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Bimanual coordination positively predicts episodic memory: A combined behavioral and MRI investigation

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ABSTRACT

Some people remember events more completely and accurately than other people, but the origins of individual differences in episodic memory are poorly understood. One way to advance understanding is by identifying characteristics of individuals that reliably covary with memory performance. Recent research suggests motor behavior is related to memory performance, with individuals who consistently use a single preferred hand for unimanual actions performing worse than individuals who make greater use of both hands. This research has relied on self-reports of behavior. It is unknown whether objective measures of motor behavior also predict memory performance. Here, we tested the predictive power of bimanual coordination, an important form of manual dexterity. Bimanual coordination, as measured objectively on the Purdue Pegboard Test, was positively related to correct recall on the California Verbal Learning Test-II and negatively related to false recall. Furthermore, MRI data revealed that cortical surface area in right lateral prefrontal regions was positively related to correct recall. In one of these regions, cortical thickness was negatively related to bimanual coordination. These results suggest that individual differences in episodic memory may partially reflect morphological variation in right lateral prefrontal cortex and suggest a relationship between neural correlates of episodic memory and motor behavior.

1. Introduction

Episodic memory is the ability to recall personal, spatiotemporally-specific events. For example, episodic memory permits recollection of one's experiences on the night of the 2016 U.S. presidential election. Although all healthy individuals apparently possess episodic memory, they do not necessarily possess it in equal measure. Anecdotally, people often remark that some individuals seem to remember events more accurately or in more detail than other individuals. More formally, scores on standardized memory tests in samples of healthy individuals vary widely and have high test-retest reliability, suggesting that individual differences in memory are fairly stable (Lo, Humphreys, Bryne, & Pachana, 2012; Woods, Delis, Scott, Kramer, & Holdnack, 2006). As noted elsewhere (Bors & MacLeod, 1996), a complete understanding of the human memory system must entail the ability to explain individual variation in memory performance. While many potential sources of individual variation have been examined (e.g., Kirchhoff & Buckner, 2006; Maguire, Valentine, Wilding, & Kapur, 2003; Wig et al., 2008), much remains to be learned. Discovering novel correlates of memory performance can direct attention to previously unconsidered sources of variation. In the present study, a potential correlate of interest was manual dexterity.

Manual dexterity has not previously been linked to episodic memory (except by implication, as described below) and the possibility of linkage might seem remote. Manual dexterity is an aspect of motor behavior, while episodic memory is a form of complex cognition. Motor behavior and complex cognition are not widely recognized as related domains. Nonetheless, relationships between the two domains have been reported. For example, Nicholls, Chapman, Loetscher, and Grimshaw (2010) examined performance on a finger-tapping task and on a composite test of general cognitive ability. Subjects who were much faster with one hand than the other (or, in other words, who exhibited strong lateralization of manual dexterity) had somewhat lower cognitive ability than subjects with smaller between-hand differences (i.e., weaker lateralization). The test of general cognitive ability administered in Nicholls et al.'s study included a measure of word-list learning to assess memory, but the authors did not report memory's specific relationship with lateralization. Also, a recent review

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(van der Fels et al., 2015) concluded that there is some evidence for positive relationships between complex motor skills (e.g., bilateral body coordination) and high-level cognitive abilities among pre-pubertal children, but evidence for a specific relationship between motor skills and episodic memory comes from a single study (Davis, Pitchford, & Limback, 2011).

Most germane to the present research is the considerable literature linking episodic memory to an aspect of motor behavior known as hand preference. Hand preference refers to the human tendency to favor one hand over the other in the execution of unimanual tasks, such as writing and throwing. Based on this tendency, people commonly classify themselves and others as either left- or right-handed. In formal research, hand preference is precisely quantified using handedness questionnaires (often called inventories; e.g., Oldfield, 1971). These self-report instruments list specific real-world activities (e.g., throwing) and query the hand used (left or right) for each, as well as the consistency of usage (e.g., whether the specified hand is used always or only usually). Based on inventory responses, individuals may be described in terms of two separable dimensions of hand preference (e.g., Annett, 1970; Lyle, Hanaver-Torrez, Hackländer, & Edlin, 2012). One dimension is *direction*, referring to which hand (left or right) is used more than the other after summing across all activities. The other dimension captures variability in how consistently the preferred hand is used (regardless of direction), and hence this dimension is known as *consistency* (or *degree*) of preference. Some people are highly consistent, using the preferred hand for nearly all tasks and on all occasions, while other people are relatively inconsistent, more frequently making use of the nonpreferred hand (for a review, see Prichard, Propper, & Christman, 2013). While direction of preference may impact memory in certain specific situations (e.g., when learning object-manipulation words; de Nooijer, van Gog, Paas, & Zwaan, 2013), it is consistency that has been more broadly linked to episodic memory.

Seminal research (Propper, Christman, & Phaneuf, 2005) compared individuals with consistent hand preference to those with inconsistent hand preference (henceforth, consistent- and inconsistent-handers, respectively) on tests of episodic memory. Inconsistent-handers exhibited superior free recall of a word list and superior recall of autobiographical diary entries. Subsequently, an inconsistent-hander memory advantage (IHMA) has been repeatedly obtained in verbal free and cued recall, manifesting as either greater correct recall or lesser false recall (Christman & Butler, 2011; Christman, Propper, & Dion, 2004; Chu, Abeare, & Bondy, 2012; Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008). IHMA has also been found in verbal associative recognition, manifesting as reduced false recognition (Lyle et al., 2012). IHMA is not limited to verbal memory, however: It has also been found on tests of source memory (Lyle, McCabe, et al., 2008) and memory for event frequency (Edlin, Carris, & Lyle, 2013). Hence, consistency of hand preference is a potent predictor of episodic memory across a range of test types and stimuli.

