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Handedness Is Related to Memory via Hemispheric Interaction: Evidence From Paired Associate Recall and Source Memory Tasks

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Strongly right (SR)-handedness is associated with poorer memory performance than nonstrongly right (nSR)-handedness (e.g., Propper, Christman, & Phaneuf, 2005). The hemispheric interaction theory states that the nSR memory advantage occurs because nSR handedness, compared with SR, is a behavioral marker for greater interaction of the cerebral hemispheres. The hemispheric interaction theory predicts that the nSR advantage should be observed exclusively on memory tasks that require hemispheric interaction. The authors tested that prediction by comparing middle-aged and older adults on two memory tasks thought to depend on hemispheric interaction (paired associate recall, source memory) and two thought not to (face recognition, forward digit span). An nSR advantage was more robust for middle-aged than older subjects and, consistent with the hemispheric interaction theory, was found only on the tasks that depend on hemispheric interaction.

Keywords: memory, handedness, hemispheric interaction, aging

Recent studies indicate that memory performance is related to handedness (Christman, Propper, & Brown, 2006; Christman, Propper, & Dion, 2004; Propper et al., 2005). These studies have not been concerned with the common distinction between left- and right-handedness. Rather, they examined memory performance as a function of whether individuals are "strongly" or consistently right lateralized in their handedness behavior or not. In everyday settings, many individuals exhibit strongly right (SR)-handedness behavior, meaning that they exclusively, or nearly so, use the right hand to perform feats of manual dexterity (e.g., writing, brushing one's teeth, using scissors). In the rest of the population, there is a wide range of nonstrongly right (nSR) behavior, including relatively "weaker" or less consistent right-handedness, and also left-handedness, which also manifests more or less strongly. Surprisingly, as summarized later, Christman, Propper, and colleagues have found that nSR handedness is associated with superior performance on some tests of memory.

To date, nSR and SR individuals have been compared in several different experimental paradigms, with nSR subjects outperforming SR subjects in some, but not all, cases. Compared to SR subjects, nSR subjects have been found to: (1) recall more items from a random word list on a free recall test (Propper et al., Experiment 1, 2005); (2) more accurately recall recent autobiographical events (Propper et al., Experiment 2, 2005); (3) recall earlier childhood memories (Christman et al., 2006); and (4) after studying lists of words that are associated with nonpresented words (Deese, 1959; Roediger & McDermott, 1995), falsely recall fewer of the nonpresented words (Christman et al., 2004). In contrast, no differences as a function of handedness have been found in recognition accuracy for words (Propper & Christman, 2004) or in word fragment completion (Propper et al., Experiment 1, 2005)—the latter being a measure of implicit memory.[1] Summarizing these results, nSR individuals have advantages over SR individuals in free recall of both laboratory and autobiographical events, but no advantage in recognition memory or implicit memory.

How can a relationship between handedness and memory be explained? Christman, Propper, and colleagues (e.g., Propper et al., 2005) theorize that the association is driven by individual differences in a third variable that is related to both handedness and memory. That variable is hemispheric interaction, which is defined as the transmission of neural signals between the left and right cerebral hemispheres via the corpus callosum and other forebrain commissures. According to this theory, nSR individuals recall better than SR individuals because hemispheric interaction is greater in the former than the latter. The hemispheric interaction

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[1] Although two experiments showed no handedness difference in recognition accuracy (i.e., discriminating old from new items), Propper and Christman (2004) did find that nSR subjects were more likely than SR subjects to report basing their recognition responses on the recollection of specific episodic details versus on a less specific feeling of knowing (see Tulving, 1985). The researchers did not assess whether this difference reflected a difference in actual ability to recollect veridical details about studied items, or merely a difference in subjects' tendency to describe their experience as remembering versus knowing.

theory of the nSR memory advantage rests on two major assumptions. The first is that handedness is, indeed, a behavioral marker for degree of hemispheric interaction. This is supported by several studies that have found that some regions of the corpus callosum, which is the largest pathway for hemispheric interaction in the brain, are larger in nSR than SR individuals (e.g., Cowell, Kertesz, & Denenberg, 1993; Habib et al., 1991; Witelson, 1985). However, it should be noted that other investigations have failed to find any relationship between handedness and the morphology of the corpus callosum (e.g., Jäncke & Steinmetz, 2003; Kertesz, Polk, Howell, & Black, 1987).

