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Interocular Transfer of Lateral Mirror-Image

Discrimination by Cats:

Evidence of Species Differences

by

Kenneth Barry Hranchuk, M.A.

A Thesis submitted to the Faculty of
Graduate Studies in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

Department of Psychology

Carleton University

Ottawa, Ontario

July 11, 1974

The undersigned recommend to the Faculty
of Graduate Studies acceptance of the thesis
"Interocular Transfer of Lateral Mirror-Image
Discrimination by Cats:
Evidence of Species Differences"

submitted by Kenneth Barry Hranckuk, M.A.,
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

.....

Thesis Supervisor

.....

Chairman, Department of Psychology

Carleton University
July 11, 1974

Interocular Transfer of Lateral Mirror-Image

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An Abstract of a Thesis presented to the
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The main purpose of the study was to resolve the issue of whether the type of interocular transfer found with split-chiasm cats tested in a two-choice discrimination box and a WGTA with lateral mirror-image form stimuli is veridical or paradoxical.

Previous research conducted by Noble (1966, 1968) who tested split-chiasm monkeys with form stimuli in a WGTA indicated paradoxical interocular transfer of lateral mirror-images. On the basis of these results Noble (1968) proposed a theory of homotopic maintenance of congruent points of the visual cortices of monkeys by callosal fibres. In later research, Berlucchi and Marzi (1970) found veridical interocular transfer effects in split-chiasm cats tested with transilluminated stimuli in a two-choice discrimination box. On the basis of their results Berlucchi and Marzi (1970) rejected Noble's theory of homotopicity.

The studies of Noble (1968) and Berlucchi and Marzi (1970) differed in three critical areas: species, apparatus and stimuli. The present study attempted to determine which of these variables may have contributed to these discrepant findings.

Eight chiasm sectioned cats were divided into two subgroups with four Subjects tested in a Grice Box and four Subjects tested in a WGTA. The stimuli were one pair of mirror-images ($< vs >$) and one pair of non-mirror-images ($+ vs \perp$). The Subjects in both groups were balanced for problem tested first, hemisphere tested first, and whether a relearning phase following a 24 trial transfer

test had the same reinforcement contingencies used during initial acquisition or if the contingencies were reversed. The dependent measures used to determine the type of transfer were percent savings following reversal or reacquisition and response latencies and choice behaviour during the 24 trial transfer test.

Following completion of reversal and/or reacquisition with the second stimuli pair the Subjects were tested to determine if the simultaneous discrimination of the mirror-image stimuli may have been mediated by a strategy of response differentiation based on the total configuration made by the stimuli (such as: > X, go right; < >, go left, (Corballis and Beale, 1970)). This test involved 200 trials, 20 of which required a Subject to respond to a pair of stimuli the same as the mirror-image S+ (i.e., either < vs < or > vs >) and 20 trials of the mirror-image S- (i.e., either < vs < or > vs >) that the Subject was last exposed to during reversal or reacquisition testing. Response latencies were recorded during each of the 40 critical test trials in both apparatuses.

The results of the experiment clearly indicated veridical interocular transfer of both pair of stimuli in the WGTA and the Grice Box. These results were supported during the transfer test in which the "untrained" eye continued to treat the original S+ as S+ and the original S- as S- in terms of choice behaviour or response latencies. Veridical interocular transfer

was also reflected in the percent savings scores found during the reversal and reacquisition phases of testing. There were positive savings for reacquisition of the mirror-images and non-mirror-images and negative savings for reversal.

The test for response differentiation indicated shorter response latencies when the S+ was presented than when the S- pair was presented. This indicated that the Subjects had in fact learned to discriminate the mirror-images on the basis of their left-right differences.

The results indicated that the differences between the Noble (1968) and the Berlucchi and Marzi (1970) findings were not related to apparatus or stimuli but did suggest a species difference between cats and monkeys at least with respect to interocular transfer.

Despite the relatively independent evolution of the neocortex of cats and monkeys (Diamond and Hall, 1969) a comparison of electrophysiological properties of the visual systems of these species suggests no gross neurological differences (Berlucchi, 1972). Behavioural differences between these two species are a more likely reason for the discrepant types of interocular transfer found. Recent work by Hamilton, Tieman and Winter (1972) and Lehman and Spencer (1973) regarding such behavioural differences are discussed.

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INTRODUCTION

Interest in the problem of the conditions under which an organism is able to distinguish left from right has been recently renewed by Corballis and Beale (1970), who have amplified the argument of Ernst Mach (1894) that a necessary condition for distinguishing left from right is an asymmetrical nervous system. In an organism that is perfectly bilaterally symmetrical, symmetrical receptor loci will give rise to symmetrical patterns of neural activity which cannot be differentiated in and of themselves. According to this argument the bilaterally symmetrical visual system of man should not be able to mediate the differentiation of left from right when the only cues available are stimuli which present equivalent visual sensations to each visual field. An instance of left-right confusion, noted by Mach (1894) and well documented since (e.g. Gibson, Gibson, Pick and Osser, 1962) is that children confuse such letters as, b and d, and p and q, which differ in their left-right orientation. Mach explained this confusion in terms of an undeveloped lateral dominance in children and the absence of asymmetrical responses such as writing with the right hand (Corballis and Beale, 1970). According to Mach the fact that this confusion is much less pronounced in adults is a consequence of the development of a motor asymmetry somewhere in the central nervous system.

There are two situations in which it is possible to

experimentally test the ability of a subject, be it man or animal, to discriminate left from right. The first is to require the subject to perform a simultaneous lateral mirror-image discrimination, for example $\langle$ vs $\rangle$ or $\square$ vs $\square$, in the absence of extra-situational asymmetrical cues. In this case the subject must make non-symmetrical responses to symmetrical stimuli, that is, the subject must always respond to one of the two stimuli regardless of spatial position. The second is to require the subject to make left-right spatial responses to stimuli which differ in respects other than left-right orientation. An example of such left-right response differentiation (Berger and Hogan, 1971) is to require the subject to go to the right arm of a T-maze when a light is present and to go to the left arm when there is no light. Corballis and Beale (1970) point out clearly that for a subject to make mirror-image responses to mirror-image stimuli it is not necessary for any left-right information to be encoded or decoded. So a task which required an animal to go into the right arm of a Y-maze when a $\square$ is at the choice point or at the end of each alley and to go into the left arm when the mirror-image stimulus is present $\square$, can be solved by the subject responding to the left-right information provided by the stimuli.

The relationship between left-right discrimination and a bilaterally symmetrical nervous system can be understood by way of example. Consider a hypothetical animal which possesses a perfectly bilaterally symmetrical nervous system with all its

sensory receptors bilaterally arranged around its vertical plane of symmetry. Such an animal could not differentiate left from right when the information it received were symmetrical stimuli. When such an animal's bilateral receptors are activated by mirror-image stimuli the only result could be an equivalent mirror-image response. Such a hypothetical animal would not be able to perform differential responses to either the left or right in the absence of asymmetrical cues. In order to perform left-right discriminations this animal would have to alter its position relative to the mirror-image stimuli and thus alter the sensations to its receptors before it could differentially respond to left or right.

The ability to perform mirror-image discriminations has been studied in many species using various experimental procedures. Experiments have been performed with children, chimpanzees, rhesus monkeys, domestic cats, rats, octopi, goldfish, rabbits, dogs, pigeons and guinea pigs (Appelle, 1972). Some investigations have been concerned only with the behavioural aspects of left-right discriminations while others are concerned with neuroanatomical and neurophysiological factors. Within these approaches a wide number of research techniques have been employed. The behavioural studies have involved different apparatus as well as different learning or discrimination paradigms. Neurophysiological approaches have included single unit recording

in different areas of the brain as well as various forms of neurological manipulation.

One aspect of what Corballis (1973) has called the "psychological problem of left and right" is concerned with interocular transfer of mirror-image and non-mirror-image stimuli and it was with this aspect that the present study was concerned. The basic question evolved from the research findings of Noble (1966, 1968), working with split-chiasm monkeys, and those of Berlucchi and Marzi (1970), working with split-chiasm cats, who tested models of the neural mechanisms underlying left-right discriminations. If the two cerebral hemispheres are in fact mirror-image duplications of one another and if this bilateral symmetry is maintained by interhemispheric homotopic (point to point) fibre connections, visual information coming from one mirror-image stimulus received by one hemisphere should be reversed when projected to the other hemisphere via the homotopic interhemispheric pathways. Therefore, if such an organism has learned a left-right discrimination with visual input being restricted to one hemisphere, it should show a preference for the negative stimulus when the untrained hemisphere is first exposed to the stimuli. Noble in fact (1968) found such a reversal effect in monkeys following section of the optic chiasm, a preparation which allows for conveniently restricting visual information into one or the other hemisphere. This reversal

effect was called "paradoxical transfer" and has been interpreted as being the result of symmetry being maintained by point to point (homotopic) commissural fibres connecting the monkeys visual cortices (Noble, 1968). Berlucchi and Marzi (1970) using a similar interocular transfer paradigm with split-chiasm cats found no evidence for such a paradoxical transfer effect. Their results indicated no reversal effect and in all cases their cats showed positive (veridical) transfer. The present study was designed to explore the factors which may have accounted for the different results found by these investigators.

The method of using interocular transfer tests to study mirror-image discrimination will be discussed following a review of behavioural studies done with children and animals and a section concerned with the neurophysiological and neuro-anatomical basis of bilateral symmetry in the visual cortices of cats and monkeys.

Behavioural Studies with Children

Mach's (1894) original observation that children tend to confuse certain letters (ie. p and q) supported his hypothesis that an approximately bilaterally symmetrical visual system such as that of Man does place restrictions on left-right discrimination. It should be noted that children do not show confusion when presented with letters in orientations other than the left-right position (ie. p and d). Mach did state that a motor asymmetry

such as writing resulted in lateralization of function and allowed such left-right discriminations to be made. Mach's early observations have been confirmed by several recent researchers.

More recently, Rudel and Teuber (1963) have found that children ranging in age from three to five years find it nearly impossible to discriminate oblique lines ($/vs\backslash$), whereas they have no problem discriminating a horizontal line from a vertical line ($-vs|$) or in discriminating vertical mirror-images ($\sqcup vs \sqcap$). Their results indicated that the deficiency in children decreases as a function of age. Rudel and Teuber interpreted their results in terms of the relative importance that vertically oriented stimuli may play in a child's visual environment. The influence of gravity on the maintenance of an upright posture provides the child with an up-down clue that may facilitate vertical mirror-image discrimination of stimuli which differ only in their horizontal or lateral aspects. They did not interpret their findings in terms of cerebral lateralization of function, but the results which indicated older children do not have difficulty discriminating lateral mirror-images are at least consistent with Mach's (1894) suggestion regarding the development of lateral dominance. The research findings and theoretical explanations of Rudel and Teuber (1963) have also been supported by Huttenlocher (1967) and Sekular and Rosenblith (1964).

Gibson, Gibson, Pick and Osser (1962) performed an extensive study with children aged four through eight that also indicated a developmental influence in mirror-image discrimination performance. Children were tested for their ability to match from sample, using as the discriminative stimuli, degrees of change from line to curve (| vs |), differences in orientation (< vs > or □ vs □), changes in perspective (+ vs +) and changes in topological transformation (⊕ vs ⊕). Their results were similar to those of Rudel and Teuber (1963) in that eight year olds performed almost perfectly while younger children had difficulty in discriminating between the mirror-image stimuli. The results were interpreted from a developmental viewpoint. Their explanation for poor mirror-image discrimination in young children was that reversals of this type are not normally a critical or determining factor for identifying objects as the same or different. They suggested that during the period from four to eight years children begin to learn that such transformations as reversal are important for distinguishing the orientations of letters (i.e., p and q). It is quite clear that the Gibson et al data are also consistent with Mach's (1894) original observations with children.

