

Superior Episodic Memory Is Associated With Interhemispheric Processing

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The dependence of episodic memories on interhemispheric processing was tested. In Experiment 1, positive familial sinistrality (FS+; e.g., presence of left-handed relatives) was associated with superior episodic memory and inferior implicit memory in comparison with negative familial sinistrality (i.e., FS–). This reflected a greater degree of interhemispheric interaction in FS+ participants, which was hypothesized as facilitating episodic memory. In Experiment 2, the authors directly manipulated inter- versus intrahemispheric processing using tests of episodic (recognition) and semantic (lexical decision) memory in which letter strings were presented twice within trial blocks. Semantic memory was superior when the 2nd presentation went to the same hemisphere as the 1st. Episodic memory, however, was superior when the 2nd presentation of a stimulus went to the opposite hemisphere. Results support an interhemispheric processing basis for episodic memories.

Relatively little research has been devoted to the possible existence of differences in memory performance as a function of handedness and as a function of the patterns of cerebral laterality that underlie handedness. However, there are both empirical and theoretical reasons to suspect the presence of systematic handedness differences in memory. From an empirical perspective, the small number of studies that have explicitly compared the recognition memory performance of left- versus right-handers yields a suggestive trend toward superiority of left-handers over right-handers. For example, Hannay and Malone (1976) compared the effects of familial left-handedness on recognition memory for nonsense words and found a nominal advantage for participants with familial left-handedness. Sherman, Kulhavy, and Burns (1976) examined recognition memory for concrete versus abstract words and found a nominal advantage for left-handers in memory for abstract words (an advantage for right-handers in memory for concrete words appeared to be mediated by superior imagery skills among right-handers). Deutsch (1978) reported superior recognition memory for musical pitch among left-handers, especially among left-handers with mixed hand preference. Annett (1992) examined memory for the Rey–Osterrieth Complex Figure among seven different handedness subgroups. A post hoc analysis, collapsing the seven groups into three groups (strong left-handers, mixed-handers, and strong right-handers) and collapsing across gender, revealed a nominal advantage for mixed-handers. Nagae (1994) exam-

ined recognition memory for line-drawing pictures and found a nominal advantage for left-handers. Finally, Martin and Jones (1998, 1999a, 1999b; Jones & Martin, 1997) have reported handedness differences in recognition memory for the orientation of everyday objects depicted on common stimuli (e.g., memory for whether the Queen of England faces left or right on British coins). However, it appears that these handedness differences depend on the orientation of the stimulus: Left-handers were better at remembering right-facing heads, whereas right-handers were superior at remembering left-facing heads. Thus, the differences between left- and right-handers likely reflected differences in motor imagery rather than differences in recognition memory per se (Martin & Jones, 1999b).

It must be noted that few of the handedness differences cited above were significant or explicitly addressed by the authors. There was also considerable variability in how handedness was measured (e.g., in terms of degree vs. direction of handedness, in terms of personal vs. familial handedness). Finally, these studies did not directly compare different types of memory, notably the episodic–semantic distinction first proposed by Tulving (1985, 1986). Tulving and others have argued for the existence of multiple memory systems, with episodic memories corresponding to the actual remembering of an event's occurrence and with semantic memories corresponding to knowledge of an event without any conscious recollection of the event's actual occurrence. A potentially important limitation of the above studies is that none have explicitly contrasted these different types of memory. Nonetheless, there is at least tentative evidence to suggest that handedness differences (and, in particular, an advantage for left- or mixed-handers) may exist in recognition (i.e., episodic) memory.

The presence of tentative empirical trends discussed above is relatively uninformative in the absence of a theoretical framework within which to explain potential individual differences in memory. However, a number of studies focusing on the neural bases of memory provide a potential

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candidate for such a framework. In essence, the hypotheses developed in this study were that (a) tests of episodic memory (i.e., recall and recognition), relative to tests of nonepisodic memory (i.e., semantic and implicit memory), would be specifically dependent on interhemispheric processing and that (b) right-handers with familial left-handedness would be superior, relative to right-handers without familial left-handedness, at episodic memory tasks because of the presumed greater degree of interhemispheric integration associated with familial (and personal) non-right-handedness. Support for each of these hypotheses is presented in turn.

Support for the hypothesis that episodic memory requires interhemispheric integration, whereas semantic memories are more unilaterally localized, comes from a review of positron emission tomography studies by Tulving, Kapur, Craik, Moscovitch, and Houle (1994). On the basis of their review, Tulving et al. (1994) proposed a hemispheric encoding/retrieval asymmetry (HERA) model of verbal episodic memory wherein the left and right hemispheres (LH and RH), particularly the prefrontal lobes, are differentially involved in semantic and episodic memory encoding and retrieval. Tulving et al. (1994) suggested that the left prefrontal cortex is responsible for both the encoding and retrieval of semantic memories; conversely, they also suggested that episodic encoding versus retrieval is associated with the left versus right hemispheres, respectively. Thus, semantic versus episodic memories appear to be associated with intrahemispheric versus interhemispheric processing, respectively, lending further support to the hypothesis that episodic memory requires integration of the cerebral hemispheres, whereas semantic memory does not.