The second assumption of the hemispheric interaction theory is that degree of hemispheric interaction has functional consequences for memory (for related ideas, see Christman, Garvey, Propper, & Phaneuf, 2003; Christman & Propper, 2001). At least in the extreme case, in which persons with little or no hemispheric interaction are compared with normal controls, this assumption is supported. Individuals who have had the cerebral hemispheres partially or completely disconnected via surgical section of the corpus callosum and/or other hemispheric commissures (i.e., callosotomy or, more generally, commissurotomy), and individuals who have failed to develop a normal corpus callosum (i.e., callosal agenesis), exhibit memory deficits relative to persons with fully developed, intact commissures (e.g., Cronin-Golomb, Gabrieli, & Keane, 1996; Geffen, Forrester, Jones, & Simpson, 1994; Jha, Kroll, Baynes, & Gazzaniga, 1997; Phelps, Hirst, & Gazzaniga, 1991; Zaidel & Sperry, 1974). Presumably, the difference in hemispheric interaction between nSR and SR individuals is not as dramatic as between split-brain individuals and anatomically normal controls, but it may be that even relatively minor differences have consequences for memory function.

In the present investigation, we sought to test an obvious prediction of the hemispheric interaction theory: The nSR advantage should be observed on memory tasks that depend on hemispheric interaction, but not on tasks that do not (see Propper et al., 2005, for similar logic). Research with commissurotomy patients and with neuroimaging techniques has identified several tasks that involve hemispheric interaction, and several that apparently do not. Below we discuss seven specific memory tasks, three that are known, or are strongly believed, to depend on hemispheric interaction via the forebrain commissures, and four that are not.

Memory Tasks That Depend on Hemispheric Interaction

Free recall (the ability to recall prior information about specific episodes with only minimal external cues) depends on hemispheric interaction, as evidenced by Phelps et al.'s (1991) finding that collosotomy patients showed lower free recall of word lists than did age- and education-matched controls. This effect is not specific to recall of individual words: Cronin-Golomb et al. (1996) found that commissurotomy patients were impaired at recalling brief stories.

As with free recall, research with commissurotomy patients has established a role for hemispheric interaction in verbal paired associate recall, which involves studying cue-target word pairs and later recalling the targets when given the cues. Several groups of researchers have found that split-brain patients show impairments on this type of memory test (Cronin-Golomb et al., 1996; Jha et al., 1997; Phelps et al., 1991).

To our knowledge, source memory, or memory for the source or origin of information (e.g., who uttered a particular statement), has not been directly investigated in split-brain patients, thereby depriving us of a strong test of whether this type of memory depends on hemispheric interaction. However, Johnson and colleagues (Johnson & Raye, 2000; Raye, Johnson, Mitchell, Nolde, & D'Esposito, 2000) have theorized that hemispheric interaction is more likely to be necessary for memory tasks requiring complex, systematic processing (e.g., source memory, free recall) than for those that can be done more heuristically (e.g., old/new recognition). Data regarding the neural correlates of source memory and old/new recognition in anatomically intact individuals are consistent with this idea. Old/new recognition, which may involve relatively cursory evaluation of reactivated information and relatively little self-initiated retrieval of additional information, is associated with right-lateralized increases in prefrontal cortex activity (e.g., Shallice et al., 1994; Tulving et al., 1994). In contrast, source memory tasks that require the self-initiated retrieval and careful evaluation of more differentiated source information tend to increase prefrontal cortex activity bilaterally (e.g., Nolde, Johnson, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1998; Ranganath & Knight, 2003). Johnson and colleagues theorize that these bilateral activations represent interhemispheric coordination of the more extensive processing necessary to perform these more complex tasks (see also Weissman & Banich, 2000).

Memory Tasks That Do Not Depend on Hemispheric Interaction

The ability to recognize previously studied words appears not to depend on hemispheric interaction. Two callosotomy patients in Phelps et al. (1991) made old/new recognition judgments about words as accurately as did age- and education-matched controls. In addition, Geffen et al. (1994) found that subjects with complete callosal agenesis were characterized by "poor delayed recall combined with relatively high recognition" (p. 258) of words. This is consistent with the notion that hemispheric interaction is, if not wholly unimportant for recognition, substantially less important for recognition than for free recall.

Hemispheric interaction via the forebrain commissures is not necessary for implicit completion of word fragments with previously studied words, because patients with complete callosotomies show normal priming effects on fragment completion tasks (provided there is only one possible completion for the fragment; Kroll et al., 2003). Note, however, that fragment completion may depend on the interhemispheric transfer of information via subcortical routes (Cronin-Golomb et al., 1996).