Over and Over (1967) have tested the possibility that memory may be an important factor for the poor discrimination of mirror-images in young children. Their hypothesis was that the

children can discriminate simultaneous presentations of such stimuli but have difficulty remembering which is the correct response from trial to trial. They suggest that such a deficit may not be attributable to a lack of sensory coding processes but rather to response variables such as intertrial intervals when a child would be required to remember the previous responses, either correct or incorrect, before the next stimulus presentation. In order to test their hypothesis, Over and Over tested children $3\frac{1}{2}$ to $6\frac{1}{2}$ years old under two conditions. One condition was a recognition task which required that the children remember to respond to a correct stimulus over a number of trials. The stimuli were presented simultaneously (either | vs— or /vs\), with one of each pair being correct and the other incorrect. The other task involved matching to sample which required the child to select a correct stimulus from a pair by comparing them with a standard. The standard was always above the test stimuli for one group of Subjects and in the middle of the test stimuli for the other group of children. The results for the simultaneous task supported Rudel and Teuber's (1963) observation that children in this age range have difficulty discriminating oblique lines but not horizontal and vertical lines. However, under matching to sample procedures the children had little difficulty selecting the oblique that was oriented in the same direction as the standard oblique.

Consequently, they have suggested that successful recognition of mirror-image oblique lines by children is dependent upon them being perceived as different as well as being remembered as such from trial to trial.

The preceding discussion included a representative sample of some of the research that has been performed with children required to discriminate mirror-image stimuli. In all the above cited literature, support for Mach's (1894) early observations of children confusing certain letters has been indicated. In an indirect manner this support lends credence to Mach's hypothesis that a bilaterally symmetrical nervous system cannot differentiate mirror-images in the absence of some asymmetrical motor response. The studies cited have interpreted their results from various theoretical approaches. Memory has been suggested as one reason children may have difficulty discriminating mirror-images (Over and Over, 1967) as well as the importance of developmental aspects (Gibson et al, 1962) and a child's visual environment (Rudel and Teuber, 1963). However, the underlying reasons for children not being able to discriminate mirror-images have yet to be fully resolved.

Behavioural Studies with Animals

The ability to perform mirror-image discrimination problems has also been studied with different species of animals, that like children possess a bilaterally symmetrical visual

system also tend to confuse lateral mirror-images to a greater degree than such stimuli arranged in other orientations. The following studies are a representative sample of the literature involved with mirror-image discrimination learning with animals.

Mach's ideas were supported by Pavlov (1937) who found that dogs could not be trained to discriminate between touch conditioned stimuli when the loci of stimulation were homologous points on two opposing limbs. Dogs trained to salivate when touched on one limb could not learn to withhold salivation when touched on the other limb. Tschirgi (1958) has stated that, like Pavlov's dogs, cats fail to discriminate touch stimuli presented to symmetrical points on opposing limbs and could not learn a conditioned discrimination problem involving responding to a circle or a square being contingent upon touch conditioned stimuli. Their results indicate that confusion of mirror-image stimuli is evident in the sensory-motor systems of the nervous system of dogs and cats, as well as the visual system. Tschirgi would agree with Mach's contention that a motor asymmetry associated with visual sensations will result in the ability to distinguish left and right. The cats mentioned by Tschirgi received touch conditioned stimuli which were symmetrically placed on opposing limbs. These touch stimuli could not be differentiated on the

basis of the required visual discriminations. Tschirgi³ does mention that cats can discriminate circles from squares when the conditional stimuli are touches of the head versus the tail.

Sutherland (1960) reported that octopi could not discriminate lateral mirror-image obliques. These results were interpreted in terms of the predominantly horizontal and vertical receptive field organization of the retina of octopi. Therefore, an oblique line in one orientation (/) would activate an equal number of vertical and horizontal receptive fields as would an oblique line in the opposite orientation (\) and result in similar visual sensations. However, even if this is a valid interpretation it probably is of limited relevance to the behaviour of mammalian species because of the dissimilar nervous systems.

Sutherland (1969) also performed a study which compared the degree to which rats, goldfish, and octopi could discriminate mirror-image stimuli. The rats were far superior to the octopi and goldfish, while the goldfish performed at a level superior to that of octopi. Sutherland's results supported the previous findings of Lashley (1938) with rats, as well as his own previous findings with octopi (Sutherland, 1960).

The degree to which discrimination of mirror-images can be performed may be dependent upon complexity of stimuli

as well as species used. Lashley (1938) reported that rats do not have difficulty discriminating between certain symmetrical pairs of figures ($\blacktriangleright$ vs $\blacktriangleleft$), but fail to discriminate others (S vs 2). These results were explained by Lashley in terms of the "conspicuous identifying elements" that the stimulus pairs possess; the lack of distinct features between a pair of stimuli increases the difficulty to discriminate between them. Lashley did not clearly define what "conspicuous identifying elements" were, other than to state that such stimuli as S vs 2 and $\backslash$ vs $/$ only provide information about the "relative position of parts which are remote from the frame of reference provided by the edges of the cards (p. 159)."

Although their study was not directly involved with lateral mirror-image discrimination, one of the eight oddity problems used by Koronakos and Arnold (1957) in a study of learning set formation in rats was a pair of oblique stimuli ($/$ vs $\backslash$) and a horizontal and vertical line pair of stimuli ($|$ vs $-$). Their results indicated that the left-right oblique problem was more difficult to discriminate than the horizontal-vertical problem, irrespective of order of presentation of the problems.

Kinsbourne (1971) tested the ability of rats to discriminate two-dimensional figures that differed in orientation.

The main purpose of the study was to determine if rats, like children (Kinsbourne and Hartly, 1968), show a "hierarchy of confusion" when presented with pairs of "p" shapes in four different orientations: 1) reversal, p vs q (most difficult); 2) reversal and inversion p vs d (less difficult than reversal); 3) inversion p vs b (more difficult than reversal and inversion); and 4) rotation, p vs ∇ (least difficult). Kinsbourne was also concerned with whether or not such a hierarchy of confusion was specific to humans and whether or not verbal mediation may be important in discrimination of orientation. The results indicated that like children and adults (Kinsbourne and Hartly, 1968) rats have the same hierarchy of difficulty in discriminating stimuli in the four orientations just described. Kinsbourne's results also indicated that verbal mediation was not a critical variable and that such a "hierarchy of confusion" may be related to "orientational disparities" that render stimuli in some orientations more discriminable than in others.

Sutherland (1963) tested four cats in an apparatus designed by Sperry et. al (1955) to determine their ability to discriminate horizontal from vertical rectangles and rectangles that were mirror-image obliques. The results revealed learning curves that were almost identical for the two problems. Sutherland also tested whether the cats were learning to discriminate

mirror-image per se or the total patterns made by the shapes when presented simultaneously. This test involved successive presentation of the stimuli after simultaneous testing had ended. All four cats showed perfect and immediate transfer of the discriminations, suggesting that the animals had learned to discriminate the obliques in terms of the differences in their orientation. Sutherland explained these above results in relation to the relative number of receptive fields in different orientations of the visual system of cats. He cited research by Hubel and Wiesel (1962) that indicated the receptive fields of the cats retina which activate single cells in the striate cortex are not oriented in a horizontal or vertical extent any more than in an oblique orientation. He refers to his earlier work (Sutherland, 1957) with octopi and goldfish. (Mackintosh and Sutherland, 1963) in an attempt to explain the differences from an evolutionary point of view. He did not state why there should be such an evolutionary influence on such discriminations but did say that oblique orientations "may be of special importance to an animal jumping from branch to branch (p. 210)".

Warren (1969) replicated Sutherland's findings in an extensive analysis of 35 cats tested in a Grice Box on four problems ($\square$ vs $\square$, $\square$ vs $\square$, $/$ vs $\backslash$, $|$ vs $-$). The purpose

of the study was to determine if Sutherland's (1963) results were related to apparatus and were due to the animals being tested with transilluminated stimuli in a dark environment devoid of all other contextual cues. Although the results bore out Sutherland's (1963) findings that cats can discriminate oblique rectangles with as much facility as they can horizontal versus vertical rectangles, the cats had more difficulty discriminating between lateral mirror-images (vs) than vertical mirror-images (vs). On the basis of the results with obliques, Warren rejected Sutherland's (1963) interpretation of the ability to perform visual discriminations in various species on the basis of the relative distribution of receptive fields that respond differentially to stimuli in specific orientations. Warren mentioned that Sutherland (1969) had also altered this view by recognizing the significance of areas beyond area 17 of the visual cortex in the analysis of visual information.

Pariss (1964) attempted to determine whether cats discriminate oblique rectangles as readily as horizontal-vertical rectangles when the stimuli are presented successively rather than simultaneously. He used an oblong box that allowed him to present the stimuli simultaneously but in such a way as to prevent the cats from viewing them together. This was achieved by placing the stimuli at each end of the box and releasing the

cats from a compartment in the centre of the box. The cats could therefore view each stimulus but could not compare them simultaneously. There were two pairs of test stimuli, a pair of horizontal and vertical lines, and a pair of oblique lines. He found that the cats that were given the oblique problem before the horizontal-vertical problem required three times as many trials to discriminate the former than the latter. When the obliques were presented after the horizontal-vertical problem, the cats took twice as many trials to learn to discriminate the oblique rectangles than the horizontal-vertical rectangles.

On the basis of his results Pariss has suggested that simultaneous discriminations may be easier for some species of animals than others. He also suggests that Sutherland's (1963) successive tests with cats may have been invalid since Sutherland had retrained his cats in the same apparatus and they may have been responding to parts of the pattern learned during original testing.

Other species such as monkeys have been extensively investigated with mirror-image discrimination learning and there is one study in particular that should be mentioned. Riopelle, Rahm, Itoigawa and Draper (1964) have found that normal monkeys trained in a modified Wisconsin General Apparatus

(WGTA) have greater difficulty discriminating lateral mirror-images than vertical mirror-images. Riopelle et al explain these findings as being a function of the manner in which rhesus monkeys inspect stimuli. They have observed that monkeys tend to inspect the lower or upper portions of a stimulus configuration rather than the lateral edges. Therefore, the extent to which stimuli are different at the bottom (or top) will determine how easily they can be differentiated. Vertical mirror-images presented laterally ($\square$ vs $\square$) are more different at the base than horizontal mirror-images presented in the same manner ($\square$ vs $\square$). This behaviour on the part of monkeys, according to Riopelle et al, is the reason vertical mirror-images are learned faster than horizontal mirror-images.

It is apparent that subjects other than children confuse left-right mirror-image stimuli more than similar stimuli in different orientations. Lateral oblique lines are apparently more difficult for children to discriminate (Rudel and Teuber, 1963) than for cats (Sutherland, 1963; Warren, 1969). However, the manner in which lateral obliques are compared may be an important factor to consider when using cats as experimental subjects (Pariss, 1964). The discrimination of lateral mirror-images such as, $\square$ vs $\square$, has proven to be a more difficult task than oblique line discriminations for cats (Warren, 1969) and

6

vertical mirror-images for monkeys (Riopelle et al, 1964).

An adequate explanation for the different degree of difficulty discriminating between these pairs of stimuli has yet to be formulated.

Neurophysiological Studies of the Visual System

Gross inspection of the neuroanatomical structures of such placental mammals as cats and monkeys indicates that they do indeed have bilaterally symmetrical nervous systems. However, in order to assume as Mach did, that this structural symmetry is also reflected in a functional symmetry, the nature of the integration between the two halves of the nervous system must be determined. The most evident neural connection between the two halves of the brain in mammals is the corpus callosum, and in order to maintain structural symmetry between the two hemispheres the interhemispheric fibres of the corpus callosum would have to interconnect homotopic points in each hemisphere. Homotopic interconnection of the two visual cortices is when a specific topological area of one hemisphere is connected to an analogous area of the other hemisphere via the fibres of the corpus callosum.

The study of such homotopic interhemispheric connections has been the subject of much research.

McCulloch and Garol (1941) utilized physiological neuronography to determine which specific areas of each cerebral

hemisphere are connected in a point to point fashion. In terms of the visual system, their results indicated that strychnization of sections of area 18 yielded strychnine spikes in homologous areas of the contralateral hemisphere. These results support callosal interconnections of general areas of the visual system of macaca mulatta.

Grafstein (1959), using more sophisticated procedures than McCulloch and Garol (1941) has found similar results with cats. Grafstein used decerebrated cats in which she partially deafferented the suprasylvian gyrus by undercutting it. The hemispheres remained connected by the corpus callosum. The procedure then involved simultaneous electrical stimulation of one area of the suprasylvian gyrus of one hemisphere and monopolar recording of the analogous area of the other hemisphere. Grafstein gave no indication of what specific area she stimulated and recorded from on the gyri. The results were as follows: "It would appear that fibres originating in cells deep in the cortex on one side end deep in the cortex on the other side, while fibres originating in superficially lying cells end superficially in the other hemisphere (p. 514)".