In an exhaustive review of the imaging literature, covering 170 experimental contrasts (i.e., brain activity in an experimental condition contrasted with brain activity in a reference or control condition) during semantic and episodic memory tasks, Cabeza and Nyberg (2000) concluded that brain "activity during semantic memory tasks has been almost always found in the left hemisphere but not in the right" (p. 20). For word fragment and stem completion measures of implicit memory, the picture is somewhat mixed: Of six relevant contrasts, three showed primarily right-lateralized activity, two showed bilateral activity, and one showed left-lateralized activity. Finally, for episodic encoding tasks using verbal materials, "prefrontal activations were always left lateralized" (p. 23), whereas "prefrontal activations during episodic retrieval are sometimes bilateral, but they show a clear tendency for right-lateralization" (p. 26).

Thus, there is some uncertainty about the exact localization of episodic encoding versus retrieval. For example, Tulving et al. (1994) reported LH encoding and RH retrieval, Halsband et al. (1998) reported LH encoding and bilateral retrieval, and Opitz, Mecklinger, and Friederici (2000) reported bilateral encoding and LH retrieval. In this sense, the exact localization of encoding and retrieval processes is not clear; the differences among studies may reflect differences in stimulus presentation or imaging technologies. However, these studies are all consistent in sug-

gesting an interhemispheric basis for episodic memories, in contrast with more consistently lateralized unihemispheric bases for semantic and implicit memory.

Research with split-brain patients indirectly implicates the role of interhemispheric integration, as mediated by the corpus callosum, in episodic memory. Recently, a study implicated the role of the corpus callosum and interhemispheric transfer in episodic, relative to implicit, memory. Cronin-Golomb, Gabrieli, and Keane (1996) examined episodic recognition and implicit word stem completion for words presented inter- or intrahemispherically in individuals with complete section of all forebrain commissures. Participants demonstrated within-hemisphere priming on the stem completion task, indicating that implicit memory can be accessed intrahemispherically; furthermore, this task can also be performed interhemispherically, which suggests that implicit memories can be shared between the hemispheres via subcortical structures. Conversely, participants' performance on an episodic recognition task was impaired regardless of presentation condition, indicating that episodic memory cannot be performed intra- or interhemispherically. This implies that the callosal section disrupts the normal interhemispheric circuitry underlying performance on episodic memory tasks. Although a same-hemisphere advantage for lateralized stimuli presented during an episodic task has been noted (Leiber, 1982), no studies have compared the size of the same-hemisphere advantage between tasks tapping episodic versus semantic memory.

In a review of memory processes in split-brain patients, Zaidel (1995) presented evidence that is also consistent with the current framework. Although Zaidel did not explicitly deal with the episodic-semantic distinction, the examples of everyday memory tasks (e.g., memory for current events, appointments, placement of common articles, parked car location) and laboratory memory tasks (e.g., paired associated learning, memory for story passages) for which split-brain patients show impairment are generally consistent with processes requiring episodic memory. Conversely, Zaidel reported that memories for things such as historical events, cooking recipes, and categorical knowledge, which are all generally consistent with semantic memories, are normal in split-brain patients. Thus, there seems to be a general consensus that the memory deficits following sectioning of the corpus callosum seem to disproportionately involve episodic memory processes, suggesting a special role of interhemispheric interaction in the encoding and retrieval of episodic, but not semantic, memories.

Given tentative support for interhemispheric versus intrahemispheric bases for episodic versus semantic memories, respectively, the hypothesized superiority of persons with personal or familial left-handedness in episodic (e.g., recognition) memory is presumed to arise from the presence of greater interhemispheric connectivity and interaction. For example, it is fairly well established that left-handedness and mixed-handedness are associated with a larger corpus callosum area (Clarke & Zaidel, 1994; Habib et al., 1991; Witelson, 1985, 1989). The precise implications of a larger corpus callosum for interhemispheric interaction are not clear; for example, it is possible that the callosal connec-

tivity is primarily inhibitory, which could, in principle, mean that larger callosa are associated with lesser interhemispheric interaction. However, given researchers' current inability to simply and directly map neural excitation and inhibition onto functional excitation and inhibition, it is just as likely that larger callosa are indeed associated with greater interhemispheric interaction.

Regarding evidence for greater functional interhemispheric integration among left-handers, the picture is somewhat mixed. For example, Hellige (1993) and Christman (1995) both concluded that, although there is tentative evidence for greater interhemispheric interaction or reduced hemispheric asymmetry among both left-handers and persons with left-handed relatives, the effects are not always robust or reliable. However, Christman (1995, 2001) noted that the majority of studies on handedness differences in interhemispheric interaction have used bilateral visual field presentation of two or more stimuli (in which separate stimuli presented to each hemisphere need to be compared), which he argued may not generalize to situations in which unitary input is presented centrally (and, hence, is equally available to both hemispheres).

That is, the nature of interhemispheric interaction (and individual differences therein) may differ between (a) situations in which input is presented bilaterally and each hemisphere processes its own separate stimulus and compares the results of its processing with the other hemisphere and (b) situations in which a single stimulus is presented centrally and each hemisphere is free to process the stimulus in its preferred manner. Thus, it is still an open question as to whether persons with personal or familial left-handedness exhibit greater interhemispheric interaction in the processing of nonlateralized input.