The right hemisphere is well known to be specialized for the recognition of faces (e.g., Haxby et al., 1996; Rapcsak, Polster, Comer, & Rubens, 1994; Sergent, Ohta, & MacDonald, 1992) and research with split-brain patients confirms that successful face recognition can occur in the absence of hemispheric interaction. Callostomy patients in Gazzaniga and Smylie's (1983) study showed no deficit relative to control subjects in recognizing faces that were processed only by the right hemisphere.

Forward digit span, which is the number of digits that can be recalled in correct order immediately after presentation, is a common immediate memory measure and it seems not to depend on hemispheric interaction. Cronin-Golomb et al.'s (1996) commissurotomy patients had normal spans, and Phelps et al. (1991) found that, in a single patient from whom they had data, span was no lower postcommissurotomy than precommissurotomy (in fact, it was numerically higher postcommissurotomy).

Relation of Prior Handedness-Memory Research to the Hemispheric Interaction Theory

If nSR handedness is a marker for greater hemispheric interaction, and if free recall but not recognition or fragment completion depends on hemispheric interaction, then nSR individuals should outperform SR individuals on tests of free recall but not recognition or fragment completion. As reviewed earlier, Christman, Propper, and colleagues have observed an nSR advantage in free recall (Christman et al., 2004, 2006; Propper et al., 2005) but not in recognition accuracy (Propper & Christman, 2004) or fragment completion (Propper et al., 2005), which is precisely what we would expect based on the hemispheric interaction theory. One reason to be cautious about drawing conclusions from existing data, however, is that some of the test comparisons were cross-experimental. Specifically, free recall and recognition tests were administered to different groups of subjects in different experiments, leaving open the possibility that the different patterns obtained for the two test types reflected sample differences, rather than differences in hemispheric interaction requirements.

The Present Investigation

As stated earlier, the goal of the present investigation was to test the hemispheric interaction theory's prediction that handedness should be related to memory exclusively on tasks that depend on hemispheric interaction. To that end, in a sample of adults aged 30 to 90 years, we compared nSR versus SR individuals on four memory measures that have not previously been examined in handedness-memory research: verbal paired associate recall, source memory, face recognition, and forward digit span. As reviewed earlier, performance on the former two measures is thought to depend on hemispheric interaction and performance on the latter two is not. The same subjects received all four tests, so, if handedness effects emerged on some tests but not others, we could infer that the pattern reflected differing requirements for hemispheric interaction and not differing subject variables.

In addition to testing the hemispheric interaction theory, in the present investigation we could examine whether the nSR memory advantage exists across the adult life span. As noted, our sample included individuals aged 30 to 90 years. Samples in previous studies of the handedness-memory relationship have consisted solely of college-aged adults. Here, we were able to test whether the nSR advantage extends into middle adulthood (30–59 years old) and beyond that into late adulthood (60–90 years old).

From the perspective of the hemispheric interaction theory, the question of whether handedness-memory effects depend on age is of interest because the corpus callosum has been found to decrease in size in late adulthood (Cowell, Allen, Zalatimo, & Denenberg, 1992; Meier-Ruge, Ulrich, Bruhlmann, & Meier, 1992; Weis, Kimbacher, Wenger, & Neuhold, 1993). This age-related decrease in callosal size may lead to changes in hemispheric interaction (Duffy, McAnulty, & Albert, 1996). If hemispheric interaction is the link between handedness and memory, and the nature of such interaction changes with age, then so too may the relationship between handedness and memory.

Finally, in the present investigation, we added an additional control to constrain inferences made between SR and nSR groups. Assuming that nSR subjects would outperform SR subjects on some of our memory measures, we assessed whether the two groups are comparable in terms of basic cognitive abilities that may mediate memory performance. We compared nSR and SR subjects on vocabulary, which reflects general crystallized intelligence, and Raven's advanced progressive matrices, which reflects general fluid intelligence (Horn & Cattell, 1967). Prior investigations have not examined whether there are handedness differences on these measures. If nSR and SR individuals are equivalent in these general intellectual abilities, then, according to the hemispheric interaction theory, we would conclude that any memory differences as a function of handedness are specifically due to the influence of hemispheric interaction, rather than to differences in general crystallized or fluid intellect.

Method

Subjects

Subjects were 161 adults (96 females) aged 30 to 90 years from the Washington University community and the Saint Louis metropolitan area who participated in a study of cognition across the life span in the laboratory of H.L.R. (McCabe, Roediger, McDaniel, Balota, & Hambrick, 2008) and who subsequently completed the Edinburgh Handedness Inventory (Oldfield, 1971), which is the measure previously used to classify individuals as nSR or SR (see the Materials and Procedure sections below for details). In order to have sufficient power to detect differences between nSR and SR individuals, we combined data from individuals aged 30 to 59 to form a single group of middle-aged subjects and combined data from individuals aged 60 to 90 into a single group of older subjects.