Grafstein, like McCulloch and Garol, found general evidence for area to area interconnection of the hemispheres

via the corpus callosum.

Hubel and Wiesel (1967), in a series of studies with cats, found that fibres in the splenium had receptive fields that were (in 31 of 34 recordings) activated by retinal stimulation along the vertical meridian of either eye. These binocularly driven cells were not activated by retinal stimulation at distances of more than 1° from the vertical meridian. Only one cell of the 34 could be activated at a maximum distance of 4° . These results indicated that the posterior callosal fibres of the cat are binocularly driven and transmit neural activity that is received in either hemisphere from the ipsilateral and contralateral areas about the vertical meridian of the retina.

These results indicate that the posterior corpus callosum maintains correspondence between the visual cortices of the two hemispheres for visual stimulation at and along the vertical meridian of both retinae of the cat.

In the same study Hubel and Wiesel also obtained evidence for heterotopic interhemispheric callosal fibre connections. Heterotopic interhemispheric connections are defined as the joining or interconnecting of two points of a bilateral nervous system which are not structurally homologous. These results were found by simultaneously recording from single visual cortical cells in each hemisphere. The electrodes were

placed in homologous areas of area 17 near the 17-18 border as well as in the 17 - 18 area of overlap and area 18. The procedure involved continuous recording from a stationary electrode in one visual area of one hemisphere and continuous recording from an advancing electrode placed at a homologous area in the contralateral visual cortex. This continuous recording allowed the experimenters to determine at what locus the two cortical cells are activated by visual stimuli presented to each eye. Utilizing this technique Hubel and Wiesel found that area 17 of one hemisphere projects directly to areas 18 and 19 of the other hemisphere. They also found projections from area 18 of one hemisphere to area 18 of the contralateral hemisphere as well as similar results for cells in the boundary between areas 17 and 18. They found no evidence for projections from area 18 of one hemisphere to contralateral area 17. In the same report Hubel and Wiesel stated that using Nauta silver-degeneration studies they had found that area 18 has numerous projections to area 18 of the contralateral side but not to area 17 of the opposite side. These later histological results would support homotopic interconnecting fibres for area 18 of the cats visual system.

Hubel and Wiesel's (1967) results have shown that area to area integration of the visual cortices is restricted to

visual stimuli presented in close proximity to the vertical meridian of the cats retinae. They have also indicated that only stimulation of the retina along the vertical meridian is relayed between the hemispheres via the corpus callosum connections in areas at and close to the border between area 17 and 18 of either visual cortex. This would suggest that stimulation of only a limited area of the visual receptors in the retinae results in transmission between the hemispheres and that the nature of these interconnections are both homotopic and heterotopic (see above).

Berlucchi, Gazzaniga and Rizzolatti (1967) also investigated the nature of the transfer of visual information via fibres in the posterior corpus callosum of the cat. Their research supported that of Hubel and Wiesel (1967).

Berlucchi et al did an extensive analysis of 17 callosal fibres and found that all were activated by stimulation of the area in close proximity to the vertical meridian of the retinae. Although these data support Hubel and Wiesel's findings there is one important difference that should be mentioned. They only found three units that were equally activated by both eyes. Of the remaining units, nine were activated by one eye and five were activated by both eyes. However, of these latter five units, stimulation of one eye resulted in superior unit responses than the other eye. As a result of these discrepancies these five units were not considered to be binocularly responsive.

In an extension of this study, Berlucchi and Rizzolatti (1968) utilized split-chiasm cats to further analyze the nature of interhemispheric interconnections across the callosal pathways. Because the crossed fibres at the chiasm are destroyed, this preparation allows one visual cortex to be activated by direct visual input from its ipsilateral eye and by indirect visual input via the corpus callosum of the contralateral eye. Through microelectrode recording, Berlucchi and Rizzolatti found that 9 out of 70 visual cortical cells driven by ipsilateral stimulation could also be activated by visual stimuli presented to the contralateral eye. These nine units were activated by stimulation along the vertical meridian (nasal side) of each retina. The area of activation was close to the area centralis and extended to approximately 10° along the vertical meridian. These findings indicate a high degree of convergence of visual stimuli presented to both eyes. In other words, particular visual stimuli will activate the same cortical neurons via direct and/or indirect visual system inputs.

In a recent review of the anatomical and physiological functions of the corpus callosum, Berlucchi (1972) has presented some relevant research concerning the interhemispheric transfer of visual information. In his discussions he mentioned the type of homotopic and heterotopic interconnections that have already been discussed (Hubel and Wiesel, 1967; Berlucchi et al, 1967).

Berlucchi also cites some unpublished research he has performed with Mascetti and Lepore. The study concerned a combination of unilateral and/or bilateral lesions of the callosally connected areas of 17, 18 and 19 of the cats visual cortex as well as unilateral lesions of sections of area 17 that lack callosal connections. The split-chiasm cats were tested for interocular transfer of eight sets of patterns, one of which was a pair of lateral mirror-images (C vs D). Interocular transfer of monocular learning occurred in all the cats regardless of the area lesioned (callosal vs acallosal). The results also indicated transfer from the lesioned side to the intact side and vice versa. In two cats that subsequently had their corpus callosum and anterior commissures sectioned, interocular transfer was totally absent. In order to refute the argument that their acallosal lesions may not have been complete, Berlucchi et al surgically removed the entire visual cortex of one hemisphere in two split chiasm cats. When tested for interocular transfer of the same pattern stimuli, one subject showed successful transfer from the lesioned to intact side and vice versa, while the other subject showed successful transfer from the lesioned to the intact side.

Berlucchi et al concluded that the interhemispheric transfer of visual pattern stimuli can occur in the absence of

the callosal connections of areas 17, 18 and 19. They state their results are in support of a proposition by Whiteridge (1965) that callosal connections in the suprasylvian and ectosylvian gyri may be the important pathways for transfer of pattern stimuli.

In summary, the studies cited in this section indicate that the connections between the visual cortices of cats via the fibres of the corpus callosum are both homotopic and heterotopic. The majority of the studies have been purely neurophysiological and have not concerned themselves with behavioural phenomenon. Only the unpublished research cited by Berlucchi (1972) attempted to reveal the relationship between interhemispheric pathways and transfer of learned pattern discriminations. In view of all the above studies the question concerning maintenance of bilateral symmetry via interhemispheric interconnections between the visual cortices of mammalian species has yet to be resolved.

Interocular Transfer of Mirror-Image Discrimination

Another important aspect of research dealing with mirror-image discrimination has centered around the role of the interhemispheric commissures in integrating the visual cortices of the two cerebral hemispheres. The primary experimental procedure used to determine the function of such neural structures as the corpus callosum is testing for interocular transfer from one hemisphere to the other.

Mello (1965, 1966a, 1966b, 1968) has performed a series of investigations concerned with interocular transfer of mirror-image patterns in pigeons.

In one of her studies, typical of the others, Mello (1966a) trained 15 pigeons under monocular testing conditions to discriminate successive presentations of: "up-down" mirror-images ($\top$ vs $\perp$), "left-right" mirror-images ($\leftarrow$ vs $\rightarrow$) and "ambiguous" figures ($\lfloor$ vs $\lceil$). The pigeons attained the initial acquisition criterion for the discriminations with equal facility. However, during retesting for interhemispheric transfer to the untrained hemisphere, which received no direct visual input during initial training, performance was variable. Interhemispheric transfer was veridical for the "up-down" problem in that Subjects continued to respond to the S+. For the "left-right" problems however, the transfer was paradoxical in the sense that the pigeons responded to the stimulus which had been S- during acquisition training. Two pairs of "left-right" mirror-images ($<$ vs $>$ and $\triangleright$ vs $\triangleleft$) resulted in mixed effects when the pigeons were tested for interocular transfer. Of the 18 tests performed with these stimulus pairs one pigeon responded to the previous positive stimulus, seven to the previous negative stimulus and ten pigeons responded at chance level. The same mixed results were found with the "ambiguous" figures ($\lfloor$ vs $\lceil$). Six of the 11 pigeons tested with these stimuli

showed no transfer, while three responded to the previous negative stimulus and two responded to the previous positive stimulus. Mello had no adequate explanation for interhemispheric reversal of the lateral mirror-images or why the lateral triangles and arrowheads did not yield the same results as the other "left-right" pairs. She stated that one difficulty in determining the interhemispheric integration of visual stimuli in the pigeon was, "... the fact that the anatomical route of interhemispheric transfer in pigeons is as yet unspecified (p. 299)".

Beale and Corballis (1967, 1968) and Corballis and Beale (1967, 1970) have performed a series of experiments in an attempt to clarify these curious findings.

Beale and Corballis (1967) found that pigeons, when viewing monocularly tend to peck a discriminative stimulus on the side of the open eye. They tested their hypothesis of "laterally displaced pecking" by determining which side of a food dish, filled with grain, would be pecked clean first by pigeons with only monocular vision. All four subjects pecked at the grain on the same side of the food dish as the open eye. On the basis of this behaviour, Corballis and Beale (1967) attempted to explain Mellos's paradoxical transfer effects. Corballis and Beale (1967) found that, in common with the data found with food dishes, pigeons with one eye occluded tended to peck to the same side of

a response key as the eye being trained. Therefore, a pigeon trained with its right eye open tends to inspect only the right half of the response key and vice versa for the left eye. Thus, they argue that lateralized oblique stimuli are discriminated on the basis of their up-down components. For a bird viewing with its right eye open, the 45° oblique would appear as the solid line in A of Fig. 1 and the 135° oblique would appear as the solid line in B of Fig. 1, and therefore the pigeons may have learned to perform this discrimination as something other than an oblique line discrimination. Beale and Corballis (1967) see this behaviour in pigeons as a possible explanation for Mellos's paradoxical transfer data. A pigeon trained with stimulus A of Fig. 1 as positive and stimulus B of Fig. 1 as negative may have transformed the problem into an up-down discrimination. A pigeon with its right eye open would only see that part of the positive oblique that appeared in the upper right quadrant of the response key. The negative oblique would only be seen in the lower right quadrant of the response key. Therefore, if the pigeon had learned an up-down discrimination as suggested, the previous negative stimulus would be treated as the positive stimulus when tested with the left eye open.

Further studies performed by Beale and Corballis (1968), Corballis and Beale (1970), Beale and Williams (1971) and Clarke and Beale (1972) also support the hypothesis of

Figure 1 Illustration of how pigeons may view oblique stimuli on a response key, as suggested by Beale and Corballis (1968).

"laterally displaced pecking" as an explanation for Mello's findings of paradoxical interocular transfer of mirror-image obliques in pigeons.

Beale, Williams, Webster and Corballis (1972) have reported data indicating that pigeons with all their inter-hemispheric commissures sectioned do not confuse mirror-image obliques. Twelve pigeons were trained to peck at a white line sloped at 60° from horizontal displayed on a green background and to withhold pecking when only the green background was displayed. Subsequent to criterion performance on the above task the pigeons were given tests of generalization. The stimuli used for these tests were six white lines ranging from 45° to 135° separated in steps of 15° . The results indicated that the six normal pigeons tested pecked a significantly greater number of times to the 60° slope and its mirror-image 120° slope. The six pigeons with all their interhemispheric commissures severed pecked only at the previous positive 60° white line. Beale et al (1972) stated that Thomas (1966) had found similar bimodal responding by normal pigeons during tests of generalization with mirror-image stimuli. On the basis of the Thomas (1966) data and their own data with normal and split-brain pigeons, Beale et al (1972) support the view that the confusion of mirror-images by normal pigeons is related to the presence of interhemispheric

commissures. Beale et al (1972) state their findings may be of relevance to the understanding of mirror-image reading and writing observed in some children.