Given our working hypotheses of (a) interhemispheric processing of episodic, relative to semantic and implicit, memories and (b) greater interhemispheric interaction being associated with personal or familial left-handedness, it was therefore hypothesized that (familial) left-handedness would be associated with superior performance on episodic, relative to nonepisodic, memory tests. In Experiment 1, we indirectly manipulated inter- versus intrahemispheric processing by comparing the performance on tests of episodic versus implicit memory of participants with versus without left-handed relatives in their immediate family. Because of logistical difficulties in procuring large and equivalent numbers of right- and left-handed participants, we used familial left-handedness as a potential marker for increased interhemispheric interaction (e.g., Gorynia & Egenter, 2000; McKeever, VanDeventer, & Suberi, 1973). In Experiment 2, we examined the neural basis of episodic (i.e., recognition) versus semantic (i.e., lexical decision) memories by using repeated presentation of stimuli to the same versus the opposite visual field (and, hence, hemisphere) as a means of directly controlling intra- versus interhemispheric processing.

A final note regarding terminology is necessary. In both Experiments 1 and 2, we used recognition tasks as a measure of episodic (and explicit) memory. In Experiment 2, we contrasted episodic recognition with lexical decision, a

commonly accepted measure of semantic memory. Conversely, in Experiment 1, we contrasted episodic recognition with a fragment completion task, which is commonly accepted as a test of implicit, not semantic, memory. In this sense, this study contrasted episodic–explicit memory with nonepisodic–nonexplicit memory, with a primary emphasis on the interhemispheric basis of episodic, relative to non-episodic, memory.

Experiment 1

Because participants with left-handed relatives may have more bilateral representation of cerebral functions, greater interhemispheric interaction, and larger corpus callosa, and because the corpus callosum has been implicated in episodic memory (e.g., Cronin-Golomb et al., 1996), we hypothesized that participants with positive familial sinistrality (FS+) would perform better on a test of episodic memory than would participants without familial sinistrality (FS–). In addition, there is evidence that personal handedness may be related to individual differences in episodic memory. Christman and Ammann (1995) found that left-handers reported fewer dissociative experiences than strong right-handers did; in particular, factor analyses revealed that this difference specifically arises from a lesser incidence of amnesia-type dissociations in left-handers (e.g., driving from point A to point B yet having no conscious recollection of the drive). To the extent that FS+ individuals resemble left-handers, this result suggests that FS+ participants may have a relative superiority in episodic memory, presumably reflecting their pattern of greater interhemispheric integration. Accordingly, in Experiment 1, we examined individual differences in episodic–explicit versus implicit memory using central presentation of stimuli, allowing us to examine the present hypothesis indirectly but under ecologically valid conditions.

Method

Participants. Participants were 180 United States Air Force recruits in their 32nd or 33rd day of basic training at Lackland Air Force Base, San Antonio, Texas. All participants were high school graduates, and all spoke English as their native language. There were 78 female participants, 97 male participants, and 5 participants for whom the gender coding was lost. Handedness was established by means of the Edinburgh Handedness Inventory (Oldfield, 1971), with participants obtaining a score of 70 or above considered right-handed. Participants' familial sinistrality was also assessed; F+ was defined as the presence of at least one left-hander in the immediate family. Participants were randomly assigned to one of three test conditions: (a) a semantic memory task wherein participants were required to complete word fragments, (b) an episodic task wherein participants were required to recognize words as having been seen previously, or (c) an episodic task wherein participants were required to recall previously seen words.

Materials. Stimuli consisted of 110 words taken from Tulving, Schacter, and Stark (1982). Words ranged from seven to eight letters in length and were low in frequency. The 110 words were divided into two groups, with half of the words being shown to participants during a study phase and half serving as distractors for the recognition and word-fragment tasks. Study and distractor lists were counterbalanced within tasks.

During the study phase, 55 words were presented serially on a computer screen, each for 5 s. The first and last five words were considered filler words to control for position effects and were not included as items on the recognition or word-fragment tests, or in subsequent analyses. Words were always presented in the same order within a list. During the test phase, participants were presented with a list of 90 word fragments (word-fragment test), a list of 90 words (recognition test), or a blank piece of paper (recall test). Word fragments were identical to those used by Tulving et al. (1982). All words and word fragments were presented in uppercase, 28-point Courier font.

Design and procedure. All instructions were presented on either 486DX or Pentium computers equipped with 17-in (43-cm) monitors. Proctors were available to aid participants if they had difficulty with any instructions. As part of a larger test battery, participants were tested in groups and seated at individual workstations in five experimental sessions. Other tests in the battery included several psychomotor and cognitive tasks and four questionnaires. Results of these other tests will be reported elsewhere and are not relevant to the present experiment.

During the study phase, participants were seated approximately 43 cm from a computer monitor on which words were presented centrally for 5 s each. Participants were given general instructions to study the words shown to them and were told that they would later be tested on them. No explicit mention of the form of testing was made, and participants were not required to respond to any stimulus presentations. Following the study phase, all participants completed a computerized version of the Edinburgh Handedness Inventory. This took approximately 2–3 min and served as a distractor.

Participants in the word-fragment group were then given a list of 90 word fragments, half consisting of words they had studied previously and half consisting of distractors. Participants were asked to complete as many fragments as possible by filling in the blanks with letters so that the fragments formed words. Participants in the recall group were given a blank piece of paper and instructed to write down as many words from the study phase as they could remember. Participants performing the recognition task were presented with a list of 90 words, half of which they had studied previously and were asked to circle those they recognized as having been shown to them. All participants were told they had 20 min to complete the task.

