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RESEARCH REPORT

Consistency of Handedness, Regardless of Direction, Predicts Baseline Memory Accuracy and Potential for Memory Enhancement

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Research has shown that consistently right-handed individuals have poorer memory than do inconsistently right- or left-handed individuals under baseline conditions but more reliably exhibit enhanced memory retrieval after making a series of saccadic eye movements. From this it could be that consistent versus inconsistent handedness, regardless of left/right direction, is an important individual difference factor in memory. Or, more specifically, it could be the presence or absence of consistent right-handedness that matters for memory. To resolve this ambiguity, we compared consistent and inconsistent left- and right-handers on associative recognition tests taken after saccades or a no-saccades control activity. Consistent-handers exhibited poorer memory than did inconsistent-handers following the control activity, and saccades enhanced retrieval for consistent-handers only. Saccades impaired retrieval for inconsistent-handers. None of these effects depended on left/right direction. Hence, this study establishes handedness consistency, regardless of direction, as an important individual difference factor in memory.

Keywords: enhancement, handedness, individual differences, memory, saccades

Recent research has documented memory differences between individuals who are consistently right-handed and those who are not. The groups that have been compared with consistent right-handers include, depending on the study, various combinations of inconsistent right-handers, inconsistent left-handers, and consistent left-handers. Although a less-salient aspect of handedness than left/right direction, how consistently individuals use one hand over the other does have an impact (Peters & Murphy, 1992). Some individuals consistently use the same hand regardless of task, whereas others switch hands between tasks or between performances of the same task. Interest in consistency and memory originated in Christman, Propper, and Dion's (2004) two-part hypothesis that, one, consistency is inversely related to interhemispheric interaction, and, two, interhemispheric interaction is positively related to memory retrieval. Both parts of the hypothesis have some tenuous support (for discussion, see Lyle & Martin, 2010). The hypothesis predicts that more-consistent individuals will have poorer memories than will less-consistent individuals, because more-consistent individuals putatively have less interhemispheric interaction. To test this surprising prediction, studies have compared consistent right-handers, who are much more common than consistent left-handers (Peters & Murphy, 1992), with the various groups mentioned earlier. Average consistency was always lower in the comparison groups, even though they sometimes included a small number of consistent left-handers. These studies supported the prediction of poorer memory among more-consistent individuals. For example, consistent right-handers exhibited less correct recall (Lyle, McCabe, & Roediger, 2008; Propper, Christman, & Phaneuf, 2005), greater false recall and recognition (see e.g., Christman et al., 2004; Lyle & Jacobs, 2010), and subjectively less-detailed memories (Parker & Dagnall, 2010; Propper & Christman, 2004).

Further spurring interest in consistency and memory is the finding that consistent right-handers, versus inconsistent comparison groups such as those described earlier, more reliably exhibit a form of memory enhancement dubbed saccade-induced retrieval enhancement (SIRE; Lyle & Martin, 2010). In SIRE studies, subjects make a series of saccadic eye movements to visual targets on a computer monitor immediately before the retrieval phase of a memory test. SIRE is deemed to have occurred if the saccades activity increases subsequent correct retrieval or decreases false retrieval versus control activities in which subjects either do not move or do freely move their eyes (see e.g., Christman, Garvey, Propper, & Phaneuf, 2003; Lyle, Logan, & Roediger, 2008). In studies examining SIRE as a function of handedness, SIRE has uniformly occurred for consistent right-handers, whereas, for inconsistent individuals, saccades have variously enhanced retrieval (Christman, Propper, & Brown, 2006; Lyle & Jacobs, 2010), had no effect (Brunyé, Mahoney, Augustyn, & Taylor, 2009), or even harmed retrieval (by increasing false recall and recognition; Lyle, Logan, & Roediger, 2008). Between-group differences in response to saccades, as in baseline memory, were initially explained by

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possible group differences in interhemispheric interaction (Lyle, Logan, & Roediger, 2008).