Campbell (1971) performed an extensive replication of some previous research by Ingle (1967) which indicated that goldfish show both paradoxical and veridical interocular transfer of left-right shapes. Ingle had found that mirror-image shapes occupying 15° of visual angle resulted in paradoxical interocular transfer, while smaller mirror-image shapes occupying 5° of visual angle resulted in veridical interocular transfer. Using a shock avoidance technique similar to Ingle, Campbell used a wider range of stimuli sizes (15° , 10° , 5°) and used the same shapes presented in an up-down orientation to test for interocular transfer. Campbell also controlled for order effects of stimuli presentation. The stimuli were white shapes mounted on black plastic and black planimetric shapes mounted on a white circle ($< vs >$ and $\vdash vs \dashv$). The stimuli were presented successively according to Gellerman's (1933) irregular sequences of trials and the goldfish were required to respond in a "go" - "no-go" fashion. The results supported Ingle's (1967) data, in that, paradoxical transfer occurred at 15° and veridical transfer occurred at 5° visual angle in all mirror-images, regardless of shape. The same shapes of all sizes presented in an up-down

fashion ($\sqrt{\text{vs}}/\Delta$ and $\perp$ vs $\top$) resulted in veridical interocular transfer. Of six fish, presented with stimuli occupying 10° of visual angle, one fish showed paradoxical transfer, four showed veridical transfer and one performed at chance level. Campbell refers to a hypothesis by Starr (1971), who has found similar results with split-chiasm monkeys. Starr has suggested that small stimuli activate small receptive fields which are connected via the forebrain commissures and are activated by stimuli of the same orientation. Paradoxical transfer results from the homotopic interconnections of the visual fields of both visual cortices in the brain. This later theory has been proposed by Noble (1968) and will now be discussed.

Direct surgical manipulations of the visual projection systems of monkeys (Noble, 1966, 1968) and cats (Berlucchi and Marzi, 1970) has been used to determine the role of the interhemispheric commissures in interocular transfer of lateral mirror-images.

Noble (1968) used monkeys in an attempt to determine what type of interhemispheric transfer occurs when Subjects are required to perform simultaneous discrimination of mirror-image and non-mirror-image stimuli. He proposed a theory based on the presence of homotopic interconnecting fibres between the two cerebral hemispheres. According to Noble the direct visual

input to area 17 is relayed to the prestriate areas 18 and 19 which in turn relay visual information to the inferotemporal area. These impulses are projected to identical loci of the opposite hemisphere by means of homotopic callosal fibres, see Figs. 2 and 3. The untrained hemisphere is therefore receiving the mirror-image of each stimulus that the eye is viewing. Therefore, the untrained hemisphere was being exposed to the problem with, in effect, the reinforcement contingencies reversed. When the untrained hemisphere is tested for transfer, the mirror-image of the positive stimulus (negative stimulus) is responded to. The direct visual input to this hemisphere was in conflict with the callosal input received during initial testing and therefore, to perform correctly, an animal must extinguish this response and then rely upon the information provided by the direct visual input.

Noble's first test of his theory was provided by two Subjects with their optic chiasm sectioned along the midline and three Subjects with both their optic chiasms and anterior commissures sectioned. Fully recovered, the Subjects were tested for interocular transfer of lateral mirror-image stimuli in a Wisconsin General Test Apparatus (WGTA). Three showed an initial chance level of responding during transfer testing. This chance level of responding to either S+ or S- rapidly changed to a preference

Figure 3 Homotopic fibres between the two hemispheres as conceptualized by Noble (1968).

for S- rather than S+. It should be noted that there was non-differential reward throughout the transfer testing phase in order to prevent any bias for either stimulus. The other two Subjects showed an initial preference for S-. Therefore, transfer was called paradoxical in that the stimulus that was nonreinforced during initial testing with one hemisphere was the preferred stimulus when the untrained hemisphere was tested for transfer. Noble (1968) explained the initial chance level responding in terms of conflicting cortical representations of the positive stimulus in the two hemispheres. When testing the second eye (hemisphere) for interocular transfer the cortical representation in the hemisphere first trained (eye now occluded) would still exert some influence over the responses during transfer testing. According to Noble, choices made on any one trial were dependent upon which hemisphere exerted the greatest amount of influence during that trial. A subsequent preference for the negative stimulus resulted when the cortical representation of the hemisphere first trained (positive stimulus) no longer exerted an influence on the cortical representation of the second hemisphere (mirror-image or negative stimulus). As an additional test of this reversal effect, Noble then retested the original eye with the same stimuli using nondifferential reward and found a perfect retention of the positive shape used during

initial training (before transfer test). Noble then trained three of these five monkeys to discriminate pairs of vertical mirror-images or bilaterally symmetrical pairs of shapes. Interocular transfer tests were veridical in every case in that Subjects' preference did not change and they continued to respond to the S+ used during initial acquisition. Noble also studied the role of the forebrain commissures in interocular transfer of lateral mirror-images by sectioning these fibres subsequent to monocular acquisition but prior to transfer testing. Two of the Subjects from the original five Subjects and one naive Subject were used. In all three Subjects there was a preference for the previously negative stimulus. Noble also performed other manipulations to determine which factors were most important in the interocular transfer of lateral mirror-images. Two Subjects with only the anterior commissure intact showed a reversal preference. This reversal effect was found with lateral mirror-images but not with vertical or bilaterally symmetrical pairs of stimuli. Noble interpreted the above results by stating that, "The reversal of preference with lateral mirror-images in the optic chiasm section monkey is mediated via the anterior commissure or the splenium of the corpus callosum (p. 149)". In three normal unoperated monkeys,

transfer of lateral mirror-images was veridical during testing of the untrained eye. Two monkeys with one optic tract sectioned yielded veridical transfer on interocular tests and in one Subject with all the forebrain commissures sectioned and the optic chiasm intact, transfer was also veridical.

Noble interpreted his results in terms of homotopic interconnecting fibres between the two cerebral hemispheres. In all cases where these fibres are intact and visual input was restricted to one of the hemispheres the results indicated a paradoxical transfer effect. However, in the event that the visual input to either hemisphere was disrupted (ie. one optic tract sectioned) or the stimuli were non-mirror images, veridical transfer occurred. Noble's monkeys did not show paradoxical transfer for vertical mirror-image or bilaterally symmetrical pairs of stimuli. He interpreted these findings simply in terms of the anatomy of the projections of optic fibres from the retina. The fibres projecting from the upper and lower halves of the retinae are not segregated and project to both hemispheres, while those of the right and left hemiretinae are segregated and project to the right and left hemispheres respectively (see Fig. 2).

In contrast to these findings Berlucchi and Marzi (1970) using an analogous paradigm with split-chiasm cats

tested in a Grice Box found evidence for veridical interocular transfer of lateral mirror-image discriminations.

The procedure involved training the Subjects to discriminate lateral mirror-images with direct visual input restricted to one eye (hemisphere). When they tested the untrained hemisphere (other eye) with nondifferential reward of the stimuli, the Subjects developed such strong position habits that the nature of the transfer, although it tended to be veridical could not be entirely determined. However, the data supporting veridical transfer came during a reversal-relearning phase with the second eye (untrained eye). They found that the Subjects required fewer trials to relearn the same discriminations as that used during original learning. On the other hand, when the reinforcement contingencies were reversed from that of original learning the Subjects required more trials to learn the discrimination than during original learning. This was attributed to the fact that the Subjects first had to extinguish responding to the original S+ before it could learn the reversed discrimination problem.

Berlucchi and Marzi (1970) refuted Noble's interpretation of homotopic interconnecting fibres between the two hemispheres by citing the electrophysiological evidence previously described (Berlucchi and Rizzolatti, 1968; Hubel and Wiesel, 1967) which suggested that at least in cats, there is a high

degree of convergence between direct visual input via the lateral geniculate nucleus (see Fig. 4) and input of interhemispheric callosal connections in the cat's visual system. In view of these electrophysiological data, Berlucchi and Marzi (1970) argued that visual information which is restricted to one cerebral hemisphere and transferred to the other hemisphere via interhemispheric pathways may not result in a mirror-image being transferred in the same manner as suggested by Noble.

It is quite apparent that there is a conflict between the basic findings of Noble (1968) and that of Berlucchi and Marzi (1970). The results of these two studies appear to have established two opposing transfer effects and the purpose of the present study was to attempt to establish the reasons for the different results.

Research Design

The main difference between Noble's (1968) research and that of Berlucchi and Marzi (1970) revolve around three critical variables: species, apparatus, and stimuli. The purpose of the present study was to determine which of these variables may have contributed to the different types of interocular transfer found by these investigators. A brief presentation of the experimental design and possible outcomes will now be presented.

Figure 4 Direct and indirect visual projections illustrating convergence in the two hemispheres as suggested by Berlucchi and Rizzolatti (1968). The diagram shows a neuron in the right visual cortex (being recorded) of a split-chiasm cat and how it can be activated by a visual stimulus which crosses the vertical meridian of the visual field.

Eight laboratory bred cats were divided into two subgroups with 4 Subjects to be tested in a Grice Box and 4 Subjects to be tested in a WGT. Following an adaptation phase in their respective apparatus, all the Subjects had their optic chiasm sectioned along the midline. At this point, monocular mirror-image and non-mirror-image acquisition and transfer testing began. During this phase the procedure was identical for both groups, other than different apparatus used. The stimuli were one pair of non-mirror images (+ vs $\perp$) and one pair of mirror-images (< vs >). The Subjects in both groups were balanced for problem tested first (either mirror-images or non-mirror-images), hemisphere trained first, and whether re-learning following transfer testing was with the same reinforcement contingencies (same S+ and S-) or reversed. Thus, as an example of the procedure used, any one Subject in either group was tested as follows. The Subject may have initially been monocularly trained to perform the mirror-image discrimination to a predetermined criterion of learning. Upon reaching criterion the Subject was then tested for interocular transfer. This involved occluding the eye of the hemisphere trained during acquisition and testing the untrained eye. During this phase a simultaneous discrimination procedure was used to test the Subjects preference of the same stimuli. Responses to either the positive or negative

stimulus were reinforced during the simultaneous transfer testing (ie. nondifferential reward). Following the interocular testing phase the Subject was retrained to criterion with S+ and S- either reversed or the same as that used during acquisition. Completion of the first reversal or reacquisition phase with the mirror-images was followed by acquisition of the non-mirror-image problem. The procedure of acquisition, interocular transfer testing and relearning was identical for the non-mirror-image pair to that used for the mirror-image pair of stimuli.

The above phase of the experimental design allowed for four combinations of results to occur in the two apparatus. Results could indicate that there was paradoxical interocular transfer of lateral mirror-images in both the WGTA and Grice Box or that transfer was veridical in each apparatus. On the other hand the results could indicate a combination of different transfer effects in the apparatus, ie. paradoxical transfer in the WGTA and veridical transfer in the Grice Box or vice versa.

Paradoxical transfer effects in both the WGTA and Grice Box would suggest that the different types of discriminanda used by Noble (1968) and Berlucchi and Marzi (1970) may have been a critical variable. Noble used form stimuli very similar to those of the present study. Berlucchi and Marzi required

their Subjects to discriminate transilluminated pattern stimuli. This difference in stimuli could have had the effect of producing different transfer effects in at least two ways. First, it is possible that Noble's monkeys may have used tactual information when they were pushing and/or manipulating the forms, such additional potential information was obviously not available to Berlucchi and Marzi's cats tested with the transilluminated patterns. Another possibility is that such a discrimination can be transferred interhemispherically via the commissures of the superior colliculus and that this is veridical transfer.

Paradoxical transfer in the WGTA and veridical transfer in the Grice Box would suggest some apparatus variable and not a stimulus difference. Such apparatus differences might be related to the type of response required in each apparatus. Subjects tested in a WGTA are required to perform a unimanual push response in order to receive reinforcement (or non-reinforcement). There is a minimal amount of mobility required of the Subject's whole body in the WGTA. In contrast, Subjects in a Grice Box are required to perform whole body responses in that they must leave a start box and physically enter one of the two goal boxes that are separated from the start box by a choice compartment. These two different modes of responding may alter the manner in which the left-right relationship of the stimuli is perceived.

Veridical transfer effects in both apparatuses would suggest that neither the type of apparatus or stimuli used is a critical variable and that there is some form of species difference in that rhesus monkeys show paradoxical whereas for some reason cats show veridical transfer regardless of testing apparatus or stimulus presentation.

Finally, veridical transfer in the WGTA and paradoxical transfer in the Grice Box would be most unexpected and difficult to interpret in view of Noble's (1968) and Berlucchi and Marzi's (1970) results.

It should be noted that when animals are tested for interocular transfer of non-mirror-images, veridical transfer was expected in both apparatus.