Compared to subjects of the same age and handedness, one nSR middle-aged subject had a composite score on the four memory measures that was more than 3 *SD* below the mean and one SR middle-aged subject had a score on our measure of general fluid intelligence that was more than 3 *SD* below the mean. These two subjects were dropped from the analyses reported below. Finally, four older subjects (3 nSR and 1 SR) did not complete all four of the memory measures as part of the original study. To preserve comparability across the four measures, these four subjects were not included in the analyses reported below. Thus, we were left with 77 middle-aged subjects (50 females) and 78 older subjects (43 females).

Materials

Following Christman, Propper, and colleagues, we used the Edinburgh Handedness Inventory to assess the handedness behavior of our subjects. The Edinburgh is a self-report measure on which respondents indicate their handedness behavior for each of 10 everyday activities (writing, drawing, using a spoon, opening jars, brushing teeth, throwing, combing hair, using scissors, using a knife without a fork, and striking a match). For each activity, the response options (and the corresponding point values for the purpose of scoring) are Always Right (+10), Usually Right (+5), No Preference (0), Usually Left (−5), and Always Left (−10). Thus, scores range from + 100 (Always Right for every activity) to −100 (Always Left for every activity) in increments of 5.

Save for the source memory tests, all of the tests used were standardized, including verbal paired associates (Wechsler, 1997b), face recognition (Wechsler, 1997b), forward digit span (Wechsler, 1997a), Shipley vocabulary (Zachary, 1986), and Raven's advanced progressive matrices (Raven, Raven, & Court, 1998). Details regarding those materials are included in the referenced sources.

There were two source memory tests (see-hear and read-anagram). For each test, a set of 80 medium-frequency concrete words was randomly selected from a larger pool of such words to serve as studied items. Each test list consisted of 40 studied words and 20 new medium-frequency concrete words. For the see-hear test, half the studied items were viewed on a computer screen, and half were heard over headphones. Headphone volume was adjusted to a comfortable level by each subject prior to study. One word was presented every three seconds. For the read-generate test, all of the words were viewed on a computer screen. Half the studied words were presented normally, and half had two adjacent letters transposed. The adjacent letters were underlined, and subjects were instructed to switch these letters in order to identify the words. Each word was presented for five seconds. In the test phase of both the see-hear and read-anagram tests, all words were presented normally on the computer screen, in the same size and font type used during study (72-point Arial).

Procedure

Subjects were administered the various measures described in the Materials section above (except for the Edinburgh Handedness Inventory) as part of a large study of cognition across the life span, conducted in H.L.R.'s laboratory (McCabe et al., in preparation). In that study, subjects aged 18 to 90 years completed an extensive battery of memory and attention measures and gave permission to the experimenters to contact them in the future about additional investigations. We mailed copies of the Edinburgh Handedness Inventory to these subjects and invited them to fill it out and return it in a self-addressed stamped envelope. Furthermore, we telephoned those individuals who did not return the Edinburgh by mail and offered them the chance to answer the questions by phone. The response rate from persons aged 18–30 was low (65.5%, n = 19/29) and so we did not include data from individuals in that age range in the analyses reported here. The response rate for persons of all other ages was 95.3% (n = 161/169).

We classified subjects as nSR or SR based on their scores on the Edinburgh Handedness Inventory. Following Christman, Propper, and colleagues, we first calculated the median Edinburgh score, which was 95 for middle-aged and older subjects alike. We then classified subjects as nSR whether their Edinburgh score was less than 95 and as SR whether their score was equal to or greater than 95. Thus, handedness behavior in the SR group was quite homogeneous with all subjects scoring either 95 or 100, but it was extremely heterogeneous in the nSR group with scores ranging from −100 to 90 (median = 80). This classification scheme yielded, among middle-aged adults, 36 nSR and 41 SR subjects, and, among older adults, 34 nSR and 44 SR subjects. Within the middle-aged and older groups, the mean age of nSR and SR subjects was comparable. Among middle-aged adults, the mean age of nSR and SR subjects was 44.0 and 45.0, respectively, and the corresponding means among older adults were 72.9 and 74.3.

