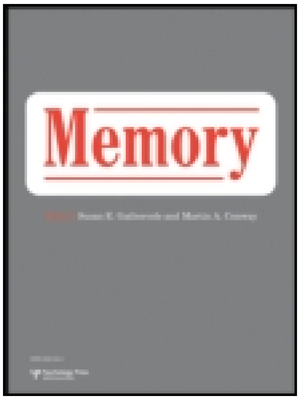

Memory
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/pmem20

Inconsistent handedness and saccade execution benefit face memory without affecting interhemispheric interaction

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Available online: 15 Sep 2011

MEMORY, 2011, 19 (6), 613–624

Psychology Press
Taylor & Francis Group

Inconsistent handedness and saccade execution benefit face memory without affecting interhemispheric interaction

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Individuals who consistently use their dominant hand for most tasks exhibit poorer memory than individuals whose handedness is relatively inconsistent, but consistent-handers' memory can be enhanced by making repetitive saccadic eye movements before attempting retrieval. One account of these effects is that inconsistent handedness and saccade execution are associated with increased interhemispheric interaction, which putatively facilitates retrieval. We tested this account by having participants classify faces as famous or novel. Faces were presented in the left and right visual fields simultaneously (bilaterally) or in one field only (unilaterally). As in prior studies, famous faces were classified more quickly and more accurately given bilateral presentation, but novel faces were not. These *bilateral gain* effects indicate that interhemispheric interaction specifically facilitates famous-face recognition, and therefore larger gains may reflect greater interhemispheric interaction. However, neither inconsistent handedness nor saccade execution increased the size of bilateral gain. Inconsistent handedness and saccade execution (the latter for consistent-handers only) did increase face-classification accuracy, but the increases were not specific to famous-face recognition, and, in fact, were somewhat stronger for novel-face identification. These results extend the beneficial mnemonic effects of inconsistent handedness and saccade execution to faces, but indicate that these benefits are not caused by increased interhemispheric interaction.

Keywords: Handedness; Saccades; Face recognition; Memory enhancement.

How can we predict which of two individuals will remember an event more completely and accurately, and how can we help people retrieve more complete and accurate memories? Recent studies suggest surprising answers to these important questions. Compared to individuals who consistently use their right hand for most tasks, relatively inconsistent right and left hand users have exhibited either more correct or less false retrieval of a wide variety of stimuli, including word lists (Christman, Propper, & Dion, 2004; Lyle, Logan, & Roediger, 2008; Propper, Christman, & Phaneuf, 2005), contextual or source details (Lyle, McCabe, & Roediger, 2008), complex visual scenes (Lyle & Jacobs, 2010), and autobiographical memories (Propper et al., 2005). Lyle, Hanaver-Torrez, Hackländer, and Edlin (in press) recently found that inconsistently handed individuals have a memory advantage over consistent left-handers, as well as consistent right-handers, indicating that, whether one's dominant hand is left or right, inconsistent usage predicts superior memory. Regarding memory enhancement, participants have exhibited either more correct or less

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This research was conducted for Alyssa E. Orsborn's undergraduate honours thesis.

http://www.psypress.com/memory DOI:10.1080/09658211.2011.595418

false retrieval of the same variety of stimuli used in handedness studies when attempting retrieval immediately after making a series of goal-directed saccadic eye movements, versus not moving or freely moving their eyes (Christman, Garvey, Propper, & Phaneuf, 2003; Christman et al., 2004; Lyle & Jacobs, 2010; Lyle, Logan et al., 2008; Parker, Buckley, & Dagnall, 2008; Parker & Dagnall, 2007, Parker & Dagnall, 2010; Parker, Relph, & Dagnall, 2008). Lyle and Martin (2010) dubbed this effect saccade-induced retrieval enhancement (SIRE).

The handedness studies cited above indicate that consistently handed individuals are most in need of memory enhancement and, remarkably, research has shown that consistent-handers are more likely to experience SIRE than inconsistent-handers. In the subset of SIRE studies that also assessed handedness, SIRE has invariably occurred for consistently handed participants, but for inconsistent participants SIRE sometimes has occurred (Christman, Propper, & Brown, 2006; Lyle & Jacobs, 2010) and sometimes has not (Brunyé, Mahoney, Augustyn, & Taylor, 2009; Lyle et al., 2010; Lyle, Logan et al., 2008; see also Shobe, Ross, & Fleck, 2009).