Following completion of reversal and reacquisition with the second stimulus pair, the Subjects were tested to determine whether the simultaneous discrimination of the mirror-image stimuli may have been mediated by a strategy of response differentiation. It is possible that the Subjects learned the discrimination by utilizing a strategy to go to the right when the stimuli were presented in one configuration (e.g., $\langle \rangle$ where $\rangle$ is S+) and go to the left when the stimuli were presented in the other configuration ($\times$). As discussed earlier, such a response

differentiation strategy does not require the discrimination of left and right, but rather requires responding to left-right stimuli that differ in respects other than just laterality (i.e., the configurations they make).

Following the completion of the reversal and re-acquisition testing with the second pair of stimuli each Subject was retrained to criterion with the mirror-image pair of stimuli. The eye last exposed to the mirror-images was the eye retrained and the same positive and negative reinforcement contingencies were maintained.

The actual test involved 200 trials, 20 of which required a Subject to respond to a pair of stimuli the same as the mirror-image S+ the Subject was last exposed to during reversal or reacquisition training (i.e., either $<vs<$ or $>vs>$). Each Subject also received 20 presentations of a pair of stimuli the same as that Subjects previous S- (i.e., either $<vs<$ or $>vs>$). Response latencies were recorded during each of the 40 critical test trials in both apparatus.

In the event the response latency data indicated no differences for the Subjects responses to either the positive or negative pair it would have to be concluded that the discrimination between the two stimuli was not on the basis of their left-right orientation. Such data would indicate that there was no preference

for either the S+ or S- and that in fact the Subjects may have utilized a strategy such as response differentiation. Slower response times during presentation of the positive pair as opposed to the negative pair would support the fact the stimuli were differentiated on the basis of their orientation. Such data as just mentioned would support the hypothesis that the positive discriminative stimulus resulted in a quicker response latency and the negative stimulus resulted in inhibition and resultant slower response times.

Subjects

The experimental Subjects were nine mongrel cats, five male and four females. One Subject, a male, was rejected due to histological analysis of the split-chiasm surgery. Of the eight remaining Subjects, two were laboratory bred while the other six were obtained from the Queen's University Vivarium. The two laboratory bred Subjects had had some prior experience in behavioural testing. This prior experience is described in Appendix A.

Apparatus

Two pieces of behavioural testing apparatus were used in the testing. The first, a Wisconsin General Test Apparatus (WGTA) (Harlow, 1949) consisted of a Subject's compartment and a response platform which allowed the experimenter to slide a test tray to and from the Subject's compartment. The Experimenter sat behind a one-way screen which could be raised or lowered and which allowed the Experimenter to observe the Subject while the test tray was forward and the Subject was responding. The Subject's compartment also had a door which could be raised or lowered for each trial.

The second behavioural testing apparatus was a Grice Box. This apparatus, similar to that described by Hirayoshi and Warren (1967), consisted of a start box, a choice area and two goal boxes. The start box had an opaque door which when raised allowed the Subject to enter the choice compartment. Each goal box contained one of a pair of stimuli which the Subject was required to discriminate. The goal boxes were fronted by a clear Plexiglas barrier that required the Subjects to enter either goal box through a four inch opening on the lateral side of each goal box. This barrier prevented the Subjects from responding too rapidly to either goal box and was designed to help eliminate positional responding.

Preoperative Procedure

Apparatus Adaptation

Prior to introduction to the behavioural testing apparatus the Subjects were assessed for paw preferences for 300 trials in a "Handedness Box" described by Warren et al (1967). Testing was administered over six sessions of 50 trials each (one session per day).

Following handedness testing, four Subjects were introduced to the WGTA and four to the Grice Box. The Subjects in the Grice Box were adapted to the apparatus by allowing them

free access to food reward (pork kidney) in either goal box. This sequence of 50 nondifferential reward trials was utilized to create consistent running from the start box to either goal box. There were no stimuli present during this phase of adaptation. The 50 trials of nondifferential reward were followed by a further 50 trials during which only one goal box or the other contained reward. Again, there were no stimuli present during these trials but the reward was visible. The Subjects were then trained to perform a simultaneous brightness discrimination task. The stimuli were two upright squares measuring 4" x 4" x $\frac{1}{2}$ " thick, one of which was painted black and the other white. Initially the brightness stimuli were paired with corresponding plastic sheets. The plastic sheets (one white and one black) were the same size as the rear walls of each goal box and made the brightness task more distinguishable. The stimuli were altered from one goal box to the other according to a balanced irregular sequence of trials (Gellerman, 1933). When the Subjects achieved a learning criterion of ten successive correct responses in any two successive 40 trial sessions, the next phase of brightness testing began. This phase involved testing the cats to the same criterion of learning with only the black and white upright stimuli present. The positive stimulus (S+) was black for two

of the Subjects and white for the other two. The Subjects were given 80 trials per day in two 40 trial sessions. Re-run self-correction trials^{*}, as described by Webster (1972), were administered on trials 10-15 and 25-30 of every 40 trial session. A response was defined as entry of one-half of the body of the Subject into a goal box. The pork kidney reward was placed behind the correct stimulus and was out of view of the Subjects until an entry into the goal box was performed and the back of the positive stimulus was inspected.

The four Subjects adapted to the WCTA were given three phases of adaptation before brightness testing was begun. The Subjects were given 100 trials of simple reach during which one foodwell of a three choice test tray was baited by putting kidney on the lip of the tray. In successive steps the Subjects were gradually required to retrieve the reinforcement from the foodwell. This phase was followed by requiring the Subjects to retrieve the reinforcement from one of two foodwells of a two-choice test tray. The final phase of this part of the adaptation involved block displacement training. This phase involved training the Subjects to displace a grey block covering one of two foodwells

^{*}The Subjects were re-run on each incorrect trial and were allowed to correct their responses. They were given the next trial after they had responded correctly on the re-run trial.

of a two-choice test tray.

Following these phases of adaptation the Subjects were trained on a brightness discrimination using the same upright squares with which the Subjects in the Grice Box were trained. The stimuli were displayed on a grey two-choice test tray, with the foodwells being 12 inches apart. Determination of which foodwell was covered by S+ (either black or white) was made according to balanced irregular sequences of trials (Gellerman, 1933). The white upright was the positive stimulus for the two Subjects and the black was positive for two. The Subjects received a total of 100 trials per day in two 50 trial sessions. The criterion for learning was 10 successive correct responses within any two successive sessions. A response during any one trial was defined as displacement of either stimulus to the extent that any portion of the outer edge of the foodwell was exposed. The paw or paw sequences used to push the block and retrieve the kidney was recorded on each trial. Re-run self-correction was also used in the WGTA during trials 13-18, 25-30 and 37-42 of each 50 trial session.

Surgical Procedure

Following adaptation to their respective apparatus, all the Subjects had their optic chiasm surgically sectioned

along the midline using a transbuccal approach described in detail by Downer (1958) and Webster (1972). The Subjects were anaesthetized with Sodium Pentobarbital (38-40 mg/kg) throughout surgery with supplementary doses being administered as needed. The surgical procedure involved placing the Subject in an upside down position with the tongue and lower jaw tied away, exposing the oralpharynx. An incision was then made through the soft upper palate exposing the nasopharynx and mucosa. The mucosa was cut with an I-shaped incision with the flaps of the incision being retracted against the lateral bones of the nasopharynx. It should be noted that all the surgery from the sectioning of the mucosa on was performed with the aid of an operating microscope. The vomer and sphenoid bones which lay over the mucosa were then thinned with the use of a drill and subsequently picked away with a dental pick. This exposed the sphenoid sinus, a cartilagenous septum within the sinus and the cranium. This septum was removed and the cranium thinned with a fine dental drill. The cranium was then picked away leaving the dura exposed. Following cutting the dura in a inverted Y-shape and retracting it, a vein lying under the chiasm was retracted and the chiasm was sectioned along the midline.

Following surgery each Subjects was given 100,000 IU of Pencillin and was observed until recovery was assured. Surgical conditions as aseptic as possible were maintained throughout each operation.

Re-adaptation

After recovery from surgery the Subjects were re-adapted to their respective apparatus. The Subjects were re-trained to criterion on the simultaneous brightness discrimination task using the same stimuli as were used during the preoperative adaptation. Only the upright stimuli were present during this phase of training. The procedure was the same as in the pre-operative apparatus adaptation in terms of correction trials, response definition and stimuli presentation. The S+ for each Subject during this phase was the same as it was during preoperative apparatus adaptation.

Occluder Adaptation

During the above re-adaptation phase both groups were adapted to having black opaque contact occluders placed over the cornea (Mishkin, Gunkel and Rosvold, 1959). The Subjects were placed in a restraining box, the cornea was temporarily anaesthetized with Opthaine solution, and the occluder, well soaked with contact

lens wetting solution, was placed over the cornea. The occluder was left in place for three or four minutes and was then removed. The same procedure was then used for the other eye. Each session of occluder adaptation involved alternate placement of the occluder until each eye had been covered twice.

Acquisition and Interocular Transfer Testing

Following recovery from surgery and apparatus re-adaptation the monocular acquisition and transfer phases of the experiment began. The procedure during this phase was identical for both groups other than apparatus used and number of training trials per session. The stimuli were one pair of non-mirror-images and one pair of lateral mirror-images. The non-mirror-image were upright forms painted black and measured four inches wide by three inches high by one inch thick and were mounted on black Plexiglas bases. The lateral mirror-image pair were also upright forms painted black, having the same dimensions as the non-mirror-image pair. Fig. 5 shows scaled illustrations of the stimulus pairs. Throughout the procedure the Subjects in both groups were balanced for problem tested first (mirror-images or non-mirror-images), eye trained first and whether the retraining following transfer testing of the other eye consisted of re-learning or reversal learning. Table 1 outlines the procedure for both groups.

Figure 5 Scaled illustrations of the mirror-image (upper) and the non-mirror-image pair of form stimuli.

Table 1

Major Phases of the Experimental Design
for Testing in the Grice Box and WGTA

Initial Acquisition-Grice Box

The four Subjects received 25 trials of nondifferential reward with their assigned stimulus pair in order to assess any preferences. All testing was against preference.

The first problem for two Subjects was the lateral mirror-image problem and for the other two Subjects the non-mirror-image problem. Within each pair of Subjects one had its left eye occluded and the other had its right eye occluded.

The stimuli were presented simultaneously with the position of S+ and S- being varied according to a balanced irregular sequence of trials. Re-run self-correction was allowed on trials 10-15 and 25-30 of each 40 trial session. Subjects received a total of 80 trials per day in two 40 trial sessions. The daily sessions were separated by five to six hours. Criterion performance was defined as ten successive correct responses during any two consecutive testing sessions. Subjects received their daily food rations following the second session of each day. Deprivation procedures were only used in cases when the Subject refused to respond in the apparatus.

Interocular Transfer Testing-Grice Box

Following attainment of criterion by the Subjects on the first problem (mirror-images or non-mirror-images) the occluder was switched so that the previously untrained eye

was exposed to the testing situation. The Subjects were then retrained to criterion on the simultaneous brightness task using the same procedure previously described¹. This phase was followed by the initial test of interocular transfer. This involved two 12 trial sessions during which each stimulus was baited with pork kidney and the position of the stimuli was varied according to balanced irregular sequences. Choice behaviour and response latencies were recorded on each trial. Measurement of response latencies involved activating a timer once the Subject left the start box and stopping it as soon as the defined response occurred.

Upon completion of the 24 trials with nondifferential reward the Subjects were retrained to criterion with the stimulus pair using the same procedure used during initial acquisition. Within each pair of Subjects trained with the mirror-image stimuli and the non-mirror-image stimuli one Subject was retrained with the same S⁺ and S⁻. The other Subject in each group was retrained to criterion with S⁺ and S⁻ being reversed from that during acquisition.

Once this second eye had reached criterion training with the second pair of stimuli began. The Subjects that were

¹The reason for training this eye on the brightness task was to eliminate position habits and to allow the Subject a period of adaptation with this eye.

trained initially with the non-mirror-images were then trained with the mirror-images and the Subjects trained initially with the mirror-images were then trained with the non-mirror images. The order of testing hemispheres of each Subject was also reversed. The procedure followed for acquisition and interocular transfer testing with the second pair of stimuli was identical to that just described for the first pair.