Results

The proportion of items correctly completed or recognized on the word-stem task or the recognition task, respectively, was not an accurate measure of participants' performance. This was because it did not take into account a baseline number of items completed by chance that had not been previously presented or that had been falsely recognized. Therefore, as recommended by Graf and Mandler (1984), we used corrected scores as the dependent measure in all tasks. For the recognition task and for the word-fragment task, this was the number of items recognized or completed that had been previously studied minus the number of items falsely recognized or completed that had not been seen previously. For the recall task, we conducted analysis on the number of words correctly recalled minus the number of words falsely recalled. Preliminary analyses yielded no significant main effects or interactions involving sex of participant (all $F_s < 1$), so subsequent analyses collapsed across this factor. We conducted a 3×2 analysis

of variance (ANOVA) on the between-subjects variables of task (word-fragment, recognition, or recall) and familial sinistrality (FS+ or FS-).

Results revealed a main effect of task, $F(2, 174) = 216.55, p < .001$, with the recognition task yielding the best performance ($n = 62, M = 29.44$), followed by the word-fragment task ($n = 56, M = 10.38$), followed by the recall task ($n = 62, M = 3.55$). There was no main effect of familial sinistrality ($F < 1$).

A Task \times FS interaction, $F(2, 174) = 2.95, p < .05$, revealed that FS- participants ($n = 26, M = 12.46$) outperformed FS+ participants ($n = 30, M = 8.30$) in word-fragment completion ($p < .05$). FS+ participants ($n = 30, M = 4.67$) outperformed FS- participants in recall ($n = 32, M = 2.44, p < .01$). Group performance was equivalent for the recognition task (FS-: $n = 33, M = 30.06$; FS+: $n = 29, M = 28.83, p > .05$; see Figure 1).

Discussion

The hypothesis that episodic–explicit memory involves integration of processing between the cerebral hemispheres, whereas implicit memory does not, was supported by the finding that FS+ individuals, who were hypothesized to exhibit greater interhemispheric interaction, performed better on a recall task compared with FS- individuals, who were hypothesized to exhibit greater hemispheric independence. If implicit memory is a unilateral phenomenon, it is possible that greater interhemispheric interaction, such as that displayed by FS+ individuals, would be detrimental to this type of memory. Future research could involve investigation of the conditions under which FS+ participants'

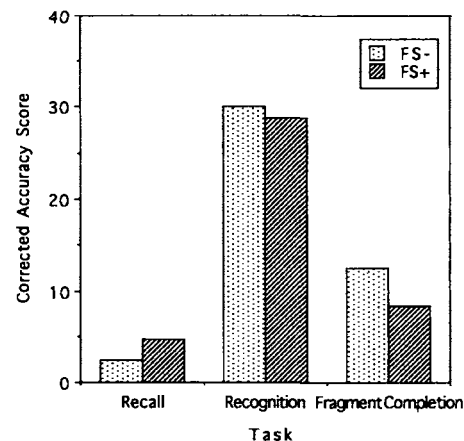


Figure 1. Corrected accuracy scores as a function of task and familial sinistrality (for recall, corrected accuracy equals number of words correctly recalled minus the number of words falsely recalled; for recognition and completion, corrected accuracy equals number of items recognized or completed that had been studied previously minus the number of items falsely recognized or completed that had not been seen previously). FS- = no left-handed relatives in immediate family; FS+ = at least one left-handed relative in immediate family.

performance on other implicit tasks suffers relative to the performance of FS- individuals.

The lack of individual differences in performance of the recognition task is somewhat puzzling, given the significant differences obtained with the other test of episodic memory (i.e., free recall). One possible explanation concerns the role of "remember" versus "know" responses in episodic recognition (e.g., Gardiner, 1988; Schacter, Verfaellie, & Anes, 1997). Remembering an item implies that participants have an explicit, consciously accessible representation of the stimulus in question. However, participants can know that they have seen a stimulus previously (e.g., on the basis of familiarity) but have no explicit, conscious representation of it. Although both judgments reflect episodic memory, remember judgments appear to involve a more direct form of conscious, episodic retrieval (e.g., Parkin & Russo, 1993) and are more susceptible to deterioration with temporal delays than are know judgments, in which resistance to temporal decay is more reminiscent of that displayed by semantic and implicit forms of memory (e.g., Gardiner & Java, 1991). To the extent that remember judgments represent a more pure measure of consciously retrieved episodic memories, it is possible that FS+ participants were biased toward successful recognition performance based on remember judgments, whereas FS- participants were biased toward know judgments. Although the present study cannot resolve this question, it is interesting that Propper and Christman (2001) found handedness differences in remember versus know judgments. Namely, in a test of recognition memory accompanied by participants making remember versus know judgments for recognized items, they found no overall differences in recognition memory between strongly right-handed and mixed-handed participants. However, strong right-handers were significantly biased toward making more know than remember judgments, whereas mixed-handers exhibited significantly more remember than know judgments. In this light, it is interesting that in the present Experiment 1, the FS- participants displayed a marginally significantly stronger degree of handedness than did the FS+ participants, $F(1, 173) = 3.62, p < .059$.

Experiment 2

Method

Participants. Participants were 84 right-handed undergraduate psychology students who received course credit for their participation. English was the native language for all participants. The Edinburgh Handedness Inventory was used to determine participants' handedness, with participants obtaining a score of 70 or above being considered right-handed; information concerning familial sinistrality was also collected and was defined as the presence (FS+) versus the absence (FS-) of at least one left-hander in an individual's immediate family. Individuals were assigned to one of two test conditions, with the result that 38 participants (23 FS-: 13 female, 10 male; 15 FS+: 8 female, 7 male) were tested on the semantic task and 46 participants (25 FS-: 19 female, 6 male; 21 FS+: 17 female, 4 male) were tested on the episodic task.

