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Efficiency of the forebrain commissures: memory for stimuli seen by the other hemisphere

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Abstract. How well will one cerebral hemisphere recognize items viewed initially *via* the other? Nonverbalizable images or words were presented to one visual field and memory for them tested in the same or the other visual field. The initially viewing hemisphere subsequently had no secure advantage in accuracy, and only for images was there a 30-ms (ca 3%) penalty in reaction time for viewing with the "other" hemisphere. Interhemispheric mnemonic communication is thus highly reliable. At longer retention intervals (1-2 min vs. 4-30 s, with accumulating added stimuli), however, recognition of words was asymmetric as to hemisphere, in that initial viewing *via* the right hemisphere was subsequently (and paradoxically) much better recognized *via* the left (other) hemisphere than was the converse situation. This suggests that the initial engram with right hemispheric viewing of words ultimately becomes established in the left, and that the right has less accurate access to a previous "left hemispheric view".

Key words: *corpus callosum*, laterality, language, visual memory, engram

INTRODUCTION

In the normal course of events, as gaze shifts from one direction to another, some items will inevitably be glimpsed within one visual field and not the other. In such circumstance there seem to be several possibilities concerning the memory formed of such an item. Most secure for sake of memory would be that callosal (and/or anterior commissural) action immediately passes a copy of the input to the other hemisphere, thereby allowing formation of a bilateral, if redundant, engram of the item. Alternatively, and more efficiently, the initially viewing hemisphere might form a unilateral engram (Doty et al. 1973), that could, however, subsequently also be accessed *via* forebrain commissural paths in the event recurrence of the input was processed first within the other hemisphere. Intermixtures of such possibilities seem likely, e.g., a weaker engram formed in the nonviewing hemisphere, with a signal somewhat degraded by transcommissural passage; or similar degradation in the signal from the second hemisphere having thereby less certain access to a unilateral engram in the first. Whatever the true arrangement, it is almost wholly dependent upon the forebrain commissures since lacking them, interhemispheric mnemonic transfer is essentially absent (e.g. Sperry 1984).

Because of the variety of manipulations available, studies on macaques have provided the firmest answers to the foregoing speculations. Formation of unilateral engrams when input is limited to a given hemisphere has been demonstrated (Doty et al. 1973), even though the splenium of the *corpus callosum* was intact and the learned response could be elicited at such time by stimulation of the other hemisphere. This may, however, be limited to the special circumstance of those experiments, in which the stimulation was direct, electrical excitation of striate cortex, i.e., the stimulus was "endogenous" in that it was initiated cortically. On the other hand, with true visual input Ringo (1993) has shown that an engram, formed in a single hemisphere, can subsequently be accessed *via* the other hemisphere that had not viewed the target item. Such querying of the initial hemisphere by the other, however, shows some loss of accuracy compared with the querying of the initially viewing hemisphere. Transmission to a nonviewing hemisphere is also effective, i.e., if one hemisphere views an item (and presumably forms an engram of it), the other hemisphere, from a commissurally transmitted "copy", also forms an engram which can serve when the initially viewing hemisphere is inactivated during the test. This engram formed in the nonviewing hemisphere (hence bilateral), that receives its engram-forming input only *via* commissural paths, is weaker than that formed in the hemisphere that actually viewed the item (Ringo 1993). A further example of commissural efficiency comes from the fact that, in macaques with split chiasm, targets given separately to the two hemispheres are consolidated. Thus, if either splenium of the *corpus callosum* or anterior commissure are intact, reaction times and accuracy in a short-term memory test (the Sternberg paradigm) reflect the total mnemonic load shared by the two hemispheres regardless of which hemisphere has viewed the item initially and which is queried (Lewine et al. 1994). It would thus appear that engrams, unilateral as to initial input, can be induced in or activated from a hemisphere that did not view the item initially. This simplistic description, of course, ignores the asymmetry that so characterizes the processing of different types of stimuli by the two hemispheres in man, a fact that will become significant in what follows below.

