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Hemispheric Cooperation in Visuospatial Rotations: Evidence for a Manipulation Role for the Left Hemisphere and a Reference Role for the Right Hemisphere

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A survey of mental rotation strategies in 210 normal subjects showed a strong tendency for right-handers to prefer rotating an object on the right and vice versa for left-handers. The differential functioning of the cerebral hemispheres during mental rotation was then assessed in 42 subjects by means of tachistoscopic presentation of two geometrical figures separately to the left and right visual fields—one of which was gravitationally stable and the other unstable. Performance was better when the unstable object was presented to the right visual field and the stable object to the left. This finding is interpreted as indicating more efficient hemispheric cooperation when the active manipulation of a mental image is performed by the left hemisphere, while the reference role is carried out by the right hemisphere. © 1994 Academic Press, Inc.

INTRODUCTION

The relative "dominance" of the cerebral hemispheres in various tasks was the central theme of most laterality research in the 1960s and 1970s (Bradshaw & Nettleton, 1983). Despite occasional mention of the possible importance of hemispheric "interactions" (e.g., Milner, 1974), the theoretical questions asked and the experimental techniques used focused

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on the topic of "Which hemisphere is better?" rather than "How do they work together?" This emphasis on the separate capabilities of the hemispheres was strongly motivated by the startling results of the early split-brain research (Sperry, 1972) and was a necessary step prior to asking questions about hemispheric interactions. Unfortunately, partly reflecting the importance of the split-brain studies, there was a strong tendency to think of even the normal brain as two semi-autonomous hemispheres which differ from the surgically divided split-brain only in the fact that intact commissural tracts allow the information in one "brain" to be sent across to the other "brain." Arguably an understanding of the subcomponents of a complex system is a necessary precursor to an understanding of the entire system, but the predominance of the "two brain" perspective meant that questions concerning the nature of hemispheric interactions, complementary development and dynamics were infrequently asked until the mid-1980s.

One technique for studying hemispheric interactions is to use traditional tachistoscopic and dichotic methods, but to present information essential to solving the task to both ears or visual fields and to manipulate the nature and left/right balance of that information. Instead of asking "Which hemisphere performs better when given information of Type A?", it then becomes possible to ask "What is the relative performance when the left and right hemispheres are processing, respectively, Type A and Type B information, and vice versa?" The difference is that the former question addresses only the question of hemispheric superiority for a given type of information processing, whereas the latter asks what combination of information presented to the left (LH) and right (RH) hemispheres maximizes systemic performance.

The "interaction" approach has the disadvantage that it includes all of the methodological difficulties of laterality research (lateralization of stimuli, limited exposure times, etc.) and adds the further complication of hemispheric interactions. It nonetheless has two principal advantages. The first is that the bilateral stimulation technique acknowledges the reality of the bilateral brain and does not pretend that either hemisphere can be tested "in isolation" in normal subjects. It is noteworthy that occipital callosal transfer times are estimated on the basis of evoked potentials to be on the order of 20 msec (e.g., Saron & Davidson, 1989; Srebro, 1987), and myelinated fibers of various diameters allow transfer in 1-25 msec (Aboitiz, Scheibel, Fisher & Zaidel, 1992). Since most behavioral responses in split visual field and dichotic tests are obtained after delays of 500 to 2000 msec, considerable interhemispheric communication may well occur prior to any response to lateralized stimulation. The second advantage of bilateral presentation of stimuli is that it reduces the problems of attentional biases since both ears or visual fields always receive relevant information.

The experimental method which we have used in the present study is a split-field tachistoscopic technique where the subject's task is always to make a same-different judgment on the information presented in the two visual fields. The idea has been to manipulate stimulus attributes in a well-understood mental rotation paradigm such that the preferred configuration of hemispheric interaction can be determined. The design of the tachistoscopic test was motivated by findings from a paper-and-pencil survey on the rotation strategies employed by normal subjects.