Acquisition and Interocular Transfer Testing-WGTA

The four Subjects assigned to the WGTA were tested for acquisition, transfer and re-acquisition in a sequence identical to that used for the Grice Box (see Table 1). The procedures followed were essentially the same as those described in the previous section. The Subjects were given the same sequence of stimulus presentations as those Subjects in the Grice Box, and variables such as eye trained first and reversal or non-reversal retraining after interocular transfer testing were balanced.

Test of Response Differentiation

Following the completion of transfer testing with the second pair of stimuli each Subject was retrained to criterion with the mirror-image stimuli. The eye last exposed to the mirror-images was the eye retrained and the same positive and negative reinforcement contingencies were maintained.

The actual test involved 200 trials, 20 of which required a Subject to respond to a pair of stimuli the same as the mirror-image S+ the Subject was last exposed to during reversal or re-acquisition training (ie. < vs < or > vs >). Each Subject also received 20 presentations of a pair of stimuli the same as the Subject's previous S- (ie. < vs < or > vs >). The two pair of stimuli were randomized within every block of five trials and were also randomized for order of presentation. Response latencies were recorded during each of the 40 critical test trials in both apparatus. In the event a Subject did not respond within a 15 second interval the trial was terminated and the Subject received a 15 second response latency score for that trial. All other procedures were the same as the phases described above.

RESULTS

Histology

Subsequent to the last stage of testing all the Subjects were perfused with normal saline and then 10% formalin. Their brains were then removed and embedded in Celloidin. Frontal sections through the chiasm, 40 μ were made and every fifth section was stained using the Weil method. The prepared slides were then examined microscopically to determine if the sections of the optic chiasm were complete. Evidence of crossed fibres at the chiasm was used as the criterion for incomplete chiasm section and rejection of the Subjects from the experiment.

Microscopic analysis of the histological slides indicated the presence of some crossed myelinated fibres in the anterior notch of the optic chiasm of one Subject. The data of that Subject has been eliminated from the experiment. The optic chiasms of the other Subjects were completely split along the midline. These results confirmed visual observations of chiasm sectioning by the Experimenter during the actual surgery. Therefore, the results are based on four Subjects tested in the Grice Box and four Subjects tested in the WGTA.

Acquisition of Discrimination--Grice Box

The Subjects trained in the Grice Box required a mean of 173 errors to attain criterion with the mirror-images and a mean of 189 errors to attain criterion with the non-mirror-images. Statistical analysis revealed that the difficulty in discriminating the two pairs of stimuli was not significantly different ($t = .25$, $df = 6$). The difference between whether the mirror-images were acquired before or after the non-mirror-images also proved to be non-significant ($t = .18$, $df = 2$ and $t = .89$, $df = 2$).

Transfer Test--Grice Box

Subsequent to each phase of acquisition (mirror-images or non-mirror images) each Subject was retrained to the brightness criterion with the eye that was occluded during acquisition. The Subjects were then given 24 trials of tests with nondifferential reward with the same stimulus pair used during acquisition. This was the first test of interocular transfer of the untrained hemisphere and always preceded retraining with the reinforcement contingencies either reversed or the same (refer to Table 1). Table 2 indicates the responses made by each Subject on each transfer problem. Although no Subjects preferred the previous negative stimulus and three responded more times to the previous positive stimulus, the difference was not significant for the non-mirror images ($\chi^2 = 2.04$, $df = 1$, $p < .20$) or the mirror-

Table 2

Number of Responses and Mean Response Latencies to the
Positive and Negative Stimuli used during Acquisition
by each Subject on Tests of Interocular Transfer
with Nondifferential Reward in the Grice Box

Subject	Choice Behaviour				Response Latency (in sec.)			
	MI ^a		NMI ^b		MI		NMI	
	S+	S-	S+	S-	S+	S-	S+	S-
Pav	12	12	12	12	2.2	3.3	2.0	2.8
Topaz	14	10	12	12	6.0	6.6	2.1	2.8
Gary	12	12	13	11	1.5	1.7	2.8	4.2
Sartre	12	12	18	6	1.5	2.2	1.1	1.3

^aMI: Mirror-Image problem

^bNMI: Non-Mirror-Image problem

images $\chi^2 = .166$, $df = 1$, $p < .70$). These results cannot be considered evidence for a veridical transfer effect. It should be mentioned that Berlucchi and Marzi (1970) using a similar test of interocular transfer with split-chiasm cats obtained results similar to those found here. Unlike the Berlucchi and Marzi test of interocular transfer the present test used response latencies as an additional dependent measure of interocular transfer. As indicated in Table 2, despite strong positional responding, each Subject in the Grice Box responded quicker to the S+ than the S-. This would indicate a preference for the previous S+ and support veridical rather than paradoxical interocular transfer of mirror-image stimuli.

Reversal and Reacquisition--Grice Box

Fig. 6 illustrates the mean errors to criterion for reacquisition and reversal of the two pairs of stimuli.

For both problems, reacquisition was not as difficult as reversal, the mean errors for the mirror-image problem being 52.5 and 251.5 respectively and the mean errors for the non-mirror-image problem being 42.5 and 385.5 respectively. Table 3 summarizes these comparisons and contains the statistical analysis.

Figure 6 Mean Errors to Criterion for Relearning and Reversal of the Non-Mirror-Images and Mirror-Images in the Grice Box

Table 3

Mean Errors to Criterion for Reversal and
 Reacquisition of the Mirror-Image
 and Non-Mirror-Image Problems
 in the Grice Box

Stimuli	Mean Errors to Criterion		<u>t</u>
	Reversal (n)	Reacquisition (n)	
Mirror-Images	251.5 (2)	52.5 (2)	3.38*
Non-Mirror-Images	385.5 (2)	42.5 (2)	13.09**

* $p < .10$

** $p < .01$

The degree of interocular transfer for the above comparisons was also assessed by calculating savings scores. These were calculated by subtracting the errors of the second eye from the first eye training errors, dividing that sum by the sum of the first and second eye training errors and then multiplying that figure by 100. Table 4. contains the percent savings for each Subject on each problem. All Subjects showed positive savings on reacquisition when compared to the savings for reversal retraining for both pairs of stimuli. This finding is definitely indicative of veridical transfer for both the mirror-image and non-mirror-image stimuli. Table 5. shows the comparisons of mean percent savings scores for reacquisition and reversal of the stimulus pairs as well as associated t-test scores. These data are also illustrated graphically in Fig. 7.

Summary of Grice Box Results

The data for the Subjects tested in the Grice Box indicated that interocular transfer of mirror and non-mirror-image pairs of form stimuli is veridical and not paradoxical. In common with the findings of Berlucchi and Marzi (1970), the transfer tests with nondifferential reward proved to be inadequate. However, the response latency data obtained during the transfer tests did support a preference for the previous positive mirror-image stimulus. In agreement with Berlucchi and Marzi (1970), the comparisons between mean errors and percent savings indicated

Table 4

Percent Savings of Individual Subjects for
 Reacquisition and Reversal of Mirror-Images
 or Non-Mirror-Images in the Grice Box

Subject	Reversal		Reacquisition	
	MI ^a	NMI ^b	MI	NMI
Sartre	+1.02%			+68.21%
Gary	-15.13%			+31.56%
Pav		-26.31%	+80.24%	
Topaz		-12.87%	+25.09%	

^aMI: Mirror-Images

^bNMI: Non-Mirror-Images

Table 5

Comparisons of Mean Percent Savings of Errors for
 Reacquisition and Reversal of Mirror-Images
 and Non-Mirror-Images in the Grice Box

Stimuli	Reversal (n)	Reacquisition (n)	<u>t</u>
Mirror-Images	-7.05% (2)	+53.05% (2)	2.06*
Non-Mirror-Images	-19.60% (2)	+49.85% (2)	3.56**

* $p < .20$

** $p < .10$

Figure 7 Mean Percent Savings of Errors for Re-acquisition and Reversal of the Mirror-Images and Non-Mirror-Images in the Grice Box

that reacquisition of the original task was facilitated and that reversal learning was retarded. These results would indicate that the type of interhemispheric information conveyed from the hemisphere first trained was not altered in such a way that would confuse relearning in the second hemisphere. This is contrary to the theory proposed by Noble (1968).

Acquisition of Discrimination -- WGTA

The Subjects trained in the WGTA required 242.3 mean errors to attain criterion with the mirror-images and 243 mean errors to attain criterion with the non-mirror-images. Statistical analysis revealed that the difficulty in discriminating the two pairs of stimuli was not significantly different ($t = .11$, $df = 6$). The difference between whether the mirror-images were acquired before or after the non-mirror-images also proved to be non-significant ($t = .30$, $df = 2$; and $t = 1.16$, $df = 2$).

Transfer Test--WGTA:

Unlike in the Grace Box, the transfer test of 24 nondifferential reward trials proved to be a sensitive indicator of interocular transfer in the WGTA. All four Subjects responded to S+ more frequently than to S- for both the mirror-image and non-mirror-image transfer tests. Table 6 indicates the responses made by each Subject on each of their transfer tests.

Table 6

73.

Number of Responses and Mean Response Latencies to the
Positive and Negative Stimulus used during Acquisition
by each Subject on tests of Interocular Transfer with
Nondifferential Reward in the WGTA

Subject	Choice Behaviour				Response Latency (in sec.)			
	MI ^a		NMI ^b		MI		NMI	
	S+	S-	S+	S-	S+	S-	S+	S-
Xerces	20	4	16	8	1.9	1.5	3.2	3.8
Olga	18	6	17	7	11.6	12.9	15.0	20.8
Q-Tip	14	10	17	7	3.4	3.6	2.9	2.8
Heathcliff	18	6	17	7	1.7	2.7	2.0	2.6

^aMI: Mirror-Image Problem

^bNMI: Non-Mirror-Image Problem

Statistical analysis indicated that 67 responses to the positive non-mirror-image stimulus was statistically significant ($\chi^2 = 15.04$, $df = 1$, $p < .001$) when compared to 29 responses to the negative non-mirror-image stimulus. The transfer test for mirror-images indicated that 70 responses to the positive stimulus was significantly greater ($\chi^2 = 20.18$, $df = 1$, $p < .001$) than 26 responses to the negative mirror-image. These results indicate substantial support for veridical transfer through the interhemispheric pathways of both mirror and non-mirror image form stimuli.

It should be noted that although response latencies to S+ and S- are included in Table 6 they are difficult to interpret because of the imbalance of choice behaviour by the Subjects to the previous S+ and S- stimuli.

Reversal and Reacquisition--WGTA

Fig. 8 illustrates the mean errors made during the reacquisition and reversal of the stimulus pairs in the WGTA.

Reacquisition of both pairs of stimuli was substantially easier than reversal. Reversal of the mirror-images required a mean of 415.5 errors as compared to a mean of 18.5 errors for reacquisition. The non-mirror-image stimuli were reacquired in an average of 74 errors while reversal required an average of 117 errors. Table 7 summarizes the

Figure 8 Mean Errors to Criterion for Relearning and Reversal of the Mirror-Images and Non-Mirror-Images in the WGTA

Table 7

Mean Errors to Criterion for Reversal and Reacquisition
 of the Mirror-Image and Non-Mirror-Image
 Problems in the Grice Box

Stimuli	Mean Errors to Criterion				
	Reversal		Reacquisition		<u>t</u>
		(n)		(n)	
Mirror-Images	415.5	(2)	18.5	(2)	7.53**
Non-Mirror-Images	117.0	(2)	74.0	(2)	1.76*

* $p < .20$

** $p < .02$

statistical analysis of the mean errors to criterion for each of the relearning phases. Fig. 8 illustrates the differences between reacquisition and reversal.

Table 8 shows the percent savings for errors made by each Subject in the WGTA during reversal or reacquisition with the stimuli and Table 9 summarizes the statistical analyses for these comparisons. The mean percent savings scores are in agreement with the results found for mean errors to criterion. In every case, reacquisition of both stimulus pairs was easier than reversal. These results, like those found in the Grice Box, are consistent with veridical transfer. Therefore, unlike Noble's (1968) split-chiasm monkeys, split-chiasm cats tested in a similar apparatus and with similar stimulus forms do not show paradoxical transfer.

The differences between the positive and negative percent savings scores are presented graphically in Fig. 9.