This question, of whether there is, indeed, a mnemonic penalty attached to viewing first with one hemisphere and then with the other, has been addressed previously, with somewhat mixed results (see Leiber 1982, Gratton et al. 1997 for review). Dimond et al. (1972) used a string of letters, easily identified as a "pattern" or by noting a single letter, if seen alone in a single visual field. If then stimuli were subsequently presented simultaneously in both visual fields, the previously seen stimulus could not be recognized if falling in the other visual field, but could be if it was unchanged in its position. There were no hemispheric differences *per se*. However, the brief interval (3 s) between first and second presentations, and the fact that the items, that actually were words, could not be identified as such, perhaps makes the phenomenon here more allied with afterimages. Somewhat similar advantages for the initially viewing hemisphere have been found by Banich and Belger (1991) and by Gratton et al. (1997) using simple length or pattern of lines.

Leiber (1982), using words that could be seen, found that when an item had been viewed initially in the LVF, it was poorly, and more slowly, recognized when viewed again *via* the RVF. The effect, however was asymmetrical, in that there was much less or no effect when the sequence was R to LVF. Rather than showing a deficit merely in consequence of the shift in viewing hemispheres, the results strongly reflect the fact that words "seen by" the right hemisphere are poorly remembered, whereas those "seen by" the left hemisphere are better recognized *via* the right hemisphere than if the right hemisphere viewed them on each occasion. At what stage the commissural connections might operate remains ambiguous, since the better engram formed by the left hemisphere might be redundantly transmitted to the right; or the right hemisphere, when called upon, might be able to access the more robust engram that had remained in the left hemisphere.

Coney and Macdonald (1988) emphasized that the pattern of results, in switching hemispheres for initial and subsequent viewing of words, was dependent upon the elapsed time (occupied by additional words as targets), a deficiency in recognition in the "crossed" condition becoming evident only after 32 s. This is compatible with the idea that the memory trace may decay much faster in the nonviewing hemisphere; but, of course, there are other possibilities. Somewhat surprisingly they failed to find the asymmetry reported by Leiber (1982).

Banich and Shenker (1994) approached the problem somewhat differently. They presented black and white, simple, nonsense drawings one, five, or nine times *via* a given hemisphere, and then assessed memory once *via* either the same or the opposite hemisphere. There was about 100 ms increase in reaction time (RT) for second presentation to a different *versus* the same hemisphere ($P \leq 0.01$); and, overall, recognition was better if the item was presented each time to the same *versus* the other VF ($P<0.01$). Reminiscent of, but opposite to Leiber (1982), for single presentations accuracy was skewed so that initial exposure *via* LVF followed by RVF recognition was substantially better than the reverse ($d' = 3.49$ *versus* 1.92, respectively). This suggests that the LVF/right hemisphere is superior for encoding the nonsense figures. Such an interpretation is supported by the fact that, overall, the LVF to LVF performance ($d' = 4.5$) bettered that of RVF to RVF ($d' = 3.68$).

Given this somewhat uncertain status of the question, whether there is a degradation in memory if an item is re-encountered in the opposite visual field, any hypothesis as to the nature of such loss, or of the success of interhemispheric mnemonic processing, must await a firm foundation of the facts. We thus chose to examine memory for words *versus* nonsense images in a demanding mnemonic task, continuous recognition, which has the added advantage of allowing some comparison between short- and long-term memory. We had a further incentive in this choice in that the characteristics of memory for these same stimuli in the exact same task had been thoroughly examined in an earlier study (Doty and Savakis 1997).

METHOD

Subjects

Sixteen subjects, 6 male, 10 female, participated in the experiments using WORDs; and one male and one female were lost from the group for the experiments on IMAGEs. No differences were found between male *versus* female subjects in any of the parameters tested. All were definitively right-handed as *per* the Edinburgh inventory (Oldfield 1971), had normal color vision, as tested with color charts (Ichikawa et al. 1978), and normal acuity, as tested with an eye chart on the computer monitor.

Basic apparatus and experimental arrangement

The experiments were conducted in a quiet, dimly lit room. Each subject was given trial runs until they were confident that they understood what was required. The subject was seated in a chair adjustable for height with chin and forehead resting against a head restraint that centered the eyes 57 cm from a computer monitor. Suitable care assured that the subject was sufficiently comfortable to maintain head position consistently throughout the testing session, usually lasting about 20 min. The experimenter followed progress of the experiment and eye position from an adjacent room, using an ISCAN infrared corneal reflection system. A Pentium computer ran the ISCAN hardware and software, which monitored eye position with an accuracy of 0.5° at 120 Hz.