A PAPER-AND-PENCIL MENTAL ROTATION TEST

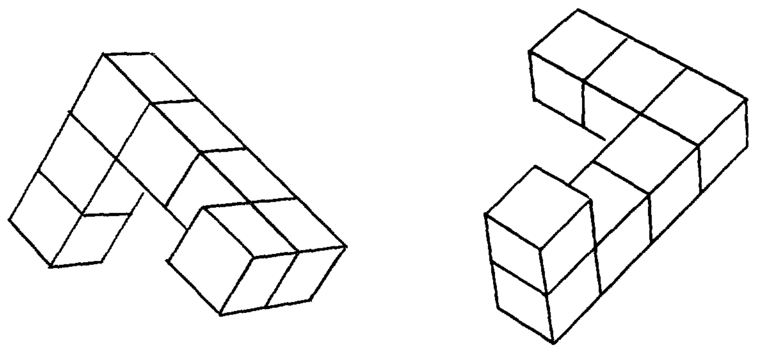
When mentally rotating one of two objects to determine if they are the same or different, most people have a tendency to rotate an askew object to the orientation of a gravitationally stable object (Shepard & Cooper, 1982). This tendency can be described as a "skewedness bias," in so far as most subjects prefer to manipulate the gravitationally unstable object and leave the stable object alone. To determine if there is also a left–right bias for such rotations, we had three groups of subjects do a pencil-and-paper test of Metzler and Shepard (1971) style geometrical rotations.

Methods

We surveyed the strategies of 210 normal subjects (160 men and women between the ages of 22 and 46, and 50 children, ages 12–14) when undertaking Shepard/Metzler-type visuospatial rotations (Shepard & Metzler, 1971) with the objects presented side-by-side (Fig. 1, top). Using 6 pairs of "same" and 6 pairs of "different" objects (both of which were presented askew, but differing in orientation by 90°), subjects were asked to respond same or different to each pair. Most subjects had no difficulty in giving the correct answer; when the occasional error was made, they were told to study it more carefully. At the end of the series of 12 trials, all subjects were told they performed well, but that the topic of research was in fact the way in which the decision was made. The subjects were then taken through the same series again, each time asked what strategy they employed to come to their same/different decision.

Results

From the survey, we found that right-handers have an overwhelming tendency to rotate the object on the right and report it to be the easier rotation to perform, and vice versa for left-handers (Fig. 1, bottom). Among the 153 (self-reported) right-handers, 128 (83%) reported that they rotated the right-hand figure more often than the left; 74 (48%) reported that they *always* rotated the object on the right and only 10 (7%) rotated the object on the left more frequently than that on the right; 18 (12%) indicated equal numbers of left and right rotations. Among the 57 left-handers (most of whom were recruited for a separate study of handedness and the immune response), 37 (66%) rotated the object on the left more often and 11 (19%) the object on the right; 25 *always* rotated the object on the left (44%). This "handedness rotation" bias was statistically highly



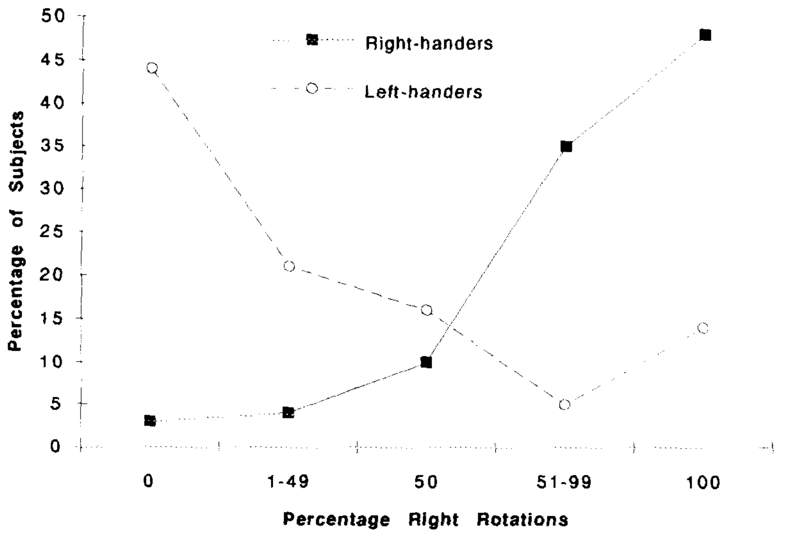


FIG. 1. Stimulus examples for the mental rotation survey are shown above. Below are shown the percentages of "right object rotations" by the 57 left-handers and 153 right-handers. The right-handers had an overwhelming tendency to rotate the object on the right, and vice versa for left-handers.

significant between the right- and left-handed groups ($df[1]$, $\chi^2 = 164.9$, $p < .0001$). There were no significant age or gender differences with regard to the preferred side for rotation. Data on accuracy were not collected.