Materials. Stimuli consisted of 72 words and 72 nonwords. Words were taken from the norms of Toggia and Battig (1978) and were all high in frequency, imagery content, concreteness, and

familiarity. Nonwords were constructed by substituting at least one letter in a word with a new letter, with the result that the letter string was meaningless in the English language. Nonwords were pronounceable and consonant with the rules of English orthography. Letter strings were five letters in length and were presented in uppercase, 24-point Helvetica font. The first letter of stimuli presented to the right visual field (RVF) and the last letter of stimuli presented to the left visual field (LVF) fell 2.0° to the right or left, respectively, of a fixation marker.

Design and procedure. The 144 letter strings were divided equally and randomly into one of four groups such that 18 words and 18 nonwords were always presented (a) twice to the RVF, (b) twice to the LVF, (c) first to the RVF and second to the LVF, or (d) first to the LVF and second to the RVF. There were six blocks of 56 trials, each block consisting of two filler items, three practice stimuli (each presented twice), and 48 experimental trials, yielded by the factorial combination of 4 Visual Field Conditions (i.e., RVF-RVF, LVF-LVF, RVF-LVF, LVF-RVF) \times 2 Stimulus Types (i.e., words vs. nonwords) \times 6 Replications. Within each visual field condition, two replications involved four intervening items between first and second presentations of the stimulus, two replications involved five intervening items, and two replications involved six intervening items. The number of intervening items was varied so that participants could not anticipate repetitions. The range of numbers of intervening items was chosen to follow the procedure used by Leiber (1982).

Occasional filler items were included in each block to provide the proper spacing between stimulus repetitions. Filler and practice stimuli consisted of an equal number of words and nonwords meeting the criteria mentioned previously, and their presentation to either the LVF or the RVF was counterbalanced across blocks of trials. Particular letter strings did not appear in more than one block of trials. Because stimuli were presented in the same order between participants within a block of trials, three versions of stimuli presentation order were constructed. Order of block presentation followed a quasi-Latin square design, with the stipulation that all three versions of a block were never presented consecutively. Words and their particular nonword counterparts never appeared in the same block of trials.

Participants were tested individually, seated approximately 43 cm in front of a computer monitor on which letter strings were presented for approximately 180 ms to either the RVF or the LVF. The same stimuli were used for both the semantic and episodic tasks. In the semantic task, participants were instructed to determine whether the letter strings formed words or nonwords (lexical decision). In the episodic task, participants were asked to determine whether they had seen that letter string previously within a block of trials (recognition).

Each trial was preceded by an auditory warning tone indicating that the participant should focus on the fixation marker (a lowercase *x*) centered on the computer screen. A letter string was flashed to either the left or right of the fixation marker 800 ms after the tone. Participants indicated whether they saw a letter string for the first or second time (episodic task) or whether they saw a word or nonword (semantic task) by pressing the appropriate key. Participants were instructed to respond as quickly and as accurately as possible and were informed that each letter string would appear only in a single block of trials. Reaction time (RT) was measured in ms and was recorded by MacLaboratory from the onset of the stimulus to the participants' response. Errors were also recorded. RTs and errors to filler and practice trials were not included in subsequent analyses.

Results

Because the central interest in the present experiment was the effect of prior experience with a stimulus (i.e., memory for a stimulus) and because the effects of such experience were not evident until the original stimulus had been repeated, we chose to use a priming measure as the dependent variable rather than the raw RT values. This allowed us to focus on hemispheric differences in priming independently from overall visual field differences in performing the lexical decision and recognition memory tasks. We determined amount of priming in the following manner: We subtracted RTs to the presentation of second stimuli from RTs to the presentation of first stimuli. We conducted RT analyses on these transformed scores and included RTs in the analyses only if the participant responded correctly on both the first and second presentations of a stimulus. It must be noted that, for the recognition task, the measure was not strictly one of priming but was rather a measure of how quickly one can recognize an item as old, relative to how quickly one can recognize it as new on its first presentation. For sake of expositional clarity, however, we refer to it as a priming measure.

We conducted an initial six-way, mixed-factorial ANOVA with two levels of each factor on both RT priming scores and on errors; the factors were Task (semantic or episodic) \times Stimulus Type (word or nonword) \times Visual Field of First Presentation (left or right) \times Visual Field of Second Presentation (same or opposite visual field as first presentation) \times Familial Sinistrality (positive or negative) \times Sex (male or female). These analyses indicated no significant effects involving sex for the error data. The only effect of sex for the RT data was an interaction between familial sinistrality and sex, $F(1, 76) = 6.95, p < .01$. This reflected the fact that among FS- participants, men ($M = 113.2$ ms) showed more priming than did women ($M = 64.9$ ms), whereas among FS+ participants, women ($M = 85.5$ ms) showed more priming than did men ($M = 47.4$ ms). Because this effect did not involve or interact with the task or visual field variables of central interest, further analyses collapsed across the factor of sex.

Results revealed a main effect of task, $F(1, 80) = 6.84, p < .01$, such that there was significantly greater priming on the semantic task ($M = 105.0$ ms) compared with the episodic task ($M = 55.6$ ms). We obtained an interaction between stimulus type and task, $F(1, 80) = 9.14, p < .003$. Analysis of simple effects revealed that priming of nonwords during the episodic task ($M = 30.0$ ms) was significantly less than priming under all other conditions (words episodic task, $M = 81.1$ ms; nonwords semantic task, $M = 114.5$ ms; words semantic task, $M = 95.5$ ms, $p < .05$).

