. Attentional theories allow for individual differences based on how well the subject attends to or utilizes the mnemonics available.

Therefore, attentional mechanisms can interpret <u>all</u> the results from the present and related experiments whereas explanations based on anatomy cannot.

Other examples of attentional processes in mirror image discriminations: Attentional mechanisms in the form of response asymmetries which aid in the discriminability of mirror-images, particularly left-right ones, have been referred to by other investigators. Animals learn quickly to turn left when one stimulus is present and to turn right when the mirror image stimulus is present. In this case the response itself serves as a mnemonic for the orientation of the discrimination, and therefore this paradigm does not qualify as mirror-image discrimination according to the definition of Corballis and Beale (1976).

Animals have been reported to invent response asymmetries to aid them in decoding mirror images. Corballis and Beale (1970a) report a pigeon that learned to discriminate binocularly mirror image oblique lines of 135° versus 45° by tilting its head. The head tilt transformed the difficult orientation discrimination into an easier one of horizontal versus vertical. Two other pigeons learned to peck a key when its left half was red and the right half was blue but to refrain from pecking when the colors were reversed. The birds learned the discrimination by standing to one side of the response key and pecking it asymmetrically. Generalization tests of various wavelengths showed that the pigeons attended to only one half of the key and knew nothing about the color on the opposite half (Clarke and Beale, 1972). Of course, animals who adopt response asymmetries in the absence of overt cues are in fact solving mirror image discriminations, since they must remember to which side to make their response.

Tieman, Tieman, Brody and Hamilton (1974) restricted attention in pigeons by fitting the birds with goggles which occluded either the dorsal, ventral, lateral, or none of the visual field. Pigeons with lateral goggles, like those with open goggles, when trained monocularly and tested for interocular transfer showed reduced, and sometimes paradoxical, transfer of left-right, but not up-down mirror images. Pigeons with dorsal (ventral) goggles, trained monocularly and tested for interocular transfer to the opposite eye which was wearing a ventral (dorsal) goggle, in contrast, displayed reduced and sometimes reversed transfer of up-down mirror images. Thus by altering the part of the visual field which was stimulated and also perhaps the part of the stimulus attended to, Tieman et al. (1974) produced results similar to those obtained with monkeys in the present study.

Human children show difficulties with left-right discriminations just as animals do (Huttenlocher, 1967; Over and Over, 1967; Rudel and Teuber, 1963; Serpell, 1971) and they also benefit from asymmetric strategies which serve as mnemonics for the orientation discrimination. Jeffrey (1958) instructed children to push a button located in the direction to which various stick figures were pointing, with the result that children previously unable to learn the discrimination were then able to master it. In addition, when told to discontinue button-pressing some children invented new mnemonic strategies, such as lifting one or the other shoulder as appropriate before responding.

Clarke and Whitehurst (1974) systematically investigated the effect of asymmetric responding on mirror image discriminability by children. Kindergarten children were asked to guess which of two circles was "good" and which was "bad". The circles were red on one side and green on the other, such that they formed up-down or left-right mirror image pairs. One group of experimental subjects who learned lateral mirror images was asked to touch a particular lateral side of the circles before responding; an analogous experimental group was asked to touch the top or bottom of vertical patterns before responding. Control groups touched the middle of the circles, both sides, or did not touch at all. All children who touched one particular side of a mirror image discrimination found the task easier than children who touched elsewhere or not at all. Furthermore, children, who responded to one side of a lateral mirror image solved the problem with "unusual ease"; in fact, every one of them reached the criterion for acquisition. In contrast, 15 out of 24 children who used a bilateral or ambiguous response failed to learn. Generalization testing showed that for all children who made a "one-sided" response, behavior was controlled solely by the colors near their place of touching.

The results of Clarke and Whitehurst's (1974) experiment compliment the present experiment with monkeys. Both monkeys and children found lateral mirror images easier to discriminate when they were required to touch either the left or the right side of the stimulus before responding. In some cases such asymmetric responding made lateral discriminations even easier than vertical ones. Both monkeys and children paid attention predominantly to cues near their place of response and used these cues as the basis of their discrimination.

Directed attention can therefore be advanced as a possible explanation for left-right confusion in the real world. As mentioned before, the environment contains a wealth of asymmetries in the vertical dimension which may be powerful enough to cause response biases or to provide a reference for coding orientation. Complimentary asymmetries in the horizontal dimension are lacking, which may account for the left-right difficulties experienced by many animals and man.

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