Discussion

We found that, when two objects with approximately equivalent gravitational instability were presented side-by-side, right-handed subjects have a strong tendency to rotate the object located on the right toward the orientation of the object on the left, and vice versa for left-handers. Most subjects report that it is easier and/or "more natural" to rotate one object or the other; most show a strong bias in one direction; and many subjects express surprise that anyone would ever rotate the object on the other side! In other words, there is a strong subjective feeling for the "right" way to perform the mental rotation. Many subjects also report that when the same/different judgment is difficult, they check their answer by rotating the object on the side opposite to that which they initially rotated. Only rarely do subjects maintain that they rotate both objects simultaneously or use a non-rotation strategy.

We refer to this tendency to rotate on the side of the favored hand as a "handedness bias" because of the strong relationship with self-reported handedness, but there is in fact a small number of subjects who show a strong rotation tendency contrary to their reported handedness, and some subjects without any apparent lateral bias. The laterality of the rotation in the mental rotation task may well be related to handedness in the sense that if corresponding 3-D geometrical objects were the stimulus materials, subjects would be likely to manipulate first the object lying closest to the favored hand. In any case, as a "mental handedness" test without any required motor behavior, the side on which a mental rotation is preferred is a strong effect.

Such survey data are suggestive of differential hemisphere involvement, but are ultimately inconclusive in so far as subjects typically scan back and forth between images and respond after several seconds. In other words, all of the visual information is presented to both visual fields and both hemispheres, and conclusions cannot be drawn concerning hemisphere involvement solely from a tendency to prefer mental rotation of objects on one side of the visual field. In order to determine if there is differential hemisphere involvement in such a visuospatial rotation task, we therefore conducted a lateralized tachistoscopic study in which the "handedness rotation" bias, i.e., the tendency to prefer to rotate an object on the left or right, was played against the "skewedness rotation" bias, i.e., the tendency to prefer rotating an askew object to the orientation of a stable object.

A TACHISTOSCOPIC STUDY

A reaction-time experiment was designed such that two geometrical stimuli were presented separately to the left and right visual fields, thus requiring cooperation between the cerebral hemispheres in order to make correct same/different judgments. Unlike the pencil-and-paper survey, however, for the tachistoscopic study, one of the pairs of objects was always presented in a gravitationally veridical (stable) orientation and one was askew. There was therefore in each stimulus pair one object which should be preferentially rotated due to its gravitational unstable state (the skewedness bias) and one object which should be preferentially rotated due to its position in the left or right visual field (the handedness bias). It was predicted that responses would be faster when the subject's handedness rotation bias (as determined from a subsequent paper-and-pencil test) was concordant with the skewedness bias. In other words, since right-rotators (usually, but not always right-handers) prefer to rotate the object on the right simply because it is on the right, but also have a tendency to rotate a gravitationally "unstable" object toward a stable one, better performance should be found when the two tendencies are concordant, i.e., when the stable object is on the left and the askew object to be manipulated is on the right. Contrarily, when the stable object is on the right, these two tendencies are discordant and, consequently, response times should be slower (see Fig. 2, top).