These studies have suggested the intriguing possibility that handedness consistency may be an important individual difference factor because it predicts both baseline memory accuracy and potential for memory enhancement. However, the prior comparisons of consistent right-handers with individuals who are not consistently right-handed leaves open the alternative possibility that what matters for memory is not handedness consistency per se but whether individuals are consistently right-handed. Also, because the groups previously compared with consistent right-handers sometimes included left-handers, some memory differences may have been due to differences in direction, not consistency.

Precisely identifying the predictor of memory accuracy and potential for SIRE is important for practical and theoretical reasons. Practically, it would be desirable to know whether all consistent individuals (left or right) carry the risk for poorer memory—and the potential for enhancement—or whether only the consistently right do. Similarly, it would be desirable to know whether all inconsistent individuals (left or right) enjoy superior memory—but limited potential for enhancement—or whether only the inconsistently right do.

Effects of handedness consistency would have theoretical implications as well. First, consider the possible effect of consistency on baseline memory performance. The neural correlates of consistency differences are intriguing as they relate to models of memory. Some regions of the corpus callosum—the major pathway for interhemispheric cortical connectivity—may be larger in more inconsistent individuals (Cowell, Kertesz, & Denenberg, 1993; Habib et al., 1991; Witelson, 1985). Although the literature is not unanimous on this neurostructural difference (Jäncke & Steinmetz, 2003; Kertesz, Polk, Howell, & Black, 1987; Welcome et al., 2009), it accords well with the finding that the corpus callosum facilitates bimanual activity (Franz, Waldie, & Smith, 2000; Sacco, Moutard, & Fagard, 2006). The corpus callosum, and the interhemispheric interaction it makes possible, currently receive little explicit attention in neurofunctional models of memory, despite the fact that the absence or severance of the pathway is known to impair memory (see e.g., Geffen, Forrester, Jones, & Simpson, 1994; Phelps, Hirst, & Gazzaniga, 1991; Zaidel & Sperry, 1974). Another neural correlate of consistency differences is that, during purely unimanual movement, more-inconsistent individuals experience greater activity in ipsilateral motor cortex and possibly other regions as well (Dassonville, Zhu, Ugurbil, Kim, & Ashe, 1997). Given that motor cortex activity may spread to frontal and parietal regions (Harmon-Jones, 2006; Peterson, Shackman, & Harmon-Jones, 2008), inconsistent individuals may experience more diffusely bilateral cortical activity. To date, the baseline strength and regional extent of bilateral activity has received little consideration in neurofunctional models of memory, despite appreciation that retrieval, except under the simplest of conditions, is typically a bilateral process (see e.g., Nolde, Johnson, & Raye, 1998; Raye, Johnson, Mitchell, Nolde, & D'Esposito, 2000). If inconsistent handedness predicts superior memory, it may necessitate expansion of current neurofunctional models of memory to specify the significance of novel factors, such as interhemispheric interaction and tonic bilaterality.

Next, consider possible consistency effects on SIRE. SIRE's cause remains to be determined. Christman et al. (2003) initially hypothesized that executing saccades enhances memory by increasing functional coordination of the left and right brain hemispheres (i.e., interhemispheric interaction), but attempts to obtain behavioral (Lyle & Martin, 2010) or electroencephalogram (Samara, Elzinga, Slagter, & Nieuwenhuis, 2011) evidence for increased interaction have not been successful. Establishing that SIRE is mediated by consistency would guide future theorizing about its cause, because any theory would have to account for different effects of saccade execution on inconsistent and consistent individuals. SIRE-specific theorizing may, in turn, advance broader theorizing about the relationship between attention and memory. In SIRE, manipulating voluntary attention (via the saccades task) affects retrieval, not during encoding or retrieval (see e.g., Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Fernandes & Moscovitch, 2000) but immediately prior to retrieval. This serial relationship between attention and memory must be explained. For example, we have hypothesized (Lyle & Martin, 2010) that, because attentional control and episodic retrieval are subserved by some overlapping and closely neighboring brain regions (Naghavi & Nyberg, 2005; Sestieri, Shulman, & Corbetta, 2010), exerting control may enhance subsequent retrieval by preengaging neural circuitry relevant to both tasks.