IHMA appears not to be explained by differences in several important cognitive abilities that could plausibly support superior episodic memory. Inconsistent- and consistent-handers have been found to score equivalently on fluid intelligence as measured by Raven's Progressive Matrices (Lyle, McCabe, et al., 2008), on executive function as measured by the Attention Networks Test (Edlin & Lyle, 2013), and on working memory capacity as measured by complex span tasks (Sahu, Christman, & Propper, 2016). In the absence of differences in these cognitive processes, neuropsychological explanations for IHMA have tended to hold sway.

Two neuropsychological hypotheses have been put forth to explain IHMA. One is that inconsistent-handers are better able to coordinate hemispherically segregated processing in the prefrontal lobes during demanding episodic retrieval tasks (Lyle, McCabe, et al., 2008). This hypothesis rests on the assumption that inconsistent-handers experience greater interhemispheric interaction than consistent-handers. This assumption is supported by findings that inconsistency is associated with greater thickness of the corpus callosum (e.g., Luders et al., 2010), greater interhemispheric transfer of skill learning (Chase & Seidler, 2008), and shorter interhemispheric transfer times (Bernard, Taylor, & Seidler, 2011; Cherubin & Brinkman, 2006). More equivocal support for the interhemispheric interaction hypothesis comes from studies that index the interhemispheric coordination of information presented separately to the left and right visual hemifields. While Lyle and Martin (2010) obtained findings supporting the idea that interhemispheric coordination is greater in inconsistent-handers than consistent-handers, Lyle and Orsborn (2011) did not.

The second neuropsychological hypothesis regarding IHMA is that inconsistent-handers have greater access to episodic retrieval processes subserved by right prefrontal cortex (Prichard et al., 2013). Right prefrontal cortex is often ascribed a special role in supporting episodic retrieval (e.g., Habib, Nyberg, & Tulving, 2003; Metcalfe, Funnell, & Gazzaniga, 1995) and it is therefore reasonable to posit that greater access to processes mediated by right prefrontal cortex might benefit episodic memory. At present, however, the only physiological data supporting the plausibility of this hypothesis come from a single study. In a resting-state EEG study conducted by Propper, Pierce, Geisler, Christman, and Bellorado (2012), inconsistent-handers exhibited hemispheric asymmetry in alpha power recorded from frontal sites such that right hemisphere activity was greater than left hemisphere activity. Asymmetric activity was not observed among consistent-handers. This finding could imply that processes subserved by right frontal regions make a greater contribution to cognition in inconsistent-handers than consistent-handers. One caveat, however, is that this study's sample size was rather small ($N = 17$).

IHMA can be taken to imply a relationship between manual dexterity and episodic memory. An intuitively appealing idea is that individuals develop a strong and consistent preference for a particular hand when they are considerably more dexterous with that hand than the other (Annett, 1985; Bishop, 1989). Indeed, many studies have revealed that consistency of preference is negatively related to lateralization of manual dexterity, meaning that greater consistency is associated with more a pronounced difference in dexterity (e.g., Badzakova-Trajkov, Häberling, & Corballis, 2011; Bernard et al., 2011; Triggs, Calvanio, Levine, Heaton, & Heilman, 2000). Hence, IHMA could be taken to suggest that episodic memory is related to a certain aspect of manual dexterity: namely, lateralization. However, there are those who have marshalled empirical evidence over the years to suggest that a relationship between manual dexterity (or proficiency) and preference is not so clear-cut (e.g., Barnsley & Rabinovitch, 1970; Porac & Coren, 1981). There is, in fact, much unshared variance between subjective measures of hand preference and objective measures of hand performance (e.g., Brown, Roy, Rohr, Snider, & Bryden, 2004; Todor & Doane, 1977; Triggs et al., 2000). To the extent consistency of hand preference is at least partially separable from manual dexterity, findings of IHMA do not unequivocally establish a relationship between manual dexterity and episodic memory. We expand on this idea in the next two paragraphs.

Because research on consistency of hand preference has relied on self-report measures of hand usage, legitimate concerns can be raised about whether it has conclusively established a relationship between episodic memory and motor behavior. People's responses on handedness inventories may not reflect their genuine everyday manual behavior. For a host of reasons (for a review, see Schwarz & Oyserman, 2001), all self-report instruments are potentially vulnerable to the charge that they do not accurately measure what they purport to measure, and there are particular concerns pertaining to handedness inventories. One concern is that handedness inventories typically query frequency of hand usage using vague quantifiers (e.g., *usually*; Bradburn & Miles, 1979), which are known to be open to differential interpretation (e.g., Griffin, 2013). It is possible that handedness inventories reveal memory differences, not between people who actually differ in hand usage, but between people who differ in interpretation of vague quantifiers. Along these lines, but in reference to other research on hand preference and cognition, two groups of authors (Badzakova-Trajkov et al., 2011; Grimshaw, Yelle, Schoger, & Bright, 2008) have argued that bias in questionnaire-taking behavior may be responsible for an apparent association between inconsistent handedness and increased levels of magical ideation.

Another concern with using consistency of hand preference to establish a relationship between motor behavior and episodic memory is that handedness inventories, like many other questions about behavior (again, see Schwarz & Oyserman, 2001) are themselves a sort of memory test. Handedness inventories ask people to recall how they have used their hands. As Edlin et al. (2013) noted, a consistent response profile could arise from failure to recall instances of using the nonpreferred hand. Hence, consistent response profiles could be associated with poorer episodic memory simply because people with poorer memory have difficulty remembering their own inconsistencies. There may be no difference in the actual incidence of inconsistency between individuals classified as consistent versus inconsistent, but only a difference in the likelihood of remembering inconsistency. This possibility cannot be readily dismissed because, when Edlin et al. assigned subjects to use their hands with varying frequencies to perform laboratory tasks, individuals classified as consistent by the inventory method exhibited poorer subsequent recall of hand-usage frequency than individuals classified as inconsistent. Individuals who have trouble recalling frequency of hand usage in the lab might have similar trouble recalling frequency of hand usage in everyday life.