Given the evidence that inconsistent handedness and saccade execution predict and enhance memory, respectively, it is paramount to determine why. Christman et al. (2003, 2004) initially hypothesised that both factors affect memory by mediating interhemispheric interaction, which the authors defined as the functional coordination of the left and right brain hemispheres. Christman et al. posited that interhemispheric interaction facilitates memory retrieval and asserted that such interaction is naturally greater in inconsistent- than consistent-handers, and is increased by making saccades (see the original reports for the rationale for these assertions). Since its introduction, this interhemispheric interaction account has dominated theorising about the cause of handedness and saccade effects on memory and been featured in all reports of the phenomena. The account has also been extended to explain benefits of inconsistent handedness and saccade execution on creativity, which was assumed to be facilitated by interhemispheric interaction (Shobe et al., 2009), and to explain consistent–inconsistent differences in various reasoning, judgement, and decision-making phenomena which were assumed to depend on interhemispheric interaction (e.g., Jasper, Barry, & Christman, 2008; Jasper, Prothero, & Christman, 2009).

To evaluate the viability of interhemispheric interaction as the causal mechanism driving handedness and saccade effects on memory, Lyle and Martin (2010) tested whether inconsistent handedness and saccade execution are, in fact, associated with greater interhemispheric interaction. We examined the effect of both factors on a task that can be performed under conditions that either do or do not require interhemispheric interaction (Banich & Belger, 1990). The task was detecting briefly presented pairs of letters that matched in identity but differed in case (e.g., *a*–*A*). Eviatar and Zaidel (1994) showed that interhemispheric interaction is necessary to detect matches of this kind when the two letters are presented to separate hemispheres (across-hemisphere), but not to the same hemisphere (within-hemisphere). Inconsistently handed participants in Lyle and Martin detected more across-hemisphere matches than consistent participants, but neither group detected more across-hemisphere matches following saccade execution versus a no-saccades control activity. Furthermore, and unexpectedly, both factors were associated with detection of more within-hemisphere matches. Thus inconsistent handedness apparently increased the interhemispheric processing that occurred on across-hemisphere trials, but saccade execution did not, while both factors increased the more purely intrahemispheric processing that occurred on within-hemisphere trials. Relating this to the interhemispheric interaction account, increased interaction was supported as a possible cause of inconsistent-handedness memory advantages, but not of SIRE. At the same time, though, the results raised enhanced intrahemispheric processing as a possible cause of both phenomena.

To explain how saccade execution might affect memory without increasing interhemispheric interaction, Lyle and Martin (2010) drew on the well-established finding from visual attention research that making goal-directed saccades activates a network of brain regions, including the frontal eye field and intraparietal sulcus (Corbetta, 1998; Corbetta & Shulman, 2002). The intraparietal sulcus, of particular interest, is also activated during many memory retrieval tasks (for reviews, see Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). Assuming the intraparietal sulcus makes a functional contribution to retrieval, we suggested saccade execution might enhance task performance by pre-activating the intraparietal sulcus, thereby possibly increasing the region's subsequent contribution. More specifically, we speculated, in line with recent theorising (Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008), that the intraparietal sulcus might help implement top-down attentional control.

In finding that inconsistent handedness was associated with superior intrahemispheric processing, in addition to superior interhemispheric interaction, and that saccade execution increased intrahemispheric processing only, Lyle and Martin's (2010) results raise questions about whether interhemispheric interaction is actually a causal factor in either inconsistent-handedness memory advantages or SIRE. However, Lyle and Martin included no memory measures to provide answers. Hence, in the present study we examined the effects of inconsistent handedness and saccade execution in a face memory procedure that simultaneously yields measures of both interhemispheric interaction and memory performance.