To test the hypothesis that consistency, regardless of direction, is a key individual difference factor in memory, the present study fully crossed consistency (consistent or inconsistent) and direction (left or right). If the hypothesis is correct, then the same relationships between consistency and memory should hold for left- and right-handers alike. Presumably because of the difficulty of recruiting enough left-handers, no study has compared sizable groups of consistent and inconsistent left-handers to determine whether they differ in baseline memory accuracy or SIRE. It bears noting, though, that two analyses including small (Kempe, Brooks, & Christman, 2009) or unreported (but presumably small; Propper et al., 2005) numbers of left-handers have been put forth as providing initial support for the hypothesis that consistency and baseline memory accuracy are negatively correlated among left-handers, as among right-handers. However, it should also be noted that Kempe et al. (2009) used what is, at best, an impure measure of memory: foreign language vocabulary learning.

Our design also allowed us to test for memory differences between left- and right-handers that were equated on consistency. Recent research has largely ignored possible effects of direction, but earlier research (Deutsch, 1978; Sherman, Kulhavy, & Burns, 1976) suggested direction might predict memory differences. This suggestion is tenuous, however, because the earlier research did not equate consistency between left- and right-handers.

The present study specifically examined memory for associations because both inconsistent handedness (Lyle, McCabe, & Roediger, 2008) and making saccades (Parker, Relph, & Dagnall, 2008) have been linked to superior associative memory. Each subject took two associative recognition tests, with retrieval following the standard bilateral saccades activity on one test and with it following the standard no-saccades control activity on the other test (both activities are detailed in the Method section). We predicted that consistent-handers, regardless of direction, would perform more poorly than would inconsistent-handers following the control task, which establishes baseline accuracy but would exhibit SIRE. Because inconsistent-handedness advantages have previously manifested, on memory measures other than associative recognition, as either more-correct retrieval (see e.g., Lyle, McCabe, & Roediger, 2008, which examined paired associate recall) or less-incorrect retrieval (see e.g., Lyle & Jacobs, 2010; Lyle, Logan, & Roediger, 2008), we predicted that one or both advantages would occur here. Regarding SIRE, Parker et al. (2008; Experiment 1) examined the effect of saccades on associative recognition in a random sample of subjects whose handedness was not reported but among whom consistent right-handedness presumably predominated, because it appears to be the most common behavioral profile (Peters & Murphy, 1992). With these subjects, Parker et al. found that saccades significantly increased correct recognition and decreased false recognition, thereby significantly increasing a measure of discrimination, *d'*. Therefore, we predicted the same effects here, at least for consistent-handers, regardless of direction. Because inconsistent-handers have, depending on the study, been unaffected, helped, or harmed by saccades, and no such explicit group had been tested previously for SIRE on associative recognition, we did not predict the effect of saccades on inconsistent-handers here but predicted the effect would be the same regardless of direction.

Method

Subjects

Subjects were University of Louisville students 18–28 years of age who received credit in psychology courses or $10 for participating. Subjects were classified (see later) as consistent-left (n = 24, 11 female), inconsistent-left (n = 24, 13 female), inconsistent-right (n = 24, 16 female), or consistent-right (n = 48, 38 female). More consistent right-handers participated due to their ready availability. Four subjects inadvertently completing the study during loud construction, and one whose difference score between the two associative recognition tests was more than 3 *SD*s from the mean, were replaced.

Materials

We used the hand preference inventory described in Lyle, McCabe, and Roediger (2008), which queries direction and consistency of handedness for 10 activities. Scores range from –100 (*exclusive left-handedness*) to +100 (*exclusive right-handedness*) in 5-point intervals.

One associative recognition test was taken from Parker et al. (2008). The study list consisted of 100 pairs of three- or four-letter unrelated words (e.g., *view–main*). The first five and final five pairs were buffers to eliminate primacy and recency effects. The test included 30 studied (or intact) pairs and 30 rearranged pairs that were combinations of two words from different pairs on the study list. In rearranged pairs, words appeared in the same left–right position in which they had been studied. If a word appeared in a rearranged pair, the word with which it had been paired at study did not appear on the test. For example, the studied pairs *view–main* and *kid–rank* were used to form the rearranged pair *view–rank*, and neither *main* nor *kid* appeared in any pair on the test. Parker et al.'s report provides additional detail about the stimuli. We created a second study list and test to the specifications of the first.