The standardized measures were administered according to their conventional protocols. The verbal paired associates task is a measure of associative recall (Wechsler, 1997b). Eight pairs of unrelated words were read to subjects at a rate of one pair every three seconds. After listening to these word pairs, subjects were given the first word in the pair and asked to produce the second. This procedure was repeated four times, with the order of the pairs presented in a different fixed random order each time. The number of correct answers, out of 32, was the measure of associative recall. The Faces test is a test of face recognition memory (Wechsler, 1997b). Subjects studied a series of 24 faces presented at a rate of one every two seconds, with a 1-s interstimulus interval. The test involved presentation of 24 studied and 24 new faces. Subjects were asked to say YES if a face presented on the test was one they studied, and NO if it was not. The number of correct answers (i.e., old items called old plus new items called new, or hits plus correct rejections) was the measure of face recognition. The digit span task was the forward digit span task from the Wechsler Adult Intelligence Scale-Third Edition (WAIS-III; Wechsler, 1997a). This test involved reading digit strings of varying lengths to subjects at a rate of one word per second, and then having them recall them in their correct serial order. The strings of digits varied in length between two and nine. Two trials of each length were presented, in a stair-step fashion, that is, the test began with trials of the shortest length and then proceeded to trials of the next longest length. The test was stopped when both trials at a given length were missed. The measure of digit span was the total number of trials for which all the items were correctly recalled in the correct serial order. The Shipley vocabulary test is a 40-item multiple choice vocabulary test (Zachary, 1986) used to assess crystallized intelligence. The subject chose a synonym to a target word from among four possible answer choices. The number of correct answers was the measure of vocabulary performance. Raven's advanced progressive matrix is a paper-and-pencil abstract reasoning task used to assess fluid intelligence. The task involved choosing one of several abstract figures to complete a series of abstract figures that adhered to a particular rule. There were 16 total items, and subjects were given 10 minutes to answer as many as possible, with the number correct serving as the measure of fluid intelligence (Salthouse, Atkinson, & Berish, 2003).

For the see-hear source memory test, subjects viewed half the studied words on a computer screen and heard the other half on headphones. Following study, subjects took a test in which they responded to words by pressing keys marked S, H, or N, to indicate whether they Saw the item, Heard the item, or the item was New. Prior to the study phase of the read-anagram source memory test, subjects practiced identifying, out loud, 18 anagrams using the letter transposition task (note that none of the subjects incorrectly identified more than one item during the practice phase). Subjects then completed the study phase in which they viewed half the words normally and solved the other half from anagrams. The test phase was identical to that of the see-hear test, except that subjects responded on the test using keys marked R, A, or N, to indicate Read, solved as an Anagram, or New.

Results

Data from each measure were submitted to separate 2 (handedness: nSR or SR) × 2 (age: middle-aged or older) between-subjects analyses of variance (ANOVA).[2] Table 1 shows group means.

Shipley Vocabulary and Raven's Progressive Matrices

Unsurprisingly, older subjects had lower scores than middle-aged subjects on Raven's progressive matrices, which assesses fluid intelligence, and higher scores on the Shipley Vocabulary Test, which taps crystallized intelligence. The effect of age was reliable for both Raven's, $F(1, 1{,}51) = 54.52$, $MSE = 6.56$, $p < .01$, $\eta_p^2 = .27$, and Shipley, $F(1, 151) = 4.07$, $MSE = 11.62$, $p < .05$, $\eta_p^2 = .026$. Analyses of these measures yielded no other significant effects (smallest p value for any other main effect or the interaction = .12). The lack of an effect of handedness indicates that nSR and SR individuals do not differ in crystallized or fluid intelligence. Having established their equivalence on these basic cognitive attributes, we turn to whether nSR and SR subjects differed on measures of memory.

Verbal Paired Associate Recall

Verbal paired associate recall was greater for middle-aged ($M = 21.1$) than older subjects ($M = 17.4$), and, more important for present purposes, nSR subjects ($M = 20.6$) had greater recall than SR subjects ($M = 18.0$). The effect of age was significant, $F(1, 151) = 8.03$, $MSE = 64.8$, $p < .01$, $\eta_p^2 = .051$, as was the effect of handedness, $F(1, 151) = 4.06$, $MSE = 64.8$, $p < .05$, $\eta_p^2 = .026$. Although the interaction was not conventionally significant, $F(1, 151) = 1.73$, $MSE = 64.8$, $p > .19$, graphical inspection of the group means (see Figure 1) makes salient the fact that the nSR advantage was much larger for middle-aged than older subjects. Indeed, the main effect of handedness appears to be driven primarily by the large effect among middle-aged subjects. Therefore, we compared nSR and SR subjects in each age group individually and found that the nSR advantage was reliable for middle-aged adults, $t(75) = 2.40$, $p < .05$, Cohen's $d = .55$, but not for older adults, $t(76) = .49$, $p = .63$.