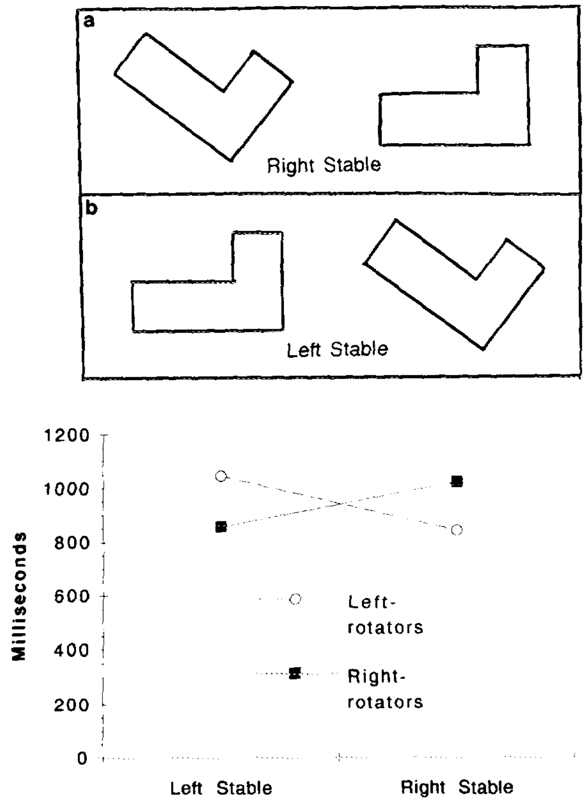


FIG. 2. Above are shown two examples of stimulus pairs in the 45° condition presented tachistoscopically. The top pair are a gravitationally "stable" object on the right and an "unstable" object on the left, and vice versa for the second pair. Comparisons between these conditions were made of the response times and number of correct responses for "same" pairs. The top pair is faster for left-rotators, whereas the bottom pair is faster for right-rotators. The mean response times were 842 ± 287 and 1045 ± 426 in the left rotator group and 1022 ± 377 and 857 ± 270 in the right rotator group.

Methods

Forty-two normal subjects (23 men and 19 women between 20 and 38 years of age) participated in the study. They were presented with pairs of geometrical objects, one of which appeared to be gravitationally stable (with its major axes running horizontally and vertically) and the other of which was presented askew from stability (one half rotated 45° or 135° clockwise and one half 45° or 135° counter-clockwise). Half of the pairs consisted of geometrically identical shapes and half were different shapes (Ls or backward Ls, sitting, standing or askew) (Fig. 2a). The stimuli subtended 2.5–4.0° of visual angle to the left and right of a central fixation cross. After 1500 msec presentation of the cross, the stimuli were presented for 150 msec, followed by a full-field random dot mask. The subjects sat approximately 50 cm from a computer screen and were required to give bilateral keyboard responses with the index fingers to "same" pairs and with the forefingers to the "different" pairs, as quickly and accurately as possible. Two seconds after a response had been recorded, the next trial began with the appearance of a fixation cross.

The test began with two practice sessions of 10 pairs of stimuli each. The first 10 were presented on the screen until a keyboard response was recorded to familiarize the subjects with the test procedure. The second practice session presented the stimuli for gradually shorter durations, from 1000 down to 150 msec. When subjects had difficulties with these practice trials, they repeated the entire set of practice trials once or at most twice, at which time all subjects said that they understood the task and thought that they could make same/different judgments.

The test session began with 4 trials which were not included in the subsequent analysis and then 96 actual trials. At the end of the test session, all subjects did a pencil-and-paper rotation task (an extended version of that described above), at the completion of which they indicated for each of 24 stimulus pairs, which of the objects they mentally rotated. Based on their responses on the paper-and-pencil test, each subject was assigned to either the left-rotator or the right-rotator group.

Results

All four (self-reported) left-handers indicated that they rotated the objects on the left in the pencil-and-paper test. Three right-handers also reported a preference for rotating the object on the left, thus giving a left-rotator group of 7 subjects and a right-rotator group of 35 subjects.

Of the 42 subjects, 6 (all right-rotators) performed at a chance level in both the 45° and 135° conditions and were discarded from the analysis. The response times and number of correct responses of the remaining 36 subjects were subjected to 2-way ANOVAs (gender and handedness rotation bias) for both the 45° and the 135° rotation conditions. The ANOVA for response times in the 45° condition showed a significant effect of the handedness bias ($df(1)$, $F = 10.869$, $p = .002$), but no gender effect ($df(1)$, $F = 2.122$, $p = .155$) and a trend for an interaction between handedness bias and gender ($df(1,1)$, $F = 3.405$, $p = .074$). Collapsing the sexes together and studying the left-rotators separately from the right rotators using paired t tests showed that the "left stable" condition was significantly faster than the "right stable" condition for right-rotators ($t(28) = -4.424$, $p = .0001$) and vice versa for left-rotators ($t(6) = 2.325$, $p = .059$) (Fig. 2b). There were no significant effects in the ANOVA for the 135° condition or for the number of correct responses in either the 45° or 135° conditions.