When two images of a well-learned (i.e., famous) face are presented simultaneously and bilaterally (i.e., one to each hemisphere at the same time), recognition is faster and/or more accurate than when a single image is presented unilaterally to either hemisphere alone (Baird & Burton, 2008; Mohr, Landgrebe, & Schweinberger, 2002; Schweinberger, Baird, Blümler, Kaufmann, & Mohr, 2003). This effect is called bilateral gain. Superior performance is not due simply to the presentation of two versus one copies of the face, because, when two images are presented one above the other on the vertical midline (instead of bilaterally), recognition is no better than in unilateral conditions (Baird & Burton, 2008). Bilateral gain also occurs for words—another class of well-learned stimuli, like famous faces—and is thought to depend on interhemispheric interaction because it was not found for words in a split-brain patient (Mohr, Pulvermüller, Rayman, & Zaidel, 1994). Also important for the present investigation is that bilateral presentation does *not* enhance identification of novel faces or novel verbal stimuli (i.e., pronounceable nonwords). Thus bilateral gain occurs specifically for recognition of previously learned stimuli, not identification of novel ones, suggesting the former is facilitated by interhemispheric interaction, but the latter is not. The plausibility of a role for interhemispheric interaction in famous-face recognition is furthermore bolstered by fMRI evidence that famous-face recognition is associated with widespread bilateral cortical activations (Leveroni et al., 2000).

We propose that the size of bilateral gain may serve as a behavioural index of degree of interhemispheric interaction. Bilateral gain size would be quantified as the amount by which recognition accuracy was higher or response time was lower in the bilateral condition versus the average of the left and right unilateral conditions. By this proposal, larger differences favouring bilateral over unilateral trials would indicate greater interhemispheric interaction. Critically, then, the interhemispheric interaction account would predict that both inconsistent handedness and saccade execution should be associated with larger bilateral gain compared to consistent handedness and a no-saccades control activity. In contrast, from Lyle and Martin's (2010) results, we would expect only inconsistent handedness to be associated with larger gain.

As for memory performance, the interhemispheric interaction account predicts that both inconsistent handedness and saccade execution should be associated with faster or more accurate recognition of famous faces because, as indexed by bilateral gain, famous-face recognition is facilitated by interhemispheric interaction. Equally important, the account predicts no effect of either factor on novel-face identification, which is *not* facilitated by interhemispheric interaction (again, as indexed by bilateral gain). From Lyle and Martin (2010), though, one might predict inconsistent handedness to be associated with superior famous-face recognition (*if* superior interhemispheric interaction is the cause of inconsistent-handedness memory advantages), but the predicted effect of saccade execution is less clear. Given Lyle and Martin's proposal that saccade execution increases top-down attentional control, and given that attentional control is important, depending on test conditions, for both achieving correct retrieval (Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Fernandes & Moscovitch, 2000) and avoiding false retrieval (Knott & Dewhurst, 2007; Skinner & Fernandes, 2008), saccade execution could conceivably increase correct recognition of famous faces, decrease false recognition of novel faces, or both. When saccade execution has preceded retrieval attempts for stimuli other than faces, saccades have sometimes increased correct retrieval, sometimes decreased false retrieval, and sometimes done both (see Lyle & Jacobs, 2010, for discussion). Critically, though, whatever the effect of saccade execution may be, Lyle and Martin's findings predict it will come *without* a concomitant increase in interhemispheric interaction (as reflected in larger bilateral gain).

To test the above predictions from the interhemispheric interaction account and Lyle and Martin (2010), we examined consistently and inconsistently handed participants' ability to classify briefly presented faces as famous or novel. Faces appeared in the left, right, or both visual fields. Participants attempted classification following saccade execution and a no-saccades control activity in within-participants fashion. We closely modelled our method on that of a prior study of bilateral gain (Schweinberger et al., 2003).

METHOD

Participants

Undergraduates aged 18–30 received credit in psychology courses for participating. We classified participants as strongly right-handed (SR; $n = 32$, 3 males, $M_{\text{age}} = 20.5$) if they scored $+80$ or higher on a hand preference inventory (see Materials below) or not strongly right-handed (nSR; $n = 32$, 5 males, $M_{\text{age}} = 20.2$) if they scored less than $+80$. We used this classification scheme to allow direct comparison with most of our prior studies. The SR-nSR division is similar to a consistent–inconsistent division, because all SR individuals are, by definition, consistent in their handedness and most nSR are inconsistent, except for strong left-handers (i.e., individuals scoring –80 or lower on the hand preference inventory), who are typically rare. Here, the nSR group included only 3 (9.4%) strong left-handers.