Presentation of stimuli and recording of response were controlled by a second Pentium computer with a Data Translation timing board providing accuracy ± 0.01 ms for measurement of the RT.

Test material

There were two types of stimuli, IMAGEs and WORDs. The former were complex, multicolored, nonobjective, nonverbalizable drawings, created with imaging software, such as CorelDraw. Examples can be seen in references (Doty and Savakis 1997) and (Kavcic et al. 2000). They have left-right symmetry, so that views from either visual field are equivalent. This is an important, and often overlooked, feature for proper interhemispheric comparison of images, since in most ordinary scenes the left and right halves of the image are not equivalent. They subtended 6x3°, width x height. Four-letter, nonoffensive English words were used, having a median usage frequency of 44.5 *per* million words, range 0-1599 (Francis and Kucera 1982). They were written with white capitals on a black background, equal to the IMAGEs in angular subtense.

The tests with IMAGEs *versus* WORDs were given at an interval of 1 week, with balanced order among subjects as to which was given first.

Procedure

The subject's task was to determine whether a presented item was NEW, i.e., had not been seen previously in the session, or that it had been seen and hence was OLD. Pressing one or the other button of a computer mouse (buttons randomly assigned across subjects) indicated the choice, which the subjects were instructed to make as rapidly as consistent with accuracy. Each trial began with illumination of the fixation point. If it was fixated steadily for 300 ms, the target item was presented for 200 ms, and if fixation had remained steady, the trial was accepted, otherwise aborted. Stimuli were lateralized to approach the center of fixation by no less than 2°, and the criterion for fixation was maintenance within a ± 0.5° horizontal, ± 1° vertical fixation window throughout the presentation. Some 3% of the trials with WORDs and 4% with IMAGEs were lost consequent to this criterion.

The intertrial interval was set at a minimum of 4 s, plus the time for the subject to fixate for the acceptable time. Only one type of stimulus, IMAGEs or WORDs was used in any session. In either case there were 240 trials, half NEW and half OLD, with the latter occurring after 0-31 intervening items, i.e., at LAGs of 1, 2, 4, 8, 16 and 32 in this continuous recognition task. Trials were arranged to be in pseudorandom order, no more than 4 items being presented consecutively in one VF, and also no more than 4 NEW or 4 OLD items consecutively. The subjects were informed of the correctness of their choice by soft beeps from the computer.

Statistical analyses

Only correct trials with an RT between 300 and 1500 ms were analyzed. Reaction times (RTs) and accuracy scores for NEW WORDs and NEW IMAGEs were analyzed with paired-samples *t*-test. Reaction times and accuracy scores for OLD WORDs and OLD IMAGEs (the critical items of interest) were entered into 2x2x2 factorial ANOVAs, with visual field (RVF, LVF), LAG (short LAGs, long LAGs), and switch (same hemisphere, different hemisphere) as within subject factors. The division into short and long LAGs, while arbitrary, does divide the trials between those with 4-30 s between first and second viewing (short LAGs 0-7 intervening items), and 1 and 2 min (long LAGs, 15-31 intervening items). All *post-hoc* analyses were carried out using the Tukey honestly significant difference test.

RESULTS

Table I presents a summary of the various comparisons between VF and the testing of recognition memory in the initially viewing (same) or initially nonviewing (different) hemisphere, and as a function of time since the initial viewing (short and long LAGs).

WORDS

Reaction times

Paired-samples *t*-test for NEW WORDs revealed significantly faster responses for RVF (913 msec) than for LVF (964 ms) (t_{15}=5.73, P<0.0005). An analysis of RTs for OLD WORDs gave a significant main effect of LAG ($F_{1,15}$=12.30, P=0.003), with faster RTs for short LAGs (871 msec) than for long LAGs (905 ms). There was also a statistically significant 3-way interaction between VF, LAG, and switch ($F_{1,15}$=4.19, P=0.06). *Post-hoc* analyses did not show statistical significance for any meaningful pairwise comparisons; however, for long LAGs, there was a tendency for faster RTs in the LVF than in the RVF regardless of the initial stimulus presentation. The peculiar feature of the LVF/right hemisphere having shorter RTs than the RVF at long LAGs (Table I) is thus not significant.