We obtained the predicted interaction between visual field of second presentation and task, $F(1, 80) = 5.05, p < .03$ (see Figure 2). The semantic task yielded greater priming when the repetition of stimuli was presented to the same visual field ($M = 114.5$ ms) than when the repetition was presented to the opposite visual field as the initial presentation ($M = 95.5$ ms). Conversely, the episodic task yielded greater priming when the repetition of stimuli was presented

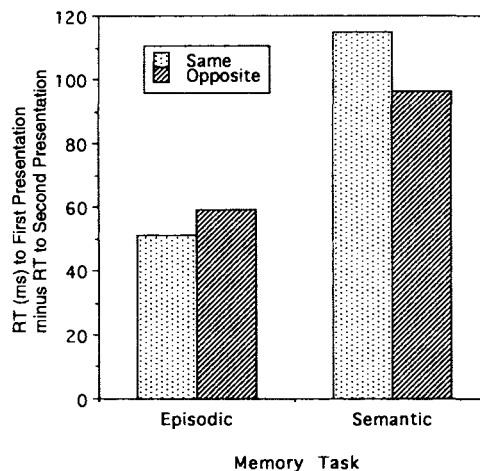


Figure 2. Magnitude of priming (first presentation RT minus second presentation RT in ms) as a function of memory task (episodic vs. semantic) and visual field of second presentation (same as first vs. opposite of first). RT = reaction time.

to the opposite visual field as the initial presentation ($M = 60.2$ ms) than when the repetition was presented to the same visual field ($M = 51.0$ ms). However, the simple effects involving within-task comparisons (i.e., same vs. opposite visual field presentations for each task separately) were not significant.

There was an interaction between stimulus type and visual field of first presentation, $F(1, 80) = 4.92, p < .03$. Analysis of simple effects revealed that words presented first to the LVF resulted in significantly more priming ($M = 98.3$ ms) than did nonwords presented first to the LVF ($M = 65.4$ ms, $p < .05$). Stimulus type did not affect priming for stimuli presented initially to the RVF (word, $M = 77.5$ ms; nonword, $M = 73.6$ ms). There was also an interaction between visual field of first presentation and visual field of second presentation, $F(1, 80) = 5.93, p < .02$, with stimuli presented twice to the RVF ($M = 87.7$ ms) resulting in more priming than stimuli presented first to the RVF and then to the LVF ($M = 63.4$ ms). Stimuli presented twice to the LVF ($M = 75.5$ ms) resulted in less priming than stimuli presented first to the LVF and then to the RVF ($M = 88.3$ ms), although analysis of simple effects yielded no significant differences.

With regard to the between-subjects variable of familial sinistrality, there was an interaction between participants' familial sinistrality and visual field of second presentation, $F(1, 80) = 4.95, p < .03$. FS- participants ($n = 48$) demonstrated more priming, regardless of task, when stimuli were presented twice to the same hemisphere ($M = 93.4$ ms), compared with when stimuli were presented to opposite hemispheres ($M = 74.5$ ms). FS+ participants ($n = 36$) exhibited more priming when stimuli were presented first to one visual field and then to the opposite ($M = 81.2$ ms), compared with when stimuli were presented to the same hemisphere twice ($M = 72.1$ ms), although analysis of simple effects yielded no significant differences (see Figure

3). All other main effects and interactions were nonsignificant, with p values above .12.

We defined *errors* as incorrect responses to the second presentation of a stimulus, given a correct response to the first presentation (we excluded conditions in which incorrect responses were given to the first presentation from all analyses). Results revealed a main effect of task, $F(1, 80) = 31.31, p < .01$, with more errors occurring during the episodic task ($M = 1.92$) compared with the semantic task ($M = 0.79$). In addition, there was a main effect of stimulus type, $F(1, 80) = 82.8, p < .01$, with more errors occurring in response to nonwords ($M = 1.95$) than to words ($M = 0.80$).

We obtained an interaction between stimulus type and task, $F(1, 80) = 21.36, p < .01$. Analysis of simple effects revealed that the greatest number of errors occurred in response to nonwords during the episodic task ($M = 2.76$), and the fewest occurred in response to words during the semantic task ($M = 0.45$), compared with other conditions (semantic task nonwords, $M = 1.13$; episodic task words, $M = 1.08, p < .05$). There was also an interaction between visual field of first presentation and visual field of second presentation, $F(1, 80) = 4.77, p < .05$, such that stimuli presented twice to the RVF resulted in significantly fewer errors ($M = 1.17$) than did stimuli presented first to the RVF and then to the LVF ($M = 1.52, p < .05$; twice to the LVF, $M = 1.40$; and first to the LVF field and then to the RVF, $M = 1.41$).

We obtained a three-way interaction between stimulus type, visual field of first presentation, and visual field of second presentation, $F(1, 80) = 9.06, p < .01$. Analysis of simple effects revealed significantly fewer errors in response to nonwords presented twice to the RVF ($M = 1.49$) compared with all other nonword presentation conditions (nonwords twice to the LVF, $M = 2.05$; nonwords first to the LVF and then to the RVF, $M = 1.99$; nonwords first to the RVF and then to the LVF, $M = 2.26, p < .05$).