Design

The experiment had a 2 (handedness: nSR or SR) $\times$ 2 (pretest activity: saccades or fixation) $\times$ 2 (face type: famous or novel) $\times$ 3 (visual field: left, right, or both) design in which all factors except handedness were within-participants. The dependent variables were proportion correct classification responses (i.e., accuracy) and mean response time for correct responses. Both variables were initially analysed via ANOVAs with the stated design.

Materials

The hand preference inventory was a modified version of Oldfield's (1971) Edinburgh Handedness Inventory (see Lyle, McCabe et al., 2008, for complete details). The inventory queries direction and consistency of hand use for 10 activities. Scores range from -100 (exclusive left-handedness) to $+100$ (exclusive right-handedness).

To present famous faces we downloaded 60 images from the Internet showing frontal headshots of individual public figures from various domains (e.g., politics, entertainment, sports). Using Adobe PhotoShop we removed all background and converted the images to greyscale and a uniform size of 1.0625 in. $\times$ 1.375 in. Images were presented on a computer monitor. The images subtended $3.5^\circ \times 4.4^\circ$ visual angle, and were centred 2.9° laterally from a central fixation cross. All faces in the edited images were recognised during central, self-paced viewing by at least 95% of an informal sample of individuals who did not participate in the experiment itself. For use on unilateral trials (see Procedure below), we also created a blurred version of each image. Blurred images were unrecognisable as depicting faces, but were of equal size and similar luminance distribution as the non-blurred images.

We also downloaded a frontal headshot of a non-famous person matching each famous face in sex, race, and approximate apparent age. Non-blurred and blurred images of the novel faces were prepared to the specifications of the famous faces.

We randomly assigned 30 famous and 30 novel faces to each of two sets, and from these sets created two blocks of face-categorisation trials. Each face (famous or novel) was tested nonconsecutively within a block in all three visual field conditions (left, right, and both). Condition order was pseudorandomly determined for each face with the constraint that the same number of faces was presented in each possible order. Famous and non-famous faces were pseudorandomly intermixed to evenly distribute the two face types throughout the block. Blocks consisted of 180 trials.

The stimulus for the saccades activity was a computerised sequence showing a black circle on a white background. The circle alternated between 13.5° left and 13.5° right of the vertical midline every 500 ms for 30 s. For the fixation activity, the circle flashed in the centre of the screen (500 ms on, 500 ms off) for 30 seconds.

Procedure

Participants first completed the hand preference inventory, and then performed one of the two pretest activities (saccades or fixation). During the pretest activities and face-categorisation test, head position was fixed by a chin rest to maintain a constant viewing distance of 17.5 in. and minimise head movement. For the saccades activity, participants moved their eyes to follow a circle that alternated between the left and right sides of the screen. For the fixation activity, participants fixated a stationary circle that flashed on and off in the centre of the screen without moving their eyes. The experimenter monitored compliance with instructions. Immediately after the pretest activity, participants performed a block of face-categorisation trials. Trials began with a central fixation cross for 1500 ms. Then either a single image of a face appeared in the left or right visual field (unilateral trials), or two identical images of the same face appeared simultaneously, one in each visual field (bilateral trials). On unilateral trials a blurred image of the face appeared simultaneously in the contralateral visual field. On all trials face presentation time was 150 ms. Participants classified faces as famous or novel. Half the participants simultaneously pressed the "z" and ">" keys with their middle fingers to respond "famous", and the "x" and "<" keys with their index fingers to respond "novel". Assignment of keys to response was reversed for the remaining participants. Each face was followed by a blank screen for 2350 ms. Response time was recorded from onset of the face to offset of the blank screen, after which the next trial began. Although participants pressed two keys to respond, only the fastest key press was recorded. Classification accuracy was also recorded.