Accuracy

Paired-samples *t*-test for NEW WORDs revealed significantly more accurate responses for RVF (85%) than for LVF (81%) (t_{15}=2.52, P=0.02). An analysis of accuracies showed a significant main effect of LAG ($F_{1,15}$= 25.74, P=0.003), with lower accuracies for long LAGs

TABLE I

Reaction time (RT) and accuracy (ACC), with Standard Deviation, for WORDs versus IMAGEs, according to NEW *versus* OLD stimuli, and presented to the SAME *versus* DIFFERENT hemispheres as OLD

	VISUAL FIELD	NEW	OLD			
			SHORT LAG		LONG LAG	
			SAME	DIFFERENT	SAME	DIFFERENT
RT -WORDS	LVF	964 ± 127 msec	885 ± 114	872 ± 134	893 ± 112	913 ± 140
	RVF	913 ± 134 msec	861 ± 127	865 ± 139	921 ± 155	892 ± 124
RT - IMAGES	LVF	928 ±1 20 msec	891 ± 130	908 ± 156	930 ± 156	981 ± 136
	RVF	935 ± 121 msec	891 ± 138	922 ± 155	978 ± 180	995 ± 198
ACC - WORDS	LVF	81 ± 9%	90 ± 8	92 ± 7	77 ± 13	84 ± 11
	RVF	85 ± 9%	93 ± 5	92 ± 5	85 ± 8	74 ± 14
ACC- IMAGES	LVF	71 ± 8%	85 ± 8	80 ± 10	70 ± 16	64 ± 20
	RVF	72 ± 9%	83 ± 9	78 ± 10	71 ± 15	69 ± 16

(80%) than for short LAGs (92%). There was also statistically significant interaction between VF and switch ($F_{1,15}=10.89$, $P=0.005$), and 3-way interaction between VF, LAG, and switch ($F_{1,15}=7.72$, $P=0.01$) as depicted in Fig. 1. Only 3-way interaction will be further analyzed since the lower level interaction is embedded within this higher level interaction.

The *post-hoc* analyses for the 3-way interaction indicated significant effects for long but not for short LAGs (Fig. 1). For the RVF accuracy was significantly better ($P=0.02$) when the second presentation of the WORD was to the same RVF/left hemisphere as compared to having the LVF/right hemisphere engaged by the second presentation (Fig. 1). The opposite tendency was present for shifting from viewing with the same LVF/right hemisphere to presenting the second view *via* the RVF/left hemisphere, $P=0.17$ (Fig. 1, Table I). The latter effect is paradoxical in that shifting from viewing by the same to the different hemisphere in this case improves performance, especially as compared to the same/different effect for R to LVF viewing, $P=0.02$ (Fig. 1). These findings were corroborated with statistically significant simple interaction for long LAGs ($F_{1,15}=12.14$, $P=0.003$), but not for short LAGs.

IMAGES

Reaction times

Differences between R vs. LVF were not significant. While there was no difference for NEW IMAGEs (Table I), an analysis of RTs for OLD IMAGES revealed a significant main effect of switch ($F_{1,13}=8.29$, $P=0.01$), with faster RTs for same hemisphere presentations (923 ms) than for different hemisphere presentations (952 ms). There was also a significant main effect of LAG ($F_{1,13}=16.09$, $P=0.002$), with faster RTs for short lags (903 ms) than for long LAGS (971 ms).

Accuracy

Again, no difference in accuracy appeared for one *versus* the other hemisphere for NEW IMAGES (Table I). For second viewing with the same *versus* different hemispheres there is a tendency ($P=0.17$) for "changing hemispheres" to yield slightly worse performance. There was a significant main effect of LAG ($F_{1,13}=44.09$, $P=0.00002$), with higher accuracies for shorter (81%) than for longer LAGs (68%).