To avoid problems inherent in using self-report measures to relate motor behavior to individual differences in episodic memory, the rather obvious solution is to instead use an objective measure of hand performance. In other words, research could examine whether individuals' episodic memory is related to their performance on laboratory tasks of manual dexterity. An affirmative result would leave no doubt as to whether motor behavior is related to episodic memory. It is not certain, however, that a performance measure of manual dexterity would relate to episodic memory in the same manner as a hand-preference measure. In a study by Badzakova-Trajkov et al. (2011), degree of preference for one hand over the other was positively correlated with lateralization of finger-tapping speed ($r = 0.661$), but only the former was related to magical ideation. This finding, although concerning a type of cognition other than episodic memory, fosters uncertainty as to whether a performance test of manual dexterity would relate to memory performance. Resolving this uncertainty is necessary for solidifying a relationship between motor behavior and memory.

Which of many possible measurable aspects of manual dexterity is most likely to be related to episodic memory? Given the documented relationship between episodic memory and consistency of hand preference, it makes sense to consider aspects of manual dexterity that have previously been associated with consistency of hand preference. There are two candidate aspects. One is lateralization of dexterity, which has already been introduced above. The second aspect of manual dexterity that has been linked to handedness consistency is bimanual coordination. Three findings are relevant here. First, Kourtis, De Saedeleer, and Vingerhoets (2014) found that inconsistent-handers' performance on a task requiring simultaneous bimanual movements was not affected by task complexity, while consistent-handers were slower on more complex tasks. Second, Gorynia and Egenter (2000) found that inconsistent-handers had a greater affinity than did consistent-handers for making rapid, alternating bimanual movements. Third and finally, Christman (1993) found that musicians who played instruments requiring temporally integrated (or coordinated) bimanual movements were more likely to be inconsistently-handed than musicians who played instruments requiring relatively independent movements. These three disparate findings converge on the idea that inconsistent hand preference is associated with advantages in bimanual coordination (for a similar conclusion, see Kourtis & Vingerhoets, 2016). Because both weak lateralization and superior bimanual coordination have been associated with inconsistent hand preference, both might reasonably be expected to bear a relationship with episodic memory. However, as we report under Results, the measure of manual dexterity utilized in the present study revealed marked individual differences only in bimanual coordination, and not in lateralization. Consequently, our focus in this report is on bimanual coordination as a possible predictor of episodic memory.

To test whether bimanual coordination is positively related to episodic memory, we utilized the Pediatric MRI Data Repository, derived from the NIH MRI Study of Normal Brain Development. Subjects in that study completed the Purdue Pegboard Test (PPT; Tiffin & Asher, 1948) and California Verbal Learning Test Second Edition (CVLT-II; Delis, Kaplan, Kramer, & Ober, 2000). The PPT has been widely used for decades to assess manual dexterity. The test involves placing pegs in small holes aligned in parallel columns under timed conditions. The PPT includes a measure of bimanual coordination, while also measuring unimanual-left and unimanual-right performance, from which an estimate of lateralization can be derived. The CVLT-II is a standardized test of word-list recall that yields measures of correct and false recall. This test was particularly apt for present purposes because several prior studies relating motor behavior to episodic memory (through the lens of consistency of hand preference) have examined word-list recall, including on the CVLT-II itself (Chu et al., 2012). Those studies have found that inconsistent-handedness is associated with significantly greater correct recall and significantly less false recall (Christman & Butler, 2011; Christman et al., 2004; Lyle, Logan, et al., 2008). We planned to regress correct recall and false recall on bimanual coordination with the predication that bimanual coordination would positively predict correct recall and/or negatively predict false recall.

As the name implies, subjects in the NIH MRI Study of Normal Brain Development also underwent MRI. This allowed us, in the event we found a relationship between bimanual coordination and episodic memory, to look for cortical morphological characteristics that might be implicated in the relationship. This was an important opportunity because no previous study of motor behavior and episodic memory has incorporated cortical morphometric analyses, despite explanations for their relationship being neuropsychological in nature. To understand how motor behavior and episodic memory might be related in the brain, we looked for brain regions in which morphological variation was associated with both PPT and CVLT-II performance. We were especially interested in the corpus callosum and right prefrontal cortex, given previous theorizing that has implicated these regions in a relationship between motor behavior and episodic memory (Lyle, McCabe, et al., 2008; Prichard et al., 2013). A sensible hypothesis was that bimanual coordination and episodic memory would, like inconsistent-handedness (e.g., Luders et al., 2010), be positively correlated with thickness of callosal subregions. Another hypothesis was that bimanual coordination and episodic memory would both related to morphological variation in right prefrontal cortex. It was difficult to predict, however, exactly which morphological characteristics might be involved, knowing only that inconsistent-handedness has been associated (via undetermined mechanisms) with increased resting activity of right frontal cortex (Propper et al., 2012). We examined cortical surface area, thickness, and volume, believing that any or all might be important.

2. Method

2.1. Participants

Data were obtained from the Pediatric MRI Data Repository (Release 4.0) of the NIH MRI Study of Normal Brain Development, a longitudinal project developed to characterize healthy brain maturation in relation to behavior in a large, multisite study (Evans & Brain Development Cooperative, 2006). This multi-center project conducted epidemiologically-based recruitment of a large, demographicallybalanced sample across a wide age range, using strict exclusion factors and comprehensive clinical/behavioral measures. A mixed cross-sectional and longitudinal design was used to create an MRI/clinical/behavioral database from approximately 500 children aged 7 days to 18 years to be shared with researchers and the clinical medicine community. Using a uniform acquisition protocol, data were collected at six Pediatric Study Centers and consolidated at a Data Coordinating Center. Enrolled subjects underwent a standardized protocol to characterize neurobehavioral and pubertal status. The data were demographically representative of the U.S. population in terms of variables including sex, race, and socioeconomic status (Waber, Forbes, Almli, & Blood, 2012). Exclusion criteria included but were not limited to IQ < 70, history of medical illness with CNS implications, and any Axis I psychiatric disorder (other than simple or social phobia, adjustment disorder, oppositional defiant disorder, enuresis, encopresis, or nicotine dependency; (see Waber et al., 2012, for a complete list of inclusion and exclusion criteria). Participants underwent brain MR imaging and extensive neuropsychological testing on up to three occasions at two-year intervals.