Table 1
Mean Shipley Vocabulary, Raven's Progressive Matrices, Verbal Paired Associate Recall, Source Memory, Forward Digit Span, and Face Recognition Scores (With SE) as a Function of Handedness and Age

Age	Measure	Handedness: nSR	Handedness: SR
Middle-aged			
	Shipley Vocabulary	33.6 (.57)	33.5 (.53)
	Raven's Progressive Matrices	8.6 (.43)	8.4 (.40)
	Verbal Paired Associate Recall	23.3 (1.3)	19.0 (1.3)
	Source Memory	.82 (.02)	.77 (.02)
	Face Recognition	38.2 (.72)	38.9 (.62)
	Forward Digit Span	12.1 (.34)	12.1 (.32)
Older			
	Shipley Vocabulary	35.4 (.58)	34.0 (.51)
	Raven's Progressive Matrices	6.0 (.44)	4.9 (.39)
	Verbal Paired Associate Recall	17.9 (1.4)	17.0 (1.2)
	Source Memory	.74 (.02)	.76 (.02)
	Face Recognition	35.4 (.74)	35.3 (.65)
	Forward Digit Span	11.8 (.35)	11.3 (.31)

Note. nSR = nonstrongly right-handedness; SR = strongly right-handedness.

Source Memory

The measure of source memory was calculated as the proportion of correctly recognized items that were attributed to the correct source (read or heard; or presented as words or as anagrams). The scores were then averaged. On this composite measure of source memory, age and handedness interacted, $F(1, 151) = 4.93$, $MSE = .01$, $p < .05$, $\eta_p^2 = .032$. Among middle-aged subjects, source memory was greater for nSR ($M = .82$) than SR ($M = .77$) subjects and the difference was significant by an independent samples t-test, $t(75) = 2.77$, $p < .01$, Cohen's $d = .64$. In contrast, among older subjects, the direction of the handedness difference was reversed, with SR subjects ($M = .76$) slightly outperforming nSR subjects ($M = .74$), but this difference did not approach significance, $t(76) = .74$, $p = .46$. Figure 2 shows this interaction graphically. Again, for completeness, we note that there was a significant main effect of age, $F(1, 151) = 7.25$, $MSE = .01$, $p < .01$, $\eta_p^2 = .046$, but not handedness, $F(1, 151) = 1.06$, $MSE = .01$, $p = .30$. In sum, there was an nSR advantage in source memory, but only among middle-aged adults.

Face Recognition

Face recognition was significantly greater for middle-aged subjects ($M = 38.5$) than older subjects ($M = 35.4$), $F(1, 151) = 20.5$, $MSE = 18.4$, $p < .01$, $\eta_p^2 = .12$, but there was no main effect of handedness, $F(1, 151) = .16$, $MSE = 18.4$, $p = .69$, nor an interaction between age and handedness, $F(1, 151) = .35$, $MSE = 18.4$, $p = .55$.

Forward Digit Span

Forward digit span was higher for middle-aged subjects ($M = 12.1$) than older subjects ($M = 11.5$) and this difference approached significance, $F(1, 151) = 3.30$, $MSE = 4.10$, $p < .08$, $\eta_p^2 = .02$. There was no main effect of handedness, $F(1, 151) = .66$, $MSE = 4.10$, $p = .42$, and no interaction, $F(1, 151) = .72$, $MSE = 4.10$, $p = .40$.

Discussion

In this study, using a sample of adults ranging from middle to late adulthood, we compared individuals exhibiting nSR versus SR handedness behavior on four very different memory measures (verbal paired associate recall, source memory, face recognition, and forward digit span). Prior research has shown that nSR individuals outperform SR individuals on various free recall tests of memory (Christman et al., 2006, 2004; Propper et al., 2005). The sole theory currently put forth to explain the nSR memory advantage is the hemispheric interaction theory, which posits that the advantage exists because nSR individuals experience greater hemispheric interaction than do SR individuals, and this imparts a

[2] In preliminary analyses, sex was included as a third variable, but it did not significantly interact with handedness on any measure and so for ease of exposition it was not included in the analyses reported below.