Discussion

The analysis of the tachistoscopic study was done using the side of the "handedness rotation bias" rather than handedness itself because it was specifically the question of which image was the more natural to rotate that was the factor of interest, not the writing hand, etc. The results for the 45° condition were unusually strong for a split-field reaction time test; 28 of the 36 subjects gave results in the direction predicted from the surveyed rotation bias, 13 of which were statistically significant intra-individual results and only one of which was significant in the direction opposite to the predicted effect.

Contrary to expectations, the results for the 135° rotation showed no significant effects in either the left- or right-rotator group. This is thought to be due to two factors: generally a poorer performance and greater RT variability at 135°, and the possibility that non-rotation strategies for the larger angle "same" pairs were used. That is, for identical objects that are 135° rotated from one another, a "mirror-symmetry" criterion can be applied after a 45° rotation of one object. Although the response times for the 135° rotations were typically longer than those for 45° rotations, as expected in a mental rotation paradigm (Metzler & Shepard, 1971), it is uncertain that mental rotation was the only cognitive process used in the decision at 135°.

Post hoc analysis of the direction of rotation and hemifield interaction showed a trend, as previously reported by others (Corballis & Sergent, 1989; Burton et al., 1992), for clockwise rotations to be faster than counter-clockwise rotations in the LVF ($t(28) = 2.62$, $p = .014$), although not vice versa in the RVF. This directional effect as related to the hemispheres might be explained in terms of the biological relevance of objects moving toward the visual midline (Corballis & Sergent, 1989), but is nonetheless a much weaker effect than the tendency for one hemisphere to be actively involved in the rotation process itself.

GENERAL DISCUSSION

Laterality studies in normal subjects, in which one hemisphere is forced to compete against or function "in isolation" from the other hemisphere, are notorious for their unreliability (Efron, 1991). Our tachistoscopic test avoids some of the problems of laterality work in requiring information from both visual fields to be used to obtain correct responses. An artificial competition between the hemispheres is therefore not demanded, and questions concerning asymmetrical attention do not arise. The task requires the normal subject with intact and callosally-connected cerebral hemispheres to make use of the visual information initially presented separately to *both* visual fields, thus requiring some level of cooperation between the hemispheres. The fact that discordant rotation tendencies significantly slowed response times suggests that one hemisphere (usually the LH) actively manipulates its visual information, while the other hemisphere is employed in a "non-dominant" reference role—*which is nonetheless as essential as the rotation itself for accurate performance.*

Studies of patients with unilateral brain damage generally indicate greater visuospatial deficits following right- than left-sided damage (Benton, 1979), but Mehta, Newcombe, and Damasio (1987) have shown that different visuospatial functions are differentially affected by unilateral lesions. Pattern completion and pattern recognition were more severely affected by RH than LH damage, but the reverse was true for Shepard/Metzler-type visuospatial rotations or the determination of line orientations. That is, when the task requires active manipulations or comparisons of visual images, rather than recognition or completion, the LH plays an important role.

Our tachistoscopic results indicate that most right-handed subjects manipulate the visual image presented to the right visual field and use the image in the left visual field as a reference against which the actively rotated image is compared. That result is thought to be consistent both with the idea that the RH is "dominant" for various visuospatial tasks requiring visual information to be held in memory and also consistent with the idea that the LH is "dominant" for mental imagery and the generation and active manipulation of visual images (Farah, 1984; Farah, Gazzaniga, Holtzman, & Kosslyn, 1985; Kosslyn, Holtzman, Gazzaniga & Farah, 1985; reviewed by Finke & Shepard, 1986; and Tippett, 1992). In so far as both hemispheres are actively involved in the tachistoscopic task, as well as presumably in everyday visual processing, labels such as "dominant" and "nondominant" are perhaps inappropriate, but it can be said that lateral control of the information provided to the visual fields has revealed favorable and unfavorable configurations which are indicative of a "manipulation" role for the LH and a "reference" role for the RH.

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