The stimulus for the saccades task was a computerized sequence showing a black circle on a white background. At a viewing distance of 24 in. (61 cm), the circle alternated between 13.5° left and 13.5° right of the vertical midline every 500 ms for 30 s. For the fixation task, the circle flashed in the center of the screen (500 ms on, 500 ms off) for 30 s.

Procedure

Subjects first completed the hand preference inventory. In prior studies, we used +80 as the a priori cutoff score between consistent right-handers and other individuals (Lyle & Jacobs, 2010; Lyle & Martin, 2010) because +80 is a common median score among undergraduates (Christman et al., 2006, 2004; Lyle, Logan, & Roediger, 2008). We extended that here by classifying individuals thusly: −80 or lower = consistent-left, –5 to –75 = inconsistent-left, +5 to +75 = inconsistent-right, +80 or higher = consistent-right.

Subjects completed the associative recognition tests via computer. They were instructed to learn word pairs for a test on which they would need to identify the exact pairs they had studied and discriminate them from rearranged pairs. During study, word pairs appeared for 3 s with a 1-s interstimulus interval. The test was self-paced. Subjects pressed *F* to indicate a pair was intact and *J* to indicate it was rearranged. Response and latency were recorded. One of the pretest activities intervened between study and test. For the saccades task, subjects moved their eyes, without moving their heads, to follow a circle that alternated between the left and right sides of the screen. For the fixation task, subjects fixated a stationary flashing circle without moving their eyes or head. The experimenter monitored compliance with instructions. Subjects took one test following saccades and the other following fixation. Order of tests and pretest activities was counterbalanced. There was a 15-min break between the two study–activity–test sequences to prevent carryover effects from the first activity. We did not constrain subjects' activities during the break.

Results

The absolute value of hand preference inventory scores did not differ between inconsistent left- and right-handers (*M*s = 59.6 and 52.9, respectively), $t(46) = 1.26$, or consistent left- and right-handers (*M*s = 91.9 and 93.2, respectively), $t(70) = 0.74$. Hence, degree of inconsistency and consistency was the same among left- and right-handers.

We initially analyzed all dependent variables from the associative recognition tests using 2 (consistency) × 2 (direction) × 2 (pretest activity) mixed-design analyses of variance in which consistency and direction were between-subjects and pretest activity was within-subject. Including gender as a covariate did not change the significance of any effects.

Discrimination

To measure subjects' ability to discriminate between intact and rearranged pairs, we calculated *d'*. The only significant effect was the Consistency × Pretest Activity interaction, $F(1, 116) = 7.32$, $p = .008$, $\eta_p^2 = .059$ (all other ps $\geq .17$). Figure 1 depicts the interaction and reveals two predicted effects. One, following fix-

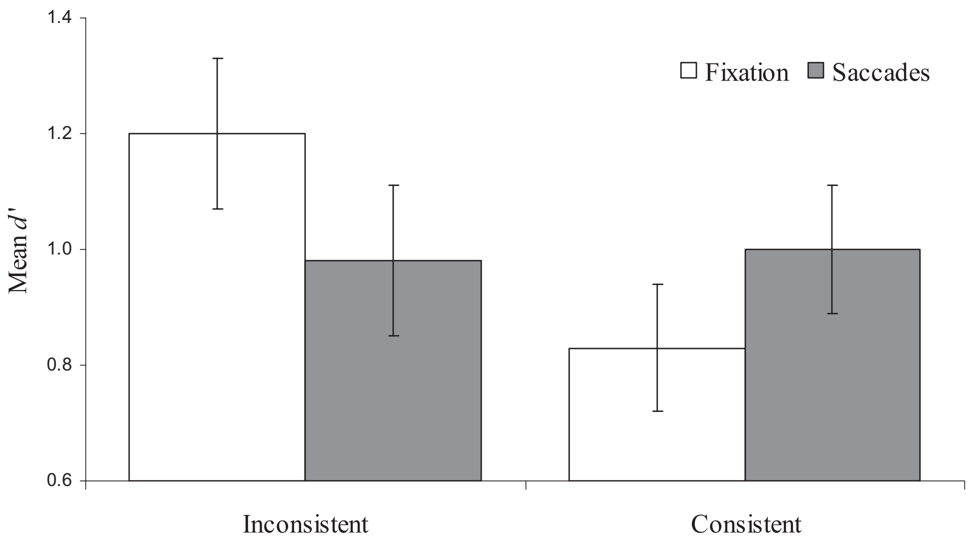

Figure 1. Mean proportion *d'*. Errors bars indicate ±1 standard error of the mean.