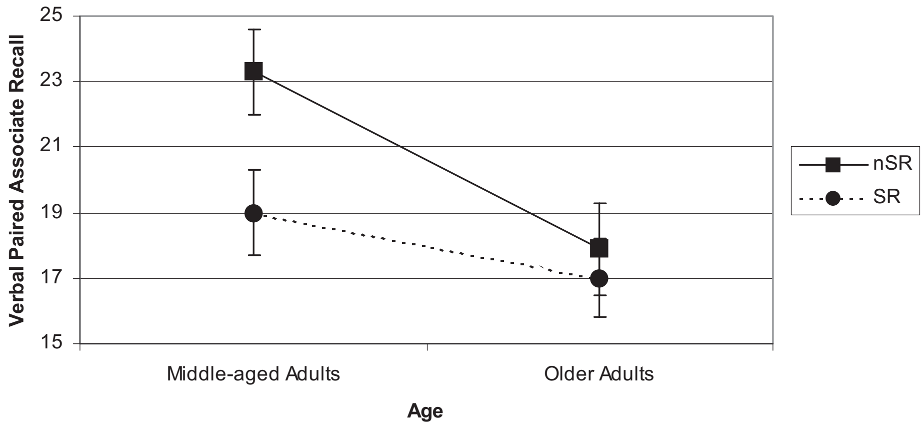

Figure 1. Mean verbal paired associate recall score as a function of handedness and age. Error bars represent ± 1 *SE*.

memorial benefit on the former. The hemispheric interaction theory makes a clear prediction, which we tested here: An nSR advantage should be observed only on memory tasks that depend on hemispheric interaction for their successful completion. Of the four memory tasks we examined, verbal paired associate recall and source memory are thought to depend on hemispheric interaction (Cronin-Golomb et al., 1996; Jha et al., 1997; Johnson & Raye, 2000; Phelps et al., 1991; Raye et al., 2000), whereas face recognition and forward digit span are not (Cronin-Golomb et al., 1996; Gazzaniga & Smylie, 1983; Phelps et al., 1991).

The prediction of the hemispheric interaction theory was borne out by our findings. An nSR advantage was observed, at least for middle-aged subjects, in verbal paired associate recall and source memory, but not in face recognition or forward digit span. On the latter two tests, nSR and SR individuals performed comparably. The same subjects completed all four tests, so it is impossible that our finding of a handedness effect on the tasks requiring hemispheric interaction, but not on the other tasks, was due to subject variables. Furthermore, given that we were able to detect a significant difference between nSR and SR individuals on verbal paired associate recall and source memory, it is unlikely that our failure to do so on forward digit span and face recognition was due to insufficient power. Finally, it is unlikely that the memory tasks that showed handedness effects did so simply because they were more difficult than those that did not. If that were the case we should have observed a handedness effect on the Raven's test, a very difficult fluid ability task.

The present results mesh neatly with past ones in supporting the hemispheric interaction theory. Christman, Propper, and colleagues have found an nSR advantage in free recall (Christman et al., 2006, 2004; Propper et al., 2005), which is dependent on hemispheric interaction (Cronin-Golomb et al., 1996; Phelps et al., 1991), but not in fragment completion (Propper et al., 2005), which is not dependent on hemispheric interaction, or word recognition (Propper & Christman, 2004), which is either not dependent on hemispheric interaction (Phelps et al., 1991), or is substantially less dependent on it than is free recall (Geffen et al., 1994). Thus, to date, the hemispheric interaction theory has successfully predicted the presence of an nSR advantage on three memory tasks thought to require hemispheric

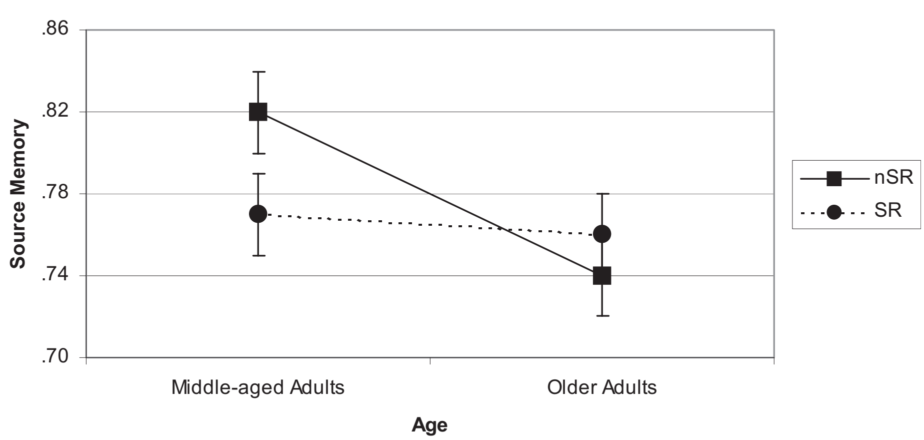

Figure 2. Mean source memory score as a function of handedness and age. Error bars represent ± 1 *SE*.

interaction (verbal paired associate recall, source memory, free recall) and the absence of an advantage on three tasks thought not to share that requirement (face recognition, forward digit span, fragment completion, word recognition).