For the purposes of this research, we first analyzed behavioral data from the subset of subjects who completed both the CVLT-II and PPT at the same timepoint. Because enrollment in the study began at age 4.5 and testing was conducted at timepoints separated by 2-year intervals, some subjects participated in all three sessions before turning 16 and becoming eligible to take the CVLT-II. Furthermore, in a small number of cases, PPT data were absent from the repository for a particular timepoint. We considered data only from the first timepoint at which a given subject completed the CVLT-II so that scores would not be contaminated by practice effects (Woods et al., 2006). This filtering process yielded data from 114 subjects. Two of these subjects had PPT subtest scores that differed dramatically from the mean. The Left Hand score of one subject was 5.5 *SD* below the mean and the Both Hands score of another subject was 4.4 *SD* below the mean. These subjects were excluded, leaving behavioral data from 112 subjects. Of these subjects, 37 (33%) had not completed the PPT at any previous timepoint, 48 (42.9%) had completed it once before, and 27 (24.1%) had completed it twice before. Although it may have been desirable to restrict analyses to subjects without previous PPT completions, the relatively small number of such subjects made this impractical. We will present evidence, however, that practice effects on the PPT were weak, at best.

Not all subjects were scanned at all timepoints and hence imaging analyses were restricted to a further subset of individuals for whom imaging data were available from the same timepoint as their previously analyzed behavioral data. This additional filtering left us with data from 93 subjects. Table 1 shows age and sex information for the subset of subjects included in our behavioral analyses and the further subset included in our imaging analyses. In line with population-wide estimates of left-hand preference (Perelle & Ehrman, 1994), 11 subjects (9.8%) reported writing with their left hand.

2.2. Behavioral tests

On the CVLT-II, subjects hear a list of 16 words belonging to four different categories (List A). Subjects immediately attempt free recall of the list in any order. This study-test sequence is repeated four more times. The five study-test cycles constitute the List A learning phase. A single study-test sequence then occurs for a second list (List B). After this begins the long-term memory phase of the CVLT-II, comprising multiple tests of long-term recall and recognition of List A. The first of these is free recall (Short-Delay Free Recall), followed by cued recall with the four category names as cues (Short-Delay Cued Recall). After a 20–30 min delay, subjects again attempt free and cued recall of List A (Long-Delay Free Recall and Long-Delay Cued Recall, respectively). These recall tests are followed by old/new sequential and two-alternative forced-choice recognition tests, but we decided a priori to analyze only the recall data. We assumed the recognition data would largely be redundant given multiple preceding recall tests. The four long-term recall tests (two free and two cued) therefore constituted our measures of episodic memory for the purpose of this research, as was also the case in Chu et al.'s (2012) study of IHMA on the CVLT-II.

Table 1
Age and sex of subjects in behavioral and MRI analyses.

	Analyses			
	Behavioral		MRI	
	Female	Male	Female	Male
N	59	53	52	41
Age (in years)	17.2	17.0	17.1	17.0

The CVLT-II has a minimum age requirement of 16 years. Individuals who enrolled in the NIH MRI Study of Normal Brain Development before the age of 16 were not administered the CVLT-II until a timepoint at which they had reached or exceeded that age. Individuals were administered the CVLT-II at all timepoints at which they were eligible.

The PPT can be administered beginning at age 6. The test board features two parallel columns of 25 small holes. At the top of the board are two cups, each containing 25 pegs. Subjects first use their right hand to place as many pegs as possible in the right column in the span of 30 s. Subjects then perform two similar tasks with the same time limit, using their left hand to place pegs in the left column and using their right and left hands simultaneously to place pegs in both columns. These tasks are known respectively as the Right Hand, Left Hand, and Both Hands subtests.[1] The Both Hands subtest measures bimanual coordination. We quantified lateralization by taking the absolute value of the difference between the Right Hand and Left Hand scores. Individuals were administered the PPT at all eligible timepoints.

2.3. Imaging data acquisition

High-resolution, T1-weighted images were acquired using a 1.5-Tesla MRI scanner from General Electric or Siemens Medical Systems. Imaging data were obtained for each participant on the day of, or within a maximum of 28 days of, psychometric testing at a given timepoint. Multiple contrasts were obtained (T1-weighted, T2-weighted, and proton-density weighted). A 3D T1-weighted spoiled gradient recalled echo sequence was selected, providing 1 mm sagittally acquired isotropic data for the entire head. Because the maximum number of slices on the General Electric scanners was 124, the slice thickness was increased to 1.5 mm. Intersite reliability was evaluated with American College of Radiology phantoms, as well as with living phantoms scanned at each site. For more details, see Evans and Brain Development Cooperative (2006).

2.4. Image Processing: Surface-Based morphometry

Cortical reconstruction and volumetric segmentation was performed with the Freesurfer image analysis suite (free- surfer-Linux-centos4_x86_64-stable-pub-v5.3.0), which is documented and freely available for download online (http://surfer.nmr.mgh.harvard.edu/). A number of deformable procedures were performed for further data processing and analysis including surface inflation (Fischl, Sereno, & Dale, 1999), registration to a spherical atlas which utilized individual cortical folding patterns to match cortical geometry across subjects (Fischl et al., 1999), parcellation of the cerebral cortex into

[1] Data from a fourth subtest of the PPT, known as Assembly, do not appear in the Pediatric MRI Data Repository. However, data from the other subtests can be interpreted independently of those from Assembly.

units based on gyral and sulcal structure (Desikan et al., 2006; Fischl et al., 2004) and creation of a variety of surface-based data including maps of cortical volume, surface area and thickness. Regressors of both PPT and CVLT-II were used to regress vertices with behavioral performance and subsequently to test the regression slope from zero (t test), which provided surface maps smoothed at 10 mm of significant vertices that passed threshold (vertex-wise $p < 0.001$). Correction for multiple comparisons was performed using Monte Carlo simulation (cluster-wise $p < 0.01$). All analyses included intracranial volume (ICV) and age as nuisance variables to control for their effects.