ation, discrimination was higher for inconsistent-handers (M = 1.18) than for consistent-handers (M = 0.83), $t(118) = 2.00$, one-tailed $p = .024$, Cohen's $d = 0.38$. Two, saccades increased consistent-handers' discrimination (M = 1.02), $t(71) = 1.72$, one-tailed $p = .045$. The interaction arose because, for inconsistent-handers, saccades did not enhance discrimination but rather significantly reduced it (M = 0.98), $t(47) = 2.02$, two-tailed p = .049. A negative effect of saccades on inconsistent-handers was not necessarily expected, but our expectations that direction would not mediate the effect of saccades on inconsistent-handers, or mediate the other two effects just described, were confirmed.

Analysis of response bias yielded no significant effects (all ps ≥ .386).

Consistency as a quasicontinuous variable. Hand preference scores vary in increments of 5 and therefore may be considered quasicontinuous, with scores progressively further from zero in either the positive (right-handedness) or negative (left-handedness) direction indicating progressively greater consistency. To determine whether consistency predicts baseline memory accuracy when consistency is treated as quasicontinuous, we calculated the correlation between the absolute value of inventory scores and *d'* in the fixation condition. The correlation was significantly negative, $r(120) = –.22$, $p = .015$, which indicates that scores progressively further from zero predicted progressively poorer discrimination. We conducted a similar analysis to determine whether consistency, when treated as quasicontinuous, predicts response to saccades. We correlated the absolute value of inventory scores with a difference score calculated as *d'* in the saccades condition minus *d'* sin the fixation condition. The correlation was significantly positive, $r(120) = .26$, $p = .004$, which indicates that scores progressively further from zero predicted progressively more-positive (or less-negative) changes in discrimination in response to saccades.

Hits and False Alarms

To explore how handedness and saccades influenced discrimination, we analyzed hits and false alarms separately (see Figure 2). Mirroring discrimination, only the Consistency × Pretest Activity interaction was significant for both hits, $F(1, 116) = 4.59$, p = .034, $\eta_p^2 = .038$, and false alarms, $F(1, 116) = 6.33$, $p = .013$, $\eta_p^2 = .052$. Following fixation, inconsistent-handers made significantly fewer false alarms (M = 0.22) than did consistent-handers (M = 0.30), $t(118) = 2.81$, one-tailed $p = .003$, Cohen's $d = 0.53$. Following fixation, inconsistent-handers also had more hits (M = 0.61) than did consistent-handers (M = 0.58), but the difference, although in the predicted direction, was not significant, $t(118)$ = 1.01, one-tailed $p = .158$. For consistent-handers, saccades significantly increased hits (M = 0.60) relative to fixation (M = 0.57), $t(71) = 1.70$, one-tailed $p = .047$. For consistent-handers, saccades did not significantly reduce false alarms (M = 0.28) relative to fixation (M = 0.31), $t(71) = 1.47$, one-tailed $p = .073$, although the effect was in the predicted direction. For inconsistent-handers, saccades significantly increased false alarms (M = 0.26), $t(47)$ = 2.25, two-tailed $p = .029$.

Response Latency

We calculated each subject's mean response latency for hits and false alarms and analyzed the response types separately. The false alarm analysis excluded nine subjects lacking at least one false alarm following both activities. Only the main effect of direction was significant for both hits, $F(1, 116) = 13.84$, $p < .001$, η_p^2 = .107, and false alarms, $F(1, 107) = 6.71$, $p = .011$, $\eta_p^2 = .059$. Left-handers were slower to make hits and false alarms (Ms = 1,754 and 2,108 ms, respectively) than were right-handers (Ms = 1,459 and 1,739 ms, respectively).