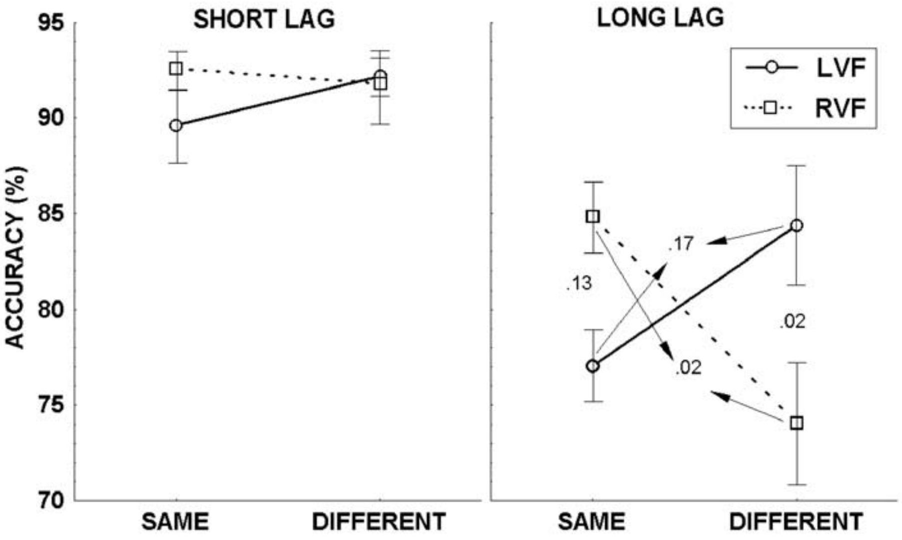

Fig. 1. Accuracy in recognition of repetition of WORDs (as OLD) at short and long LAGs. "SAME" indicates viewing with the same hemisphere for both NEW and OLD presentations, whereas DIFFERENT signifies that the viewing hemisphere changed between initial (NEW) and repeat (OLD) presentations. The Legend indicating VF thus refers to that used for initial viewing.

NEW/OLD analyses

In order to investigate the differences between NEW and OLD trials (i.e., LAG 32 aggregated across same and different VFs) the RT and accuracy scores were analyzed in 2x2 factorial ANOVA with VF (LVF, RVF) and NEW/OLD as within subject factors. An analysis for WORDs, as expected, revealed a significant main effect of NEW/OLD ($F_{1,15}$=12.69, P=0.002) for accuracy, although not for RTs. *Post-hoc* analyses indicated that NEW WORDs were better identified (83%) than OLD WORDs (76%).

Similarly, for IMAGEs, there was also a significant main effect for NEW/OLD for accuracy ($F_{1,13}$=6.60, P=0.02); *post-hoc* analyses indicating that the NEW IMAGEs (72%) were better evaluated than the OLD IMAGESs (62%). On the other hand, the RTs for IMAGEs, in addition, showed a statistically significant main effect of NEW/OLD ($F_{1,13}$=7.22, P=0.02) with shorter RT for NEW IMAGEs (932 ms) than for the OLD IMAGEs (984 ms).

DISCUSSION

The continuous recognition paradigm

The multiple switching from one to the other hemisphere/VF had no apparent effect upon the general format of the results expected in the continuous recognition task, e.g., there were shorter RTs and greater accuracy at shorter lags, with progressively increasing RT and diminished accuracy as time and number of intervening items increased. The values for WORDs and IMAGEs, the latter being more difficult and requiring somewhat longer RTs (Table I), were highly concordant with those found previously for the identical materials and procedure, with normal, foveal viewing (Doty and Savakis 1997). Thus, the parafoveal viewing herein is unlikely to be a factor in any of the results. An important carryover from the earlier results is support for the supposition that the data herein for long LAGs at 1-2 min do indeed reflect long-term memory. The earlier data (Doty and Savakis 1997) showed that some 70% of the WORDs, seen twice for 200 ms each time, and 60% of the IMAGEs viewed for 2 s on each occasion, could be recognized after an interval of 1 week.

An interesting peculiarity should be noted in the fact that the average RT for OLD IMAGEs is longer than that for evaluations when the IMAGE is NEW. This was present at LAG 32, but unremarked, in the previous study, and was also present for WORDs as well (Doty and Savakis 1997). This poses a challenge for explaining what transpires in the open-ended, "infinitely exhaustive" search of memory putatively required for identifying an item as NEW. Put the other way, why should it take even longer to identify an item that really has been subjected to mnemonic processing. We propose that the answer is available from the work of Rugg and his colleagues (Doyle and Rugg 1998, Rugg et al. 1998), showing that once an item has been viewed, the cortical potential evoked by a second presentation of the item differs significantly from that evoked in the naive state, whether or not the subject can identify the repetition as such. In other words, viewing an item ineluctably establishes some trace of that event, whether or not it can subsequently be retrieved consciously, or remains a "hidden", implicit memory (Schacter et al. 1993). Indeed, Gratton et al. (1997) found prior exposure of one hemisphere to a simple stimulus thereafter distinguished that hemisphere's evoked response to bilateral presentation of that stimulus. Thus, for the present instance, when an item is viewed for the first time, its mnemonic appraisal proceeds along less complicated lines than if, as on repetition, there is additionally a second process to contend for the decision, the implicit memory, as evidenced by the change in the evoked response; and the second process adds to the time required.