It is important to note that, for the first time in the published literature, we tested for, but did not find, differences between nSR and SR individuals on Shipley vocabulary, a measure of crystallized intelligence, or on Raven's advanced progressive matrices, a measure of fluid intelligence. Hence, we found no evidence that nSR individuals' superiority on certain memory tasks could be attributed to them possessing greater crystallized or fluid intelligence.

The Shipley vocabulary test is, of course, also a measure of verbal ability and from that perspective it is notable that nSR subjects did not score higher on it, because prior evidence of an nSR memory advantage has come primarily from tests of memory for verbal materials, including individual words (Christman et al., 2004; Propper et al., Experiment 1, 2005) and autobiographical events that were written down in a journal (Propper et al., Experiment 2, 2005). The lack of a handedness difference in vocabulary suggests that the prior and current findings of an nSR advantage in memory for verbal stimuli is not the result simply of superior verbal proficiency in nSR individuals. Converging evidence that handedness differences in memory are not specific to verbal content is the present finding of an nSR memory advantage for nonverbal source information.

A goal of the present investigation, in addition to testing the hemispheric interaction theory, was to explore whether the nSR memory advantage extends across the adult life span. Prior studies have examined the handedness-memory relationship only in college-aged adults. Here, our subjects were in middle and late adulthood. Among middle-aged subjects, there was a clear handedness-memory association: On both verbal paired associate recall and source memory, nSR subjects had higher scores than SR subjects (see Figure 1). Thus, the nSR memory advantage is not a fleeting feature of young adulthood, but rather extends well into midlife.

This study yielded no clear evidence that the nSR memory advantage extends beyond middle into late adulthood. In source memory, there was no evidence whatsoever of an nSR advantage among older adults. Indeed, nSR subjects had numerically lower scores than SR subjects. In verbal paired associate recall, there was a main effect of handedness and no reliable interaction with age, reflecting the fact that, among both middle-aged and older subjects, scores were higher for nSR subjects. However, the nSR advantage was not individually reliable for older subjects as it was for middle-aged ones. Therefore, we cannot conclude with any confidence that, in late adulthood, there is an nSR advantage on either source memory or verbal paired associate recall.

Given our very preliminary understanding of the nSR memory advantage in young and middle adulthood, any attempt to explain why the effect would be eliminated in late adulthood must be highly speculative. Nevertheless, if we draw on the hemispheric interaction theory and assume that the advantage depends on hemispheric interaction, then two potential explanations suggest themselves. The first is that, in late adulthood, the difference in hemispheric interaction between nSR and SR individuals may be reduced relative to early life. The major pathway for hemispheric interaction, the corpus callosum, is known to decrease in size in old age (Cowell et al., 1992; Meier-Ruge et al., 1992; Weis et al., 1993). Perhaps, as the corpus callosum gets progressively smaller, the difference in callosal size (and hence hemispheric interaction) between nSR and SR individuals is reduced.

A second possibility is that, while nSR individuals may experience greater hemispheric interaction than SR individuals throughout adulthood, the consequences may be less uniformly positive in old age than in middle or young age. Neuroimaging research has shown marked variability between older adults in how they activate the cerebral hemispheres during memory tasks (Cabeza, Anderson, Locantore, & McIntosh, 2002). Specifically, some older adults appear to recruit the same neural network as younger adults but it is inefficient for them, while other older adults recruit a different and highly efficient network. Greater hemispheric interaction may enhance the operation of an efficient network, but be of little value (or perhaps even be detrimental) in the service of an inefficient one. Thus, greater hemispheric interaction associated with being an nSR individual may cease to confer a uniform memory advantage in old age. As stated, these accounts are speculative and only additional research, perhaps employing neuroimaging techniques, can reveal whether they have any merit.

Concluding Remarks

In this article, we have demonstrated that the memory advantage for nSR individuals over SR individuals is not limited to cases like those studied previously by Christman, Propper, and colleagues in which memory is tested via free recall. At the same time, we have shown that the nSR advantage is, indeed, limited and does not amount to generically "better memory" for nSR individuals. More important, we were able to predict, based on the hemispheric interaction theory, which memory tasks would and would not show the handedness effect. This supports the intriguing idea that handedness truly is a marker for functionally meaningful differences in hemispheric interaction. An important next test of the theory will be to use brain imaging techniques to compare callosal area and function in nSR versus SR individuals and to determine whether any differences are correlated with performance on the tasks implicated by behavioral studies as being dependent on hemispheric interaction. If future research also supports the theory, handedness may emerge as a new, methodologically convenient lens through which to examine how hemispheric interaction gives rise to remembering.

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