2.5. Image processing: corpus callosum width

The corpus callosum cross section in the medial sagittal plane was located in each MRI using affine transformations to stereotaxic space (MNI-152). The region $\{(x, y, z) \mid x = 0, -50\,\text{mm} \le y \le 50\,\text{mm}, -10\,\text{mm} \le z \le 40\,\text{mm}\}$ was transformed from standard space into MRI scanner space, and the T1-weighted image was resampled on this plane at 0.25 mm resolution. A hybrid edge-detection/region-growing segmentation method identified likely corpus callosum white matter in this slice. White matter outside the corpus callosum, particularly in the fornix, was manually excluded. The result was checked against the original T1-weighted image for anatomical accuracy.

Thickness of the corpus callosum was measured at 100 uniformly spaced locations along the medial axis of the structure from splenium to rostrum. The medial axis is found by solving the Eikonal equation $\|\nabla T\| F = 1$ for T in a two-dimensional domain bounded by the outline of the corpus callosum in the mid-sagittal plane, where the velocity function F is the Euclidean distance map of the CC interior, $F(y,z) = \min_{(y_0,z_0 \notin CC)} \sqrt{(y-y_0)^2 + (z-z_0)^2}$ (El-Baz, Casanova, Elnakib, Gimel'farb, & Switala, 2010). The medial axis is the path following the gradient of T from the start point with $T = 0$ to the end point where T takes its maximal value on the domain. The start point is initially taken to be the most posterior point on the corpus callosum, and the method is iterated with the end point of the previous run becoming the start point of the next run. Convergence is reached after only three iterations with no further change in the end point. Subsequently, the start and end points cut the corpus callosum outline into two segments, inferior and superior. Solving the Laplace equation $\nabla^2\phi = 0$ inside the corpus callosum, with Dirichlet boundary conditions on these two segments, one can compute a unique field line at any point within the corpus callosum. The arc length of that field line is the estimated thickness w of the corpus callosum at that location. Analysis treated corpus callosum width as a linear function of both PPT and CVLT measures, including ICV as a nuisance variable.

3. Results

3.1. Behavioral analyses

In the long-term memory phase of the CVLT-II, subjects recalled the same list of words (List A) on four separate tests. Unsurprisingly, the mean number of words correctly recalled (out of 16) ranged only narrowly from 12.2 to 12.9 across the four tests. Similar means were obtained by Chu et al. (2012) in their study revealing IHMA on the CVLT-II. Furthermore, scores on the four tests were highly intercorrelated, as shown in Table 2. In the interest of data reduction, we summed correct recall across tests to yield a single measure of total correct recall with a potential maximum of 64 (range = 25–64, $M = 50.3$, $SD = 9.5$). Regarding false recall, the repository included the total number of non-presented words erroneously recalled by each subject across the four tests (often called *intrusions*). We used this as our measure of total false recall (range = 0–12, $M = 2.3$, $SD = 2.8$).

PPT performance resembled that observed in prior research with subjects in the same age range (Mathiowetz, Rogers, Dowe-Keval, Donahoe, & Rennells, 1986). Right Hand performance ($M = 14.4$) was best, followed by Left Hand ($M = 13.9$) and Both Hands ($M = 11.3$). All pairwise comparisons were significant, smallest $t(111) = 3.33$, $p = 0.001$, Cohen's $d = 0.32$. We calculated lateralization as planned and found that the sample mean ($M = 1.2$) differed significantly from 0, $t(111) = 11.34$, $p < 0.001$, Cohen's $d = 0.31$, indicating that manual dexterity was lateralized in this sample. However, the magnitude of lateralization was small in absolute terms and there was little variability in scores. Nearly two-thirds of the sample (65.2%) had a score of either 0 or 1, severely limiting this variable's meaningfulness as an individual difference measure. We therefore do not consider lateralization further as a variable of interest. Table 3 presents intercorrelations between subtest scores, age, sex (dummy coded as female = 1, male = 2), writing hand (dummy coded as right = 1, left = 2), and number of prior PPT completions (0, 1, or 2). Scores on each subtest were moderately positively correlated with the others, as is typical (Tiffin & Asher, 1948). In addition, scores on each subtest were positively correlated with age and female subjects tended to score higher on all subtests than did male subjects, as has previously been reported for teenaged individuals (Mathiowetz et al., 1986). Effects of writing hand on these subtests were not particularly pronounced, as in Judge and Stirling's (2003) study of teenaged individuals, with the exception that left-handers were significantly worse than right-handers on the right-hand subtest. Correlations between subtest performance and number of prior PPT completions were not significant, although all were positive, suggesting that any practice effects were weak and not readily statistically detectable.

A multiple linear regression was conducted to identify factors that predicted total correct recall on the CVLT-II. We entered predictors in two sequential blocks. In the first block, we entered sex, age, and writing hand in stepwise fashion. Sex and age were included because both were correlated with PPT performance and it was important to determine whether they predicted correct recall before assessing the predictive power of the PPT itself. Writing hand can serve as a proxy for overall direction of hand preference (Perelle & Ehrman, 1994) and, although direction of hand preference has not previously been linked to episodic memory (Lyle et al., 2012) and the number of left-handed writers in this dataset was small, we deemed it worth including for exploratory purposes. In the second block, we entered Both Hands scores, along with Left Hand and Right scores, in stepwise fashion. Left

Table 2
Correlation matrix of CVLT-II recall tests.

		1	2	3
1	Short-Delay Free			
2	Short-Delay Cued	0.81		
3	Long-Delay Free	0.84	0.82	
4	Long-Delay Cued	0.84	0.88	0.87

Note: All correlations are significant at $p < 0.001$.