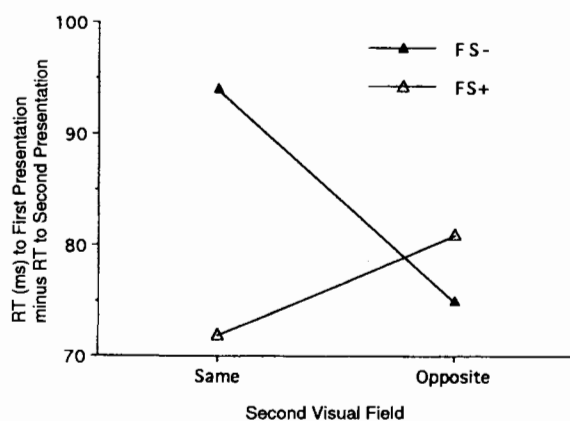


Figure 3. Magnitude of priming (first presentation RT minus second presentation RT in ms) as a function of familial sinistrality (FS- = no left-handed relatives in immediate family; FS+ = at least one left-handed relative in immediate family) and visual field of second presentation (same as first vs. opposite of first). RT = reaction time.

Post hoc analysis revealed an interaction between participants' familial sinistrality and visual field of first presentation, $F(1, 84) = 6.40, p < .05$. FS+ participants made the most errors when stimuli were presented first to the RVF, whereas FS- participants made the most errors in response to stimuli presented first to the LVF; however, simple effects were not significant.

Discussion

The results support the hypothesis that episodic-explicit memory is an interhemispheric phenomenon, whereas semantic-implicit memory is more intrahemispheric in nature. Although we predicted a same-hemisphere advantage for both the implicit fragment completion and episodic recognition tasks, results actually reveal an opposite-hemisphere advantage for the task accessing episodic memory. This is a rather counterintuitive finding. It would seem reasonable to expect that presentation of a stimulus twice to the same neural structure (i.e., cerebral hemisphere) would result in greater priming than would presentation of a stimulus twice but to different cerebral structures, regardless of task. The finding of an opposite-hemisphere advantage for magnitude of priming in the episodic task suggests that this type of memory is critically reliant on interhemispheric integration of processing.

With regard to Tulving et al.'s (1994) HERA model of episodic encoding and retrieval, the results offer qualified support for their theory. Although the general notion of interhemispheric versus intrahemispheric processing involved in episodic versus semantic memory, respectively, is supported, specifics of the HERA model are not. According to the model, episodic memory encoding and retrieval take place in the left and right prefrontal cortex, respectively, whereas the encoding and retrieval of semantic memories occur in the left prefrontal cortex. It may have been expected that, for the episodic task, the greatest amount of priming would occur when stimuli were presented first to the RVF/left hemisphere and second to the LVF/right hemisphere; however, we obtained the opposite-hemisphere advantage in the episodic task in equal magnitude regardless of the visual field of first presentation. Similarly, it may have been predicted that the greatest amount of priming for the semantic task would have occurred for stimuli presented twice to the RVF or left hemisphere. Indeed, this was the case; participants performing the semantic task did demonstrate the most priming when stimuli were presented twice to the RVF or left hemisphere, although the effect was not significant.

Although this discrepancy on the episodic task cannot be resolved on the basis of the present results, a number of methodological differences between the two studies may play a role. First, the correspondence between physiological data (as in the Tulving et al., 1994, study) and behavioral data (as in the present study) is not always straightforward. Second, the Tulving et al. article covered only studies using central presentation of input, thus allowing the encoding and retrieval systems considerable flexibility in determining which cortical regions handled which aspects of the task.

The use of lateralized presentation of input in the present experiment, however, served to externally constrain which hemisphere performed encoding versus which performed retrieval. That is, if there is a choice (e.g., as with central input projected to both hemispheres), then perhaps the left versus right hemispheres assume control over episodic encoding versus retrieval, respectively. When input to be encoded or retrieved is projected to a single hemisphere, however, then perhaps that hemisphere assumes processing control regardless of its preferred mode. If so, the present results suggest that episodic memory is generally benefited by between-hemisphere separation of encoding versus retrieval, independent of which hemisphere performs initial encoding operations.

In addition to the predicted Task \times Presentation Condition interaction, we also obtained an interaction between participants' familial sinistrality and same-different presentation condition. Across both tasks, FS+ versus FS- participants demonstrated opposite- versus same-hemisphere advantages, respectively, in magnitude of priming. It is important, however, that familial sinistrality did not factor into the Task \times Visual Field of Second Presentation interaction, showing that both FS- and FS+ participants demonstrated similar interhemispheric effects for episodic and semantic memory.

The finding that FS+ participants tended to display an opposite-hemisphere priming advantage may reflect a greater propensity toward bilateral processing in right-handed FS+ participants (e.g., Kee, Bathurst, & Hellige, 1983; McKeever, 1990, 1991; Varney & Benton, 1975; Zurif & Bryden, 1969). In addition, other research has indicated that personal, and presumably familial, left-handedness is associated with a larger corpus callosum (Burke & Yeo, 1994; Cowell, Allen, Kertesz, Zalatimo, & Denenberg, 1994; Habib et al., 1991; Kertesz, Polk, Howell, & Black, 1987), and it has been suggested that the relative size of this brain structure influences the amount of information transfer between the cerebral hemispheres, with a larger corpus callosum possibly encouraging more interhemispheric transfer of information (e.g., Christman, 1993, 1995, 2001; Dimond & Beaumont, 1972; Honda, 1982; McKeever & Hoff, 1983; Moscovitch & Smith, 1979; Potter & Graves, 1988; Verillo, 1983). To the extent that FS+ individuals share characteristics with personal left-handers, then FS+ participants may also exhibit greater interhemispheric integration. Because the exact influence of familial sinistrality on aspects of interhemispheric processing is still unclear, conclusions regarding greater interhemispheric interaction in FS+ participants must be considered speculative.