Discussion

The primary purpose of this study was to determine whether consistency of handedness, regardless of direction, predicts differences in baseline memory accuracy and potential for SIRE. The results were clear: Consistent subjects had poorer associative memory (especially, more false recognition) than did inconsistent subjects in the fixation (i.e., baseline) condition, and SIRE (espe-

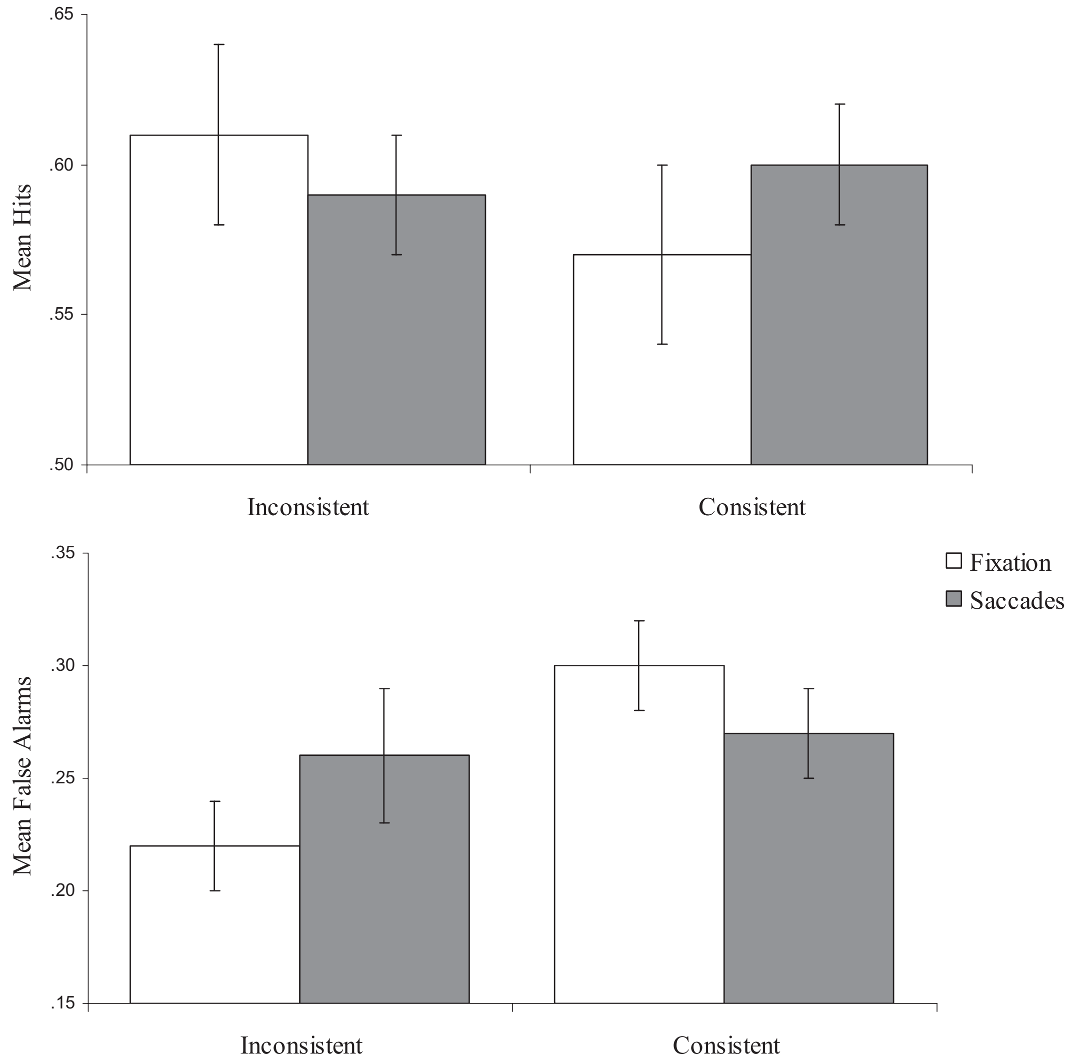

Figure 2. Mean proportion hits (top) and false alarms (bottom). Errors bars indicate ±1 standard error of the mean.

cially, increased hits) occurred for consistent, but not inconsistent, subjects. Critically, we found for the first time that consistency had these same effects among left- and right-handed subjects that were equated on consistency scores from a hand preference inventory. Direction of handedness did not qualify the key interaction of consistency and pretest activity. Hence, consistency of handedness, regardless of direction, emerged as an important individual difference factor in memory.