Table 3
Correlation matrix of PPT subtest scores and subject characteristics.

		1	2	3	4	5	6
1	Right Hand						
2	Left Hand	0.59**					
3	Both Hands	0.62**	0.56**				
4	Age	0.21*	0.26**	0.24*			
5	Sex	−0.38**	−0.20*	−0.27**	−0.07		
6	Writing Hand	−0.21*	−0.05	−0.18	0.07	0.17	
7	# of Prior PPT Completions	0.18	0.11	0.13	−0.17	−0.03	−0.08

Note: Sex dummy coded as 1 = female, 2 = male. Writing hand dummy coded as 1 = right, 2 = left.
* $p < 0.05$.
** $p < 0.01$.

Hand and Right Hand scores were included because they were correlated with Both Hands scores. The results were straightforward: The only significant predictor was Both Hands, which was positively related to total correct recall, $\beta = 0.31$, $t(111) = 3.41$, $p = 0.001$. The regression model incorporating this predictor was significant, $F(1, 110) = 11.61$, $p = 0.001$.

We conducted a second multiple linear regression, identical in design to the first, for total false recall. Again, the only significant predictor was Both Hands, which was negatively related to false recall, $\beta = -0.24$, $t(111) = 2.60$, $p = 0.011$. The regression model was significant, $F(1, 110) = 6.76$, $p = 0.011$.

We repeated the regressions reported above restricted to the small subset of subjects ($N = 37$) whose initial PPT scores came from the same timepoint as their initial CVLT-II data. The key findings were that, for correct recall, Both Hands remained a significant predictor, $\beta = 0.42$, $t(36) = 2.54$, $p = 0.016$, while, for false recall, the predictive power of Both Hands did not reach statistical significance, $\beta = -0.24$, $t(36) = 1.40$, $p = 0.171$, but standardized Beta was exactly the same as in the analysis of all subjects. For both correct and false recall, standardized Beta weights were larger for Both Hands than for Left Hand or Right Hand and neither Left Hand nor Right Hand were significant predictors. These findings argue against the possibility that practice effects on the PPT contribute to a relationship between bimanual coordination and episodic memory.

3.2. Neuroimaging analyses

3.2.1. Corpus callosum

Having established that Both Hands scores covaried with total correct recall and total false recall, we next sought to determine whether any of those measures covaried with callosal width. We calculated partial correlations between the three measures and corpus callosum width at each point along the medial axis, controlling for age, sex, writing hand, Left Hand scores, Right Hand scores, and intracranial volume. Both Hands scores did not correlate significantly with callosal width at any point. There were some significant correlations between total correct recall and width (all positive), and between total false recall and width (all negative). Although these correlations are theoretically sensible, in that they suggest that greater callosal thickness is associated with superior episodic memory (i.e., more correct and less false recall), the number of significant correlations ($N = 8$) did not exceed the number expected by chance ($N = 10$).

3.2.2. Surface-based morphometry

Whole brain surfaced-based morphometry (cortical volume, surface area and thickness) was used to investigate neural correlates of Both Hands, total correct recall and total false recall scores, as our previous analyses focused on these variables. Increased Both Hands scores resulted in a significant relationship with decreased cortical thickness in the anterior right middle frontal gyrus (MFG; BA 9/46; Fig. 1a). Increased total correct recall resulted in a significant relationship with increased surface area in the anterior right middle frontal gyrus (MFG; BA 9/46; Fig. 1b); this region was nearly identical to the one identified in the Both Hands regression. Increased total correct recall also resulted in a significant relationship with increased surface area in inferior frontal gyrus/pars orbitalis (IFG/BA 47; Fig. 1b). In addition, while an area in the right anterior-inferior temporal gyrus (ITG) passed vertex-wise thresholding, it did not pass cluster-wise thresholding. Analyses examining total false recall resulted in no significant findings.

4. Discussion

To advance our understanding of the origins of individual differences in episodic memory, we sought to establish whether memory performance is predicted by bimanual coordination and, if it is, to identify cortical morphometric characteristics that might be implicated in the relationship. We found that bimanual coordination, as indexed by Both Hands scores on the PPT, positively predicted correct recall and negatively predicted false recall on the CVLT-II. This means that individuals who exhibited superior bimanual coordination tended to remember more items that had actually been on a word list and fewer words that had not—a hallmark pattern of superior episodic memory and strikingly similar to what has been found when comparing inconsistent-handers to consistent-handers. Although we found, as in prior research (Mathiowetz et al., 1986; Tiffin & Asher, 1948), that Both Hands performance was significantly related to age, sex, and unimanual performance, none of those variables were associated with superior episodic memory and cannot account for the predictive power of bimanual coordination. These results provide solid evidence for a positive relationship between motor behavior and episodic memory. Such a relationship has previously been suggested by studies using consistency of hand preference as a measure of motor behavior (e.g., Lyle, McCabe, et al., 2008; Propper et al., 2005), but the reliance of those studies on a self-report measure left open the possibility that the relationship between motor behavior and episodic memory was more apparent than real. The present study, in contrast, is more definitive.

Because we utilized an existing data repository and did not have control over which measures were administered, we do not have consistency of hand preference data for the subjects in this study. We therefore do not know whether greater bimanual coordination was associated with greater inconsistency of hand preference in this study (although that relationship has been found elsewhere; Christman, 1993; Gorynia & Egenter, 2000; Kourtis et al., 2014). Consequently, we cannot make claims about whether bimanual coordination and consistency of hand preference are independent predictors of episodic memory or simply two manifestations of a common predictive factor. While that is an interesting issue to resolve in future research, the contribution of the present research does not rest on our ability to resolve it here. To solidify a relationship between motor behavior and episodic memory, it was critical to test the predictive power of an objective performance measure, regardless of whether such a measure is correlated with a self-report measure (Badzakova-Trajkov et al., 2011; Grimshaw et al., 2008). Moreover, the present study contributes entirely novel data concerning a cortical morphometric relationship between motor behavior and episodic memory, as discussed next.