Left hemispheric dominance for WORDs

It is certainly no surprise that recognition of NEW WORDs *via* the RVF held an overall advantage of some 50 ms and 4% in accuracy compared to viewing *via* the LVF. For transcommissural engram formation (Table I, DIFFERENT), however, the consequences of this left hemispheric linguistic dominance is of considerable interest. As can be seen in Table I, it is manifest only at the longer LAGs, as maintained by Coney and Macdonald (1988). From Fig. 1, confirming Leiber (1982), it can be seen that a WORD viewed initially by the right hemisphere (LVF) is much better recognized when it is then subsequently viewed by the left hemisphere (RVF), and that this level of recognition is comparable to that found with viewing by the left hemisphere on both occasions. From Table I it might be inferred, *ab initio*, that this is simply a "speed/accuracy tradeoff", i.e., it took an additional 21 ms for a 10% gain in accuracy (913 ms/84% vs. 892 ms/74%) for the second viewing by right *versus* left hemisphere (Fig. 1). This is peculiarly selective, however, for the same applies for the reverse case of viewing *via* the same hemisphere, i.e., L vs. RVF in Fig. 1 (893 ms/77%, 921 ms/85%, respectively). In any event, there was no statistically significant positive correlation between accuracy and RTs for long LAGs at either the trial or individual subject level.

The seeming paradox of better accuracy for viewing "right hemisphere items" *via* the "left hemisphere", however, is fully, and most simply, explained if, upon initial viewing, the right hemisphere were to transmit a copy to the left hemisphere, which then forms its own engram of the event. The reason for proposing such transmission is that, if the right hemisphere views on both occasions, recognition is inferior to that just noted when the left hemisphere provides the second viewing. In the other case, when the linguistically efficient left hemisphere has viewed the WORD initially, putatively making a secure engram, subsequent viewing *via* the right hemisphere either presents trouble accessing this engram on the left, or must access the derivative and poorer engram that has been stored on the right from the transcommissural copy sent by the left hemisphere on initial viewing. The RTs (Table I), unfortunately, are too unstable and too similar to support either of these interpretations; and transcommissural time may be too short to be detected.

Lack of dominance for IMAGEs

Use of IMAGEs was intended to provide a contrast in hemispheric lateralization to that of WORDs, i.e., it was anticipated that they would favor the right hemisphere, as noted above for the use of black and white designs by Banich and Shenker (1994). Failure to find an effect of laterality may simply be characteristic of our more complex, colored images or, more likely, that the symmetry of these images made them more readily recognizable when viewed from the perspective of the other hemisphere. In any event, the effects of switching hemispheres was relatively small, a significant difference of some 30 ms overall between viewing *via* the same *versus* the other hemisphere, and a consistent, though minor, tendency for slight diminution in accuracy (Table I).

CONCLUSIONS

While conforming well to expectations for this demanding task of continuous recognition with the use of either WORDS or IMAGES, the results revealed only minimal or no cost for interhemispheric recognition. The only significant effect for second viewing by a different hemisphere was the 3% increase in RT for recognizing IMAGES with the second hemisphere. The human commissures thus seem remarkably efficient in dispelling this potential problem (seemingly a bit better than macaques - Ringo 1993), although they cannot defeat the asymmetry imposed by hemispheric specialization. The validity of this transcommissural action can be seen in the work of Doyle and Rugg (1998) where, upon viewing a word *via* either visual field, responses can be seen in both hemispheres within 150 ms.

With this definition of commissural capability, and its interaction with cerebral dominance, it will now be feasible to assay the "strength" of the engram formed in each hemisphere when only one views the target initially. Such measure can probably be achieved with judicious use of unilateral masking, presented simultaneously with initial or second viewing, thus enhancing confinement of the engram, or its readout, to a chosen hemisphere.

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