Summary of WGTA Results

When considering the dependent measures of interocular transfer (mean errors, percent savings and transfer test) in the WGTA, the results support veridical rather than paradoxical interhemispheric transfer. Evidence for veridical transfer is most significant when considering the results of the transfer test and comparisons of mean percent savings scores for errors.

Table 8

Percent Savings of Individual Subjects for Reacquisition
and Reversal of Mirror-Images and Non-Mirror-Images
in the WGTa

Subject	Reversal		Reacquisition	
	MI ^a	NMI ^b	MI	NMI
Xerces		-18.34%	+69.53%	
Olga		+17.53%	+63.63%	
Q-Tip	-29.64%			+46.62%
Heathcliff	-15.98%			+60.13%

^aMI: Mirror-Images

^bNMI: Non-Mirror-Images

Table 9
 Comparisons of Mean Percent Savings of Errors for
 Reacquisition and Reversal of Mirror-Images
 and Non-Mirror-Images in the WGTA

Stimuli	Reversal (n)	Reacquisition (n)	<u>t</u>
Mirror-Images	-22.75% (2)	+66.50% (2)	10.13**
Non-Mirror-Images	-.42% (2)	+53.35% (2)	2.8*

* $p < .20$

** $p < .01$

Figure 9 Mean Percent Savings of Errors for Re-acquisition and Reversal of the Mirror-Images and Non-Mirror-Images in the WGT

Results of the Response Differentiation Test

The results of the test for response differentiation indicated strong support for veridical transfer in both pieces of testing apparatus and also that the Subjects were performing a left-right discrimination and had not transformed the mirror-image problem into a response differentiation task along the lines suggested by Beale and Corballis (1968). Table 10 summarizes the differences between response latencies to an S+ pair ($\langle \langle$) and an S- pair ($\rangle \rangle$) of stimuli.

The Subjects in both pieces of testing apparatus responded faster when the S+ pair of stimuli was presented than when the S- pair was presented. Observations made by Experimenter at the time of testing indicated that Subjects were "confused" when presented with the pair of S- stimuli. In the majority of cases when this confusion was observed the Subjects tended to shift from goal box to goal box in the Grice Box and from foodwell to foodwell in the WGTA. This shifting behaviour was a major factor for the longer response latencies to the S- pair. In fact, two of the Subjects refused to respond within the 15 second response criterion (Xerces twice and Olga six times). Such refusal to respond never occurred when the S+ pair was presented. During the test trials when the S+ pair was presented the Subjects performed in

Table 10

Mean Response Latencies to the S+ and the S- Pair
in the Grice Box and the WGTA during the
Test of Response Differentiation

Apparatus	Mean Response Latency (in seconds)		<u>t</u>
	S+	S-	
Grice Box	1.95	3.60	6.60**
WGTA	1.67	5.84	3.48*

*p < .05

**p < .01

the same manner as during acquisition phases of the experiment. The Subjects simply responded to either positive stimulus.

The different mean response latencies are illustrated in Fig. 10.

Summary of the Results

Interocular transfer of mirror-image and non-mirror image form stimuli via the interhemispheric pathways of split-chiasm cats is veridical rather than paradoxical. This veridical transfer effect has been found to occur in both the Grice Box and WGTA. Fig. 11 summarizes the major results of the experiment.

Group results in the Grice Box indicated substantial support for veridical transfer. When considering mean errors to criterion, the comparisons between reacquisition and reversal of the two pairs of stimuli has shown that relearning in the second hemisphere is facilitated when the reinforcement contingencies remain the same as during initial acquisition and that relearning is considerably retarded when the reinforcement contingencies are reversed. Group comparisons on mean percent savings scores are consistent with the results found with mean errors. The 24 trials transfer test with nondifferential reward did not indicate support for either veridical or paradoxical transfer in spite of the fact three Subjects did show a slight preference for the previous S+

Figure 10 Mean Response Latencies to the S+ and S- Pairs in the Grice Box and WGTA During the Test of Response Differentiation

WGTA 85.

Figure 11 Summary of the Major Results in the WGTA and the Grice Box

2 2
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and none of the Subjects indicated a preference for the previous S-.

The results obtained in the WGTa also indicated veridical transfer of mirror and non-mirror-image form stimuli. Like in the Grice Box, maintaining the same reinforcement contingencies during testing of the untrained hemisphere facilitated acquisition while reversal resulted in no facilitation at all. The same comparisons for mean percent savings scores are in support of the mean errors results. The 24 trial nondifferential reward transfer test in the WGTa revealed strong support for veridical interocular transfer of both mirror and non-mirror-image stimuli. The previous positive mirror-image was highly preferred over the previous negative mirror-image stimulus as was the previous positive non-mirror-image preferred over the previous negative non-mirror-image.

The test of response differentiation yielded data showing that the Subjects in both pieces of testing apparatus had in fact learned to discriminate the lateral mirror-image pair on the basis of their left-right orientation. If in fact the Subjects had learned to discriminate the stimuli on the basis of pair configurations (ie. $><$, go right and $<>$, go left) preferences should have been greatly

disrupted when << or >> were presented. However, during the present test of response differentiation the Subjects did show fast responding when presented with the positive pair and confusion when presented with the negative pair.

DISCUSSION

The major objective of the present research was to attempt to clarify the nature of interhemispheric transfer of mirror-image and non-mirror-image form stimuli in split-chiasm cats. The questions revolved around Noble's (1968) findings of paradoxical transfer of three-dimensional form mirror-image stimuli in split-chiasm monkeys tested in a WGTA, and Berlucchi and Marzi's (1970) conflicting findings of veridical transfer of transilluminated mirror-image pattern stimuli in split-chiasm cats tested in a Grice Box. The research design attempted to resolve these different findings by using parameters that would indicate whether or not such differences were related to stimuli, behavioural testing apparatus, or species differences. The procedures used to determine whether interocular transfer was paradoxical or veridical included a 24 trial test of preference, a relearning and reacquisition phase and a test of response differentiation. The results indicated that interhemispheric transfer of mirror-image form stimuli in split-chiasm cats tested in both a Grice Box and a WGTA was veridical rather than paradoxical.

The 24 trial transfer test with nondifferential reward supported veridical interocular transfer in both apparatuses.

During this test all the Subjects tested in the WGTA indicated a strong preference for the positive (used during acquisition) mirror-image stimulus indicating that the untrained hemisphere received the same information during learning as the hemisphere originally trained.

The 24 trial nondifferential reward transfer test in the Grice Box, in terms of choice behaviour, indicated that only one of the four Subjects did not show complete positional responding. This Subject responded to S+ on 14 of the 24 test trials. The results found in the present transfer test are similar to those of Berlucchi and Marzi (1970) who, using a similar test, also failed to detect differential choice behaviour in a Grice Box. The test used in the present study was, however, more powerful than that used by Berlucchi and Marzi in that response latencies were recorded on all 24 trials. All 4 Subjects responded consistently faster when the S+ as opposed to the S- stimulus was in their preferred goal box. This would indicate that despite the lack of preference in terms of choice behaviour, the Subjects showed veridical transfer as reflected in response latencies.

The findings of Warren and McGonigle (1969) concerning the use of nondifferential reward during tests for transfer and

generalization may be an explanation for the poor choice behaviour during the 24 trial transfer test in the Grice Box of the present research, and that of Berlucchi and Marzi (1970). Warren and McGonigle found that discriminations tend to become disrupted when testing with differential reward is changed to testing with non-differential reward. The animals develop strong position habits which of course interfere with the assessment of stimulus preferences.

In common with Berlucchi and Marzi's (1970) study, the results of the present experiment have shown that the most effective means of determining the type of inter-hemispheric transfer in split-chiasm cats was an analysis of reversal and reacquisition differences when the second eye is tested subsequent to the first eye. Veridical transfer is indicated by facilitated reacquisition and retarded reversal learning, whereas paradoxical transfer is indicated by retarded reacquisition and facilitated reversal learning.

The reversal and reacquisition data of the present experiment indicated that reacquisition of the mirror-images was facilitated while reversal learning was retarded. When considering mean errors and mean percent savings scores to criterion, all the comparisons between reacquisition and

reversal of the two pairs of stimuli indicated veridical interhemispheric transfer in split-chiasm cats tested in both the Grice Box and WGTA.

Noble's (1968) major tests of interocular transfer of mirror-image stimuli involved testing the untrained hemisphere with nondifferential reward. He did not have any relearning tests of interocular transfer such as was used in the present study and in the Berlucchi and Marzi (1970) study. In view of Warren and McGonigle's (1969) discussion of the use of nondifferential reward, an interocular test using reversal and reacquisition for assessing interhemispheric transfer of mirror-images should be considered in future research using split-chiasm monkeys.

In reviewing the literature only one instance (Sutherland, 1963) was found where the experimenter tested cats for the possibility that mirror-image discrimination may have been a result of response differentiation. Subsequent to criterion performance with mirror-image obliques (/vs\), Sutherland (1963) presented each of his four normal cats with the same stimuli in a successive discrimination paradigm. This enabled Sutherland to determine whether or not his Subjects had learned to discriminate the obliques

on the basis of their left-right orientation or because of the total configuration ($\langle \rangle$ vs $\langle \rangle$) created by the stimuli. Sutherland's Subjects showed immediate transfer from the simultaneous to the successive discrimination tasks. This allowed Sutherland to conclude that his Subjects had indeed learned to discriminate left and right oriented oblique rectangles.

The present test of response differentiation with split-chiasm cats is in direct consort with Sutherland's findings. When comparing mean response latencies for responding to the previous positive and negative stimulus, it was found that the Subjects in both apparatus responded faster to the previously positive mirror-image than to the previously negative mirror-image.

The present study and Sutherland's (1963) study have indicated that cats, both normal and chiasm sectioned, do not discriminate lateral mirror-images on the basis of response differentiation ($\langle \rangle$, go right or $\langle \rangle$, go left). No such study has yet been reported for the split-chiasm monkey discriminating lateral mirror-images.

In hand with the behavioural results just described, the theoretical explanations offered by Berlucchi and Marzi.

concerning the type of indirect visual information a hemisphere receives via interhemispheric callosal fibres was supported. The results of the present study with cats are not consistent with Noble's hypothesis of a homotopic interconnecting system via the corpus callosum between the two visual cortices as being a major factor for paradoxical results with split-chiasm monkeys tested in a WGTA.

The results found in the present study would indicate that the different types of interocular transfer of lateral mirror-images found for split-chiasm cats and monkeys is not related to type of testing apparatus or discriminanda used. Split-chiasm cats tested with form stimuli in a WGTA show veridical transfer of mirror-image stimuli. The results of the study are supported by all the dependent measures used to determine interocular transfer of mirror-image form stimuli in split-chiasm cats.

However, the data do suggest a species difference between cats and monkeys insofar as interocular transfer of lateral mirror-images is concerned.

A possible explanation for the differences between cats and monkeys on tests of interocular transfer of mirror-images may be attributed to the divergent evolution of neocortex in these species as suggested by Diamond and Hall

(1969). However, it is not probable that these species are so different in their evolutionary development as to indicate a interhemispheric interconnecting system as different as suggested by the results of the present study. In fact, Berlucchi (1972) cites electrophysiological and anatomical research indicating that the callosal connections of the visual cortices in cats, monkeys, rabbits, and rats are essentially the same.

There are however, other factors that should be considered when testing different species on tests of interocular transfer of mirror-image stimuli. Variables such as response strategies and utilization of other sensory modalities may differentiate how different species may acquire left-right discriminations and how such discriminations may transfer from one hemisphere to the other during subsequent tests. The following theoretical discussion will consider some of these variables.

There are many different factors that experimenters should consider when using interocular transfer tests of visual stimuli in split-chiasm subjects. Some such factors could be related to the involvement of the somatosensory systems. During initial acquisition in a transfer test

paradigm, pushing stimuli displayed on a test tray may provide Subjects with cues about the learning situation that can be readily transferred to a transfer test relearning phase of an experiment. Somatosensory cues during original learning could be received from hand or paw manipulation of discriminanda, running from a start box to the goal box or shifting the body and/or head from one stimulus to the other in a two-choice simultaneous discrimination task. The type of information just described could readily transfer to a relearning situation despite the fact that the visual information may not as readily transfer from the original learning situation. This effect during testing may influence the degree to which any particular Subject will re-establish responding to the appropriate stimulus. In other words when considering the transfer of visual information from one situation to another, experimenters must also consider the transfer of stimuli via other sensory modalities.