Our neuroanatomical analyses suggest that the relationship between bimanual coordination and episodic memory may be rooted in morphological characteristics of right lateral prefrontal cortex. Specifically, increased Both Hands scores were related to decreased cortical surface area of the right anterior MFG (BA 9/46), while increased total correct recall was related to increased surface area of the same region of right anterior MFG (BA 9/46), as well as right IFG (pars-orbitalis/BA 47). These two findings may seem at odds (decreased cortical thickness, increased surface area), but theoretical accounts for cortical development may be illuminating. Over the course of development, it is thought that the prefrontal cortical mantle pulls inferiorly and laterally from the midline (i.e., superior frontal gyrus; BA 4/6/8), as increased cortical tissue is required to support higher-level executive functions putatively mediated by the lateral prefrontal cortex (LPFC, BA 9/46; Paus, 2005). This increase in cortical tissue is manifest in a more complex gyrification pattern and increased surface area of the LPFC. While speculative, increased right hemispheric utilization by individuals with greater bimanual coordination may increase this developmental process and thus show greater decreases in cortical thickness and increases in surface area.

Furthermore, as we can only speculate as to why bimanual coordination would be negatively related to right LPFC thickness, we can offer an alternative explanation that draws on the known relationship between bimanual coordination and consistency of hand preference (Christman, 1993; Gorynia & Egenter, 2000; Kourtis et al., 2014). Recent studies (Arning et al., 2013; Robinson, Hurd, Read, & Crespi, 2016) have shown that inconsistency and consistency are associated with

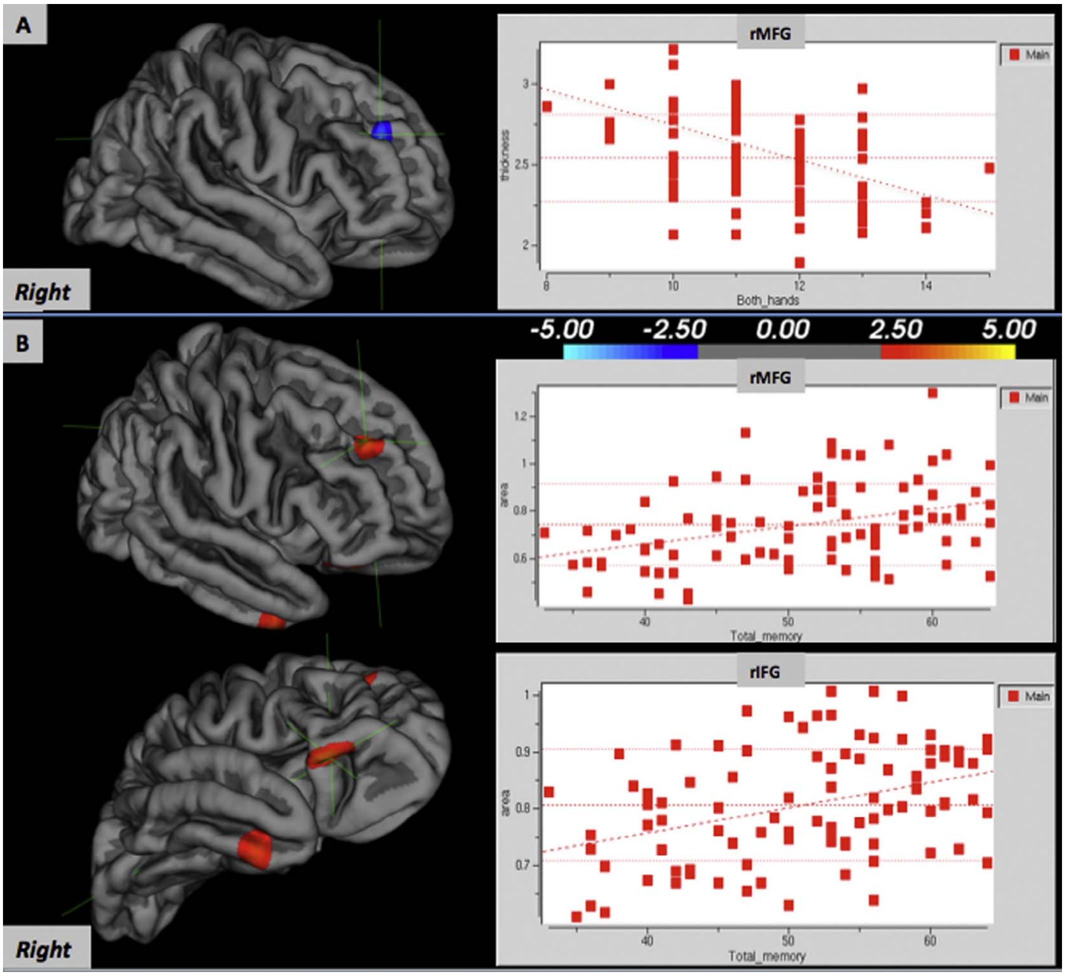

Fig. 1. (a) Surface-based morphometry showing the location and negative regression slope between Both Hands and cortical thickness. The only region passing both vertex and cluster-wise threshold was right middle frontal gyrus (rMFG). (b) Surface-based morphometry showing the location and positive regression slope between CVLT total memory and cortical surface area. Regions passing both vertex and cluster-wise threshold were right middle frontal gyrus (rMFG) and right inferior frontal gyrus (rIFG). Of note, right anterior-inferior temporal gyrus did not pass cluster thresholding.

different polymorphisms of a gene thought to be involved in development of brain asymmetries (PCSK6, proprotein convertase subtilisin/kexin type 6). It could be that these polymorphisms result in differential asymmetry of LPFC thickness. This could possibly help to explain why asymmetric resting alpha levels—indicating greater right- than left-hemisphere activity—have been observed among inconsistent-handers but not among consistent-handers (Propper et al., 2012). Perhaps certain PCSK6 polymorphisms are common, not only among inconsistent-handers, but among individuals who exhibit relatively good bimanual coordination. This possibility is not out of the question given a relationship between bimanual coordination and consistency of hand preference and given the fact that PCSK6 has already been shown to have some pleiotropic effects (Robinson et al., 2016). One could then hypothesize that genetic factors are responsible for the relationship between bimanual coordination and right LPFC thickness.