Furthermore, the superiority of FS+ participants on episodic memory tasks found in Experiment 1 was not obtained in Experiment 2. Two possible explanations can be provided. First, Experiment 1 used central presentation of stimuli, whereas Experiment 2 involved lateralized presentations. Individual differences in interhemispheric interaction may differ as a function of both hemispheres having equal access to input (as in central presentation) versus hemispheric access being directly determined by location of input (as in lateralized presentation). Second, it is possible

that the effects in Experiment 1 were partially mediated by marginally significant differences in strength of handedness between FS- and FS+ participants. In contrast, there were no differences in Experiment 2 in strength of handedness between FS- and FS+ participants ($F < 1$).

General Discussion

The present experiments provide tentative behavioral support for (a) the existence of individual differences in memory performance as a function of task and familial sinistrality and (b) the existence of between- versus within-hemisphere processing advantages in episodic versus non-episodic memory, respectively. In Experiment 1, within- versus between-hemisphere processing was manipulated indirectly by comparing the performance of FS+ versus FS- participants, with the assumption that FS+ participants would exhibit relatively greater degrees of interhemispheric interaction, which in turn was hypothesized to selectively benefit episodic memory. Results are consistent with our framework, as FS+ versus FS- status was associated with superior performance in episodic-explicit versus implicit memory tasks, respectively. In Experiment 2, when within- versus between-hemisphere processing was directly manipulated by presenting subsequent input to either the same or the opposite hemisphere as the initial presentation, superiority in episodic versus semantic memory was associated with between- versus within-hemisphere presentation of input, respectively.

The results of Experiment 1 have important potential implications for research into memory and cognition. The presence of individual differences in episodic memory tasks as a function of familial sinistrality suggests that studies of individual differences in memory should pay attention to familial (and probably personal) handedness. At the very least, restriction of participant samples to strongly right-handed FS- participants would provide for the most homogenous pool. At best, the presence of systematic individual differences in episodic memory could provide a useful tool in developing formal models of memory processes (e.g., taking into account systematic differences in interhemispheric interaction). In a related vein, studies of amnesic syndromes may benefit from taking handedness into account, as the greater interhemispheric interaction and superior episodic memory displayed by FS+ individuals could have systematic relations to both severity of amnesia and anatomical locus of brain damage.

The results of Experiment 2 provide direct behavioral evidence for an interhemispheric division of labor in episodic encoding and retrieval. Current models of the neural bases of memory systems are not sufficiently advanced as to provide an explanation for this effect. That is, it is not clear why episodic memories benefit from an interhemispheric division of labor, whereas semantic and implicit memories benefit from unihemispheric processing. For example, the HERA model is descriptive primarily when it comes to interhemispheric issues. The focus of attention in testing such models has been on intrahemispheric differences between memory systems (e.g., the role of lateral temporal

areas in episodic encoding versus the role of medial-temporal areas in semantic retrieval). An admittedly speculative account for these findings involves the fact that episodic memories have two components: (a) the memory event itself and (b) the spatial and temporal context surrounding that event. Given the fact that the left-lateralized implicit memories involve retrieval of the event itself, in the absence of explicit retrieval of the spatiotemporal context, it may be the case that the specific events and stimuli are stored in the left hemisphere, whereas the surrounding spatiotemporal context is stored in the right hemisphere. Although this is likely to be an overly simplistic notion, it does suggest possible ways to test it. For example, the retrieval of the spatiotemporal context surrounding an event, in the absence of explicit memory for the event itself, is a fairly common metacognitive failure (e.g., remembering that one had an interesting thought earlier in the day while sitting at one's desk but being unable to recall the thought itself). The proposed account predicts that such metacognitive failures would be associated with right-lateralized cortical activity.

The present findings also shed light on a potential neural mechanism underlying *childhood amnesia*, the absence of episodic memories for the first 3 or 4 years of life. Namely, the offset of childhood amnesia (i.e., the onset of episodic memory; Bruce, Dolan, & Philips-Grant, 2000; Eacott & Crawley, 1999; Perner & Ruffman, 1995) roughly coincides with the maturation and myelination of the corpus callosum (Giedd et al., 1996; Knyazeva & Farber, 1991; Witelson & Kigar, 1988; Yakovlev & Lecours, 1967). To the extent that the present results suggest that interhemispheric integration underlies episodic memories, a functional corpus callosum should be critical in the formation of such memories. Thus, perhaps the maturation of the corpus callosum during early childhood is at least partly responsible for the offset of childhood amnesia.

In conclusion, the present experiments provide initial support for the hypothesis that the retrieval of episodic memories is at least in part dependent on interhemispheric interaction. Participants with greater degrees of interhemispheric interaction displayed superior episodic memory (Experiment 1), and presentation conditions that forced interhemispheric interaction were associated with superior episodic memory (Experiment 2). This hypothesis has recently received further support with the finding that alternating leftward-rightward eye movements, which activate the right and left hemispheres in parallel (e.g., Bakan & Svorad, 1969) and therefore presumably enhance interhemispheric interaction, lead to improvements in episodic-explicit, but not implicit, memory (Christman & Garvey, 2000).

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Received November 13, 2000

Revision received June 1, 2001

Accepted June 4, 2001 ■