The above is directly related to whether or not lateral mirror-image information relayed via other sensory systems may be paradoxical and override any veridical effects shown by the visual system. A possible example of this could be Noble's work where there was tactual information from the form stimuli available to his monkeys. Ettlinger and Elithorn (1962) have shown that monkeys required to tactually discriminate

lateral mirror-image stimuli (C vs C) with one hand showed paradoxical transfer when tested with the other hand. If such were the case for the Subjects used by Noble, he actually may have found a mixed effect of weak veridical transfer in the visual system and a strong paradoxical effect in the sensory-motor system. This could have resulted in the paradoxical information dominating the veridical information from the visual system. In discussing handedness in his experiment, Noble (1968) has stated that: "Although there was a tendency for the hand contralateral to the open eye to be more frequently used than the other there is no evidence that the hand used affected the results, (p. 131)".

Cats would not get the same amount of tactile feedback by simply pushing a block as a monkey which may actually handle the block as well as push it back to expose the foodwell. The above may be one explanation for the type of transfer that Noble found versus the type of transfer Berlucchi and Marzi have found. Berlucchi and Marzi's cats received no tactile information at all due to the fact that they were required to discriminate transilluminated stimuli.

Another important factor in discussing the transfer of stimuli from one situation to another is the manner in

which the Subject has learned to respond. Scanning the stimuli during simultaneous discrimination in a WGTA may readily transfer to a relearning (transfer test) phase of the experiment. The development of such a behaviour during acquisition may facilitate the rate of relearning. Some Subjects tend to closely inspect one stimulus at a time, whereas, others tend to sit back in the response compartment and scan the discriminanda with a sweeping motion of the head. In the Grice Box, response strategies also differ for individual subjects. Some Subjects respond very rapidly during the initial phase of acquisition and then over time begin to slow down and inspect the stimuli from the choice compartment. In other cases Subjects tend to develop this latter response strategy quicker and rather than run rapidly from start box to goal box, they stop in the choice area and inspect the stimuli before entering a goal box. Therefore in the WGTA we have instances of passively sitting back in the response compartment and scanning the stimuli by shifting the head from left to right as well as a situation of more active scanning where the Subject approaches a stimulus, shifts to the other, then shifts back and eventually responds to either the positive or negative stimulus. In the Grice

Box the situation is similar in that scanning can be active as well as passive. The Subject in most cases must go from goal box to goal box in order to scan the stimuli before responding. Those Subjects that tend to respond very rapidly in the Grice Box during initial phases of training begin to slow down and inspect the stimuli subsequent to a series of sessions during which correction trials alter their running speed. At this point the Subjects begin to learn to inspect both goal boxes rather than run rapidly from the start box to either goal box in a random manner. It is at this point that actual discrimination learning appears to develop.

A good illustration of how degree and type of transfer can be influenced by the manner in which a Subject responds can be found with the behaviour of Sartre. When considering savings, Sartre showed a slight paradoxical effect with the mirror-images. This Subject required 290 errors to reverse the mirror-images as compared to 296 errors during acquisition, (see Table 4). In terms of percent savings (1.02%) this Subject showed no transfer. This was a result of either the type of information received from the untrained hemisphere or other reasons related to the experimental situation. The other Subject (Gary) in the

mirror-image reversal group tested in the Grice Box showed -15.13% savings.

One possible explanation why Sartre may have shown this slight paradoxical effect with the mirror-images (first pair tested with) is related to the manner in which he responded during acquisition. Unlike the other three Subjects tested in the Grice Box, Sartre responded very rapidly to either goal box once the door to the start box and the Plexiglas barrier were raised. During initial stages of acquisition the Subject ran into the barrier on every trial and did not stop to inspect the stimuli. Over sessions of acquisition training this rapid running behaviour decreased, and the Subject began to inspect the stimuli in each goal box.

When compared to the other Subjects, Sartre made over twice as many errors to reach criterion with the mirror-images than the other three subjects. Sartre required 296 errors while the other Subjects required an average of 132 errors (see Appendix B for individual trials and errors). Therefore, the shift from rapid, non-attentive responding to slower running and inspection of the stimuli may be reflected in the reversal phase of transfer testing for this subject.

More recently, Hamilton, Tieman and Winter (1973) have reported some research that is directly related to

the present discussion. Hamilton et al trained split-chiasm monkeys to perform a successive discrimination of asymmetrical stimuli ($\cup$ vs $\cap$ and $<$ vs $\times$). The Subjects were trained in an apparatus that prevented head movements and allowed the experimenter to control which eye or hand was to be tested. Their results indicated that their monkeys fixated the centre of a stimulus and did not scan even though scanning would have been beneficial. As a result of blindness in both temporal visual fields the stimuli were very difficult to discriminate when the left eye was open. The rotated stimuli would appear as $\cup$ vs $\cup$ and $<$ vs $<$ rendering them almost impossible to discriminate. Discrimination of the same stimuli was easy for the left eye when the stimuli were rotated 180° (ie. $-$ vs $>$ and $-$ vs $>$). The same results were found when the right eye was tested.

Hamilton, Tieman, and Winter (1973) have offered an explanation for Noble's (1968) paradoxical transfer results found with lateral mirror-images. They offer the explanation making the assumption that Noble's monkeys did fixate to the centre of the stimuli. They argued that discrimination of $<$ vs $>$ will result in paradoxical transfer since the arrows will appear as this $<$ vs $>$ when viewed with the right eye and when the left eye is tested

for transfer these same stimuli will appear as such, $\angle$ vs $\rangle$. Therefore, the discrimination to be performed is no longer one of lateral mirror-images, but rather a simple pattern discrimination. Thus, if $\angle$ was the positive stimulus and $\rangle$ was the negative stimulus for the right eye, $\rangle$ would become the positive stimulus for the left eye and $\angle$ the negative stimulus. The results of such an experiment would indicate paradoxical transfer of lateral mirror-image stimuli. Contrary to Hamilton's monkeys, Noble's monkeys were unrestrained and were required to perform simultaneous form discriminations. However, Lehman and Spencer, (1973) have demonstrated that split-chiasm monkeys with restricted head and body movements tested on simultaneous discrimination in a modified WGTa also fixate to the centre of stimuli, thus restricting their view to the contralateral half of the discriminanda. Hamilton et al emphasize the importance of stimulus selection when performing research with split-chiasm animals.

In a further test of interocular transfer of mirror-image stimuli in split-chiasm monkeys, Hamilton,

Tieman, and Brody (1973) have confirmed the Hamilton, Tieman and Winter (1973) findings just discussed. This study involved requiring normal and split-chiasm monkeys to match from sample two pairs of transilluminated pattern stimuli presented in left-right ($<$ vs $>$ and $\vdash$ vs $\dashv$) and up-down ($\vee$ vs $\wedge$ and $\perp$ vs $\top$) orientations. Following extensive training with non-mirror-images the mirror-image stimuli were presented to the Subjects with a system of polarized lenses that allowed the Experimenter to present the sample to one eye and the two-choice stimuli to the other eye. The normal Subjects performed correctly on all the tests while the split-chiasm Subjects were inconsistent with the left-right problems. The split-chiasm Subjects performed similar to the normals on all the up-down matching to sample tasks. The first left-right problem ($<$ vs $>$) resulted in paradoxical transfer in two of three Subjects tested. All three Subjects showed veridical transfer when tested with the second left-right problem ($\vdash$ vs $\dashv$). Hamilton *et al* (1973) rejected Noble's hypothesis as an explanation for the paradoxical transfer their Subjects had shown with the left-right stimuli. They argued that such a structural model as Noble's, which is based on anatomical connections, should result in reversal in all cases of interocular transfer of left-right mirror-

image stimuli. They also rejected a hypothesis presented by Corballis and Beale (1970) which suggested that the orientational differences of asymmetrical stimuli may readily be detected by animals and children but that memory of such left-right differences may be lacking and result in continued difficulty to discriminate such differences. Hamilton et al (1973) rejected such a hypothesis since their matching to sample task was a perceptual problem and did not require memory of left-right differences.

Hamilton, Tieman and Brody (1973) explained the shift from paradoxical transfer to veridical transfer of their Subjects in behavioural terms. They hypothesized that their Subjects may have utilized one of two response strategies during their initial training. The Subjects may have fixated the centre of the stimuli (as described above) or they may have used a code that said, "the arrow-head that points toward my blind visual field is correct," (Hamilton, Tieman and Brody, 1973) (p. 423)." They suggest that these strategies were probably extinguished during training with non-mirror-image stimuli and that the Subjects then relied upon direct veridical commissural input as discussed by Berlucchi and Marzi (1970).

The above results obtained by Hamilton and his associates are very similar to the numerous studies performed by Corballis and his associates. Paradoxical transfer effects found with pigeons (Mello, 1965, 1966, 1968) have been explained from a response asymmetry point of view. Similar to Hamilton's monkeys, pigeons tend to view only half of the response key that is ipsilateral to the open eye. Therefore, pigeons show paradoxical transfer in the same manner as Hamilton's monkeys. To date there has been no research performed to analyze the possibility that split-chiasm cats may utilize response asymmetries to discriminate lateral mirror-image stimuli.

Assuming that the manner in which Subjects inspect stimuli and also respond to stimuli becomes part of their behavioural repertoire in any particular apparatus and whether or not such factors are carried over to a transfer test situation is very important to consider when discussing type of transfer. Although this discussion has centered around many different factors that may influence degree of transfer, there are no specific data from the present study that can lend support for the amount of transfer of such factors. However, it is

certainly the case that such factors may influence inter-ocular transfer and further experimentation should be carried out in order to determine the importance of such variables. The results of the present research suggest that future studies be oriented to studying behavioural phenomena that are associated with the problems of left-right discriminations.

An area of research that has yet to be explored involves the developmental aspects concerned with discriminating lateral mirror-images. That maturational level is an important factor for such an ability in children has already been fully discussed (see Introduction). Studies attempting to determine whether or not mirror-image discrimination in animals is dependent on the developing nervous system have yet to be performed. This may prove to be a fruitful area of research in the future.

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Appendix A
Prior Experience of Subjects.

Approximately four months prior to the actual study reported here Gary and Topaz had had 538 and 588 trials respectively of visual nonreversal shift testing. This testing was in a WGTA and was to be used as an apparatus adaptation. However, the nonreversal shift task proved to be too difficult and was abandoned in favour of brightness testing. It should be noted that this prior experience of Topaz and Gary took place in a WGTA which should not have influenced their behavior in their subsequent testing in the Grice Box.

Appendix B

**Trials and Errors to Criterion for all
Phases of Acquisition, Relearning and
Reversal with the Mirror-Images and
Non-Mirror-Images**

Table 11

Trials and Errors to Criterion during
Acquisition, Relearning and Reversal
of the Mirror-Images and Non-Mirror-
Images by Subjects Tested in the

Grice Box

	Mirror-Images					
	Acquisition		Relearning		Reversal	
	Trials	Errors	Trials	Errors	Trials	Errors
Pav	243	73	53	8		
Topaz	357	162	293	97		
Gary	380	157			395	213
Sartre	642	296			632	290

Non-Mirror-Images

	Acquisition		Relearning		Reversal	
	Trials	Errors	Trials	Errors	Trials	Errors
	Trials	Errors	Trials	Errors	Trials	Errors
Pav	586	217			731	372
Topaz	736	308			828	399
Gary	295	125	159	65		
Sartre	253	106	72	20		

Table 12

Trials and Errors to Criterion during
Acquisition, Relearning and Reversal
of the Mirror-Images and Non-Mirror-
Images by Subjects Tested in the WGTA

	Mirror-Images					
	Acquisition		Relearning		Reversal	
	Trials	Errors	Trials	Errors	Trials	Errors
Olga	209	63	62	14		
Xerces	355	128	80	23		
Q-Tip	530	197			907	363
Heatchcliff	860	339			889	468

	Non-Mirror-Images					
	Acquisition		Relearning		Reversal	
	Trials	Errors	Trials	Errors	Trials	Errors
Olga	408	191			376	134
Xerces	184	69			208	100
Q-Tip	446	250	225	91		
Heathcliff	425	229	177	57		

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