Not necessarily expected, but supporting two previous experiments (Lyle, Logan, & Roediger, 2008), consistency also predicted potential for saccade-induced impairment. Specifically, saccades harmed inconsistent subjects, whether left or right, by increasing false recognition. In the three experiments now showing harm for inconsistent subjects, saccades increased false recall or recognition of individual or paired words. In contrast, when saccades did not affect inconsistent subjects (Brunyé et al., 2009), or affected them positively (Christman et al., 2006; Lyle & Jacobs, 2010), the to-be-retrieved memories were not simple verbal ones but more complex autobiographical or visual ones. For consistent-handers, SIRE occurred for all these memory types. This emerging pattern suggests saccade-induced impairment may be more material-specific than enhancement.

The present findings have methodological and theoretical implications. Heretofore, a methodological problem in handedness-memory research has been irregular treatment of left-handers owing to the lack of data regarding how their memories compare with right-handers'. For example, some studies (see e.g., Lyle, McCabe, & Roediger, 2008) combined left-handers, regardless of consistency, with inconsistent right-handers, whereas others (Christman et al., 2006; Propper et al., 2005) combined inconsistent left- and right-handers but excluded consistent left-handers. Hence, the present findings support the method of forming groups of consistent- and inconsistent-handers, irrespective of direction.

Regarding theory, it is now clear that the challenge is to explicate why consistency per se, rather than the presence or absence of consistent right-handedness, is related to memory. Presumably, motor behavior does not affect memory accuracy or response to saccades directly. Rather, consistent and inconsistent individuals may differ in interhemispheric interaction (see e.g., Cowell et al., 1993; Habib et al., 1991; Witelson, 1985) and/or in cortical activity in motor regions and beyond (Dassonville et al., 1997), causing differences in encoding and/or retrieval processes that affect memory accuracy. Furthermore, the different baseline neural states of consistent and inconsistent individuals may interact differentially with cortical activations caused by making goal-directed saccades in SIRE studies. Brain imaging studies have revealed that making saccades to visual targets activates a frontoparietal cortical network (see e.g., de Haan, Morgan, & Rorden, 2008; Ettinger et al., 2008; Petit, Clark, Ingeholm, & Haxby, 1997). This network is involved not only in saccade execution but more generally in goal-directed allocation of attention (Corbetta & Shulman, 2002), and a key component region of the network, intraparietal sulcus, is implicated in episodic retrieval (Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008). We hypothesize that saccade-induced activation of attention- and retrieval-related cortical regions may interact with different baseline neural states in consistent and inconsistent individuals to produce new temporary states that, respectively, either facilitate or impair retrieval processes (and possibly other cognitive processes; see Shobe, Ross, & Fleck, 2009). Obviously, more research is needed to explore these possibilities.

A secondary purpose of this study was to test for memory differences between left- and right-handers. Direction was not related to any measure of memory accuracy. Hence, we did not extend previous findings of direction-based memory differences (Deutsch, 1978; Sherman et al., 1976). It remains for future research to resolve whether this is because we examined associative memory, whereas previously obtained differences were in memory for tones and highly concrete words, or because we equated consistency of left- and right-handers, whereas prior research did not. There was one direction-based difference in our study, however: Left-handers, regardless of consistency, were slower than right-handers to make both correct (hits) and incorrect (false alarms) memory judgments. Although not predicted, this is reminiscent of the finding (Wright, Hardie, & Rodway, 2004) that left-handers were slower than right-handers to initiate responding on a problem-solving task (i.e., the Tower of Hanoi task), and it resonates with the idea that left-handers are more inhibited (Wright, Hardie, & Wilson, 2009), or less proactive (Rogers, 2009), than right-handers. Left-handers' tendency to respond more slowly may have consequences when memory judgments must be made quickly, and therefore this area may warrant additional study.

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