Conclusions regarding the positive relationship between episodic memory and right LPFC surface area are more substantive, due to the abundance of research examining memory performance and the LPFC. Increased surface area of LPFC is thought to indicate increased function (Dickerson et al., 2009; Shaw et al., 2012), in relation to better performance on total correct recall. It is not surprising that these regions indicated significant relationships with CVLT-II performance due to their long hypothesized involvement in controlled episodic/semantic memory retrieval (Corbetta & Shulman, 2002; Depue, 2012; Snyder, Banich, & Munakata, 2011). Theoretically, the function ascribed to the MFG has been maintaining working memory representations that guide behavior (Depue, 2012; Depue, Orr, Smolker, Naaz, & Banich, 2015; Snyder et al., 2011), whereas the IFG has been suggested to be involved in the selection of semantic information, which MFG would likely access in support of executive function, through its connections to inferior temporal regions (Corbetta & Shulman, 2002; Petrides & Pandya, 2002; Snyder et al., 2011). Therefore both regions, while performing separate functions, coordinate to select episodic memory information that can be used to support top-down control of behavior. While it is beyond the scope of the current paper to speculate on neural hemispheric laterality, it is noteworthy that findings of right hemispheric increased LPFC surface area may reflect the consequence of additional recruitment of neural pathways over time. Supported by many functional neuroimaging studies, findings indicate frequent recruitment of the right hemisphere during episodic memory retrieval (Henson, Shallice, & Dolan, 1999; Konishi, Wheeler, Donaldson, & Buckner, 2000; Nyberg et al., 2003). Therefore, the relationship between increased right LPFC surface area and better episodic memory performance may reflect increased recruitment.

In contrast to the promising findings we obtained regarding right LPFC, we found no evidence that callosal thickness is involved in the relationship between bimanual coordination and episodic memory. Performance on the Both Hands subtest of the PPT was not significantly correlated with callosal thickness at any of 100 points along the length of the commissure. The Both Hands subtest requires making synchronous, identical movements with the two hands and it may be that this type of bimanual coordination does not rely on callosal communication and is not related to callosal metrics (Fling et al., 2011). Or it may be that bimanual coordination and episodic memory are more strongly related to white matter integrity than to callosal thickness—a relationship we could not have seen without diffusion tensor imaging. We did find, however, that callosal thickness was significantly positively correlated with correct recall at a few points and significantly negatively correlated with false recall at a few different points. These correlations could be taken to support the idea—often put forth in relation to IHMA (e.g., Lyle, McCabe, et al., 2008; Propper et al., 2005—that individual differences in episodic memory stem from individual differences in degree of interhemispheric interaction, but a major caveat is that the number of significant correlations did not exceed the number expected by chance alone given an alpha level of 0.05. Hence, unless these correlations can be replicated, we must entertain the possibility that they are spurious.

4.1. Limitations and future directions

Several limitations bear noting. First, the age range of subjects was highly restricted (16–19 years). Most prior research linking motor behavior—in the form of consistency of hand preference—to episodic memory has been conducted on college students, mostly aged 18–22 years (but see Lyle, McCabe, et al., 2008). Hence, the age range of subjects in the present research partially overlapped with that of subjects in another relevant literature, which is a positive, but we obviously cannot say whether an identical relationship between bimanual coordination and episodic memory exists for younger or older individuals. Promisingly, however, subjects who were enrolled into the NIH MRI Study of Normal Brain Development at ages 6–15 years were administered the children's version of the CVLT, and also took the PPT and underwent MRI scanning. We intend to examine those data in a future study. Of possible relevance, one study of pre-pubertal children has already found that bilateral body coordination, which is somewhat similar to bimanual coordination, was positively related to episodic memory (Davis et al., 2011).

A second limitation is that, in this sample, there was little variability in lateralization of manual dexterity as measured by the PPT and therefore we could not appropriately address whether individual differences in lateralization were related to individual differences in episodic memory or brain morphometry. Future research could utilize alternative measures of lateralization, which may not present the same problem, such as the difference between right- and left-unimanual fingertapping (e.g., Badzakova-Trajkov et al., 2011; Nicholls et al., 2010).

Third, we examined only a single measure of bimanual coordination and one on which coordination demands were fairly minimal. One factor that is assumed to make coordination tasks more demanding is the requirement of asynchronous hand movements (e.g., Fling et al., 2011). Future research could examine whether alternative measures of bimanual coordination, and especially those that are more demanding, also predict episodic memory.

Fourth, although we assessed episodic memory specifically for verbal stimuli, we were not able to assess whether the relationship between bimanual coordination and episodic memory was in any way impacted by the neural organization of language in our subjects. This may be worth examining in future studies given that the neural organization of language has been shown to vary with consistency of handedness (e.g., Knecht et al., 2000).

Fifth and finally, the current study examined morphological data only, which was regressed with behavioral data. While morphological regressions with behavioral data can provide insight about putative neural mechanisms, data concerning brain function and white matter integrity (from functional MRI and diffusion tensor imaging, respectively), would be of considerable value in future studies.

4.2. Conclusions

Despite the limitations just noted, the present research is the first to show that a performance measure of motor behavior can be used to predict episodic memory. This is important because, as described in the Introduction, studies of consistency of hand preference—by virtue of their reliance on self-report measures—have left room to doubt whether motor behavior is actually related to memory. Furthermore, the present research is the first to suggest that individual differences in bimanual coordination and episodic memory may have their origins in morphometric variation of right lateral prefrontal cortical regions.

Author note

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This manuscript reflects the views of the authors and may not reflect the opinions or views of the NIH.

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