After the first block there was a 15-minute break during which participants performed an unrelated filler task to prevent carryover effects from the first pretest activity. After the break participants performed the other pretest activity followed by a second block of face-categorisation trials. At the midpoint of each block participants repeated the pretest activity they performed at the start of the block. Order of pretest activity and test block was counterbalanced.

RESULTS

Accuracy

Bilateral gain. Figure 1 shows we obtained bilateral gain for famous faces, which were classified correctly more often when presented bilaterally ($M = 0.82$) versus unilaterally in either visual field ($M_{\text{left}} = 0.76$, $M_{\text{right}} = 0.75$). In contrast, novel faces were classified about equally accurately in all visual field conditions ($M_{\text{both}} = 0.87$, $M_{\text{left}} = 0.88$, $M_{\text{right}} = 0.86$). The face type $\times$ visual field interaction was significant, (2, 124) = 19.22, $p < .001$, $\eta_p^2 = .24$, as was the gain from presenting famous faces bilaterally versus in either visual field individually, smallest $t(63) = 5.35$, $p < .001$.

No higher-order interactions involving face type and visual field were significant (smallest $p = .13$), suggesting neither handedness nor pretest activity affected the size of the bilateral gain effect. To confirm this we directly examined the magnitude of bilateral gain (for famous faces only) by averaging each participant's proportion correct in the unilateral conditions and subtracting the mean from the participant's proportion correct in the bilateral condition. The larger this difference score, the larger the bilateral gain. We submitted difference scores to a 2 (handedness) $\times$ 2 (pretest activity) ANOVA. Overall, mean gain was 0.07, and, as depicted in Figure 2, this did not vary significantly as a function of handedness, pretest activity, or their interaction (smallest $p = .27$).

Inconsistent-handedness advantage. Inconsistent handedness was not associated with larger bilateral gain, but Figure 3 shows that nSR participants' face-classification responses were more accurate than those of SR participants.

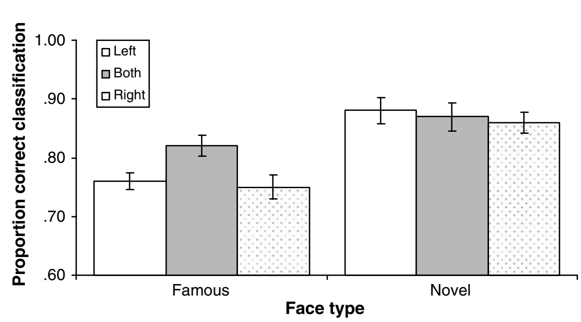

Figure 1. Mean proportion correct face-classification responses as a function of face type and visual field. Errors bars are 95% within-participants confidence intervals (Cousineau, 2005).

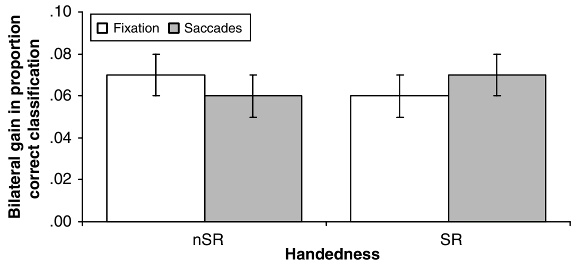

Figure 2. Mean bilateral gain in proportion correct classification of famous faces as a function of handedness and pretest activity. Each participant's bilateral gain was calculated as proportion correct on bilateral trials minus proportion correct on the average of left and right unilateral trials. Errors bars indicate ±1 *SEM*.

Critically, nSR participants classified both famous ($M = 0.80$) and novel ($M = 0.89$) faces more accurately than did SR participants ($M_{famous} = 0.76$, $M_{novel} = 0.84$). The main effect of handedness was significant, $F(1, 62) = 7.33$, $p = .009$, $\eta_p^2 = .11$. The difference was individually significant for novel faces, $t(62) = 2.17$, $p = .034$, Cohen's $d = 0.63$, but not famous faces, $t(62) = 1.61$, $p = .113$.

SIRE. Saccades did not increase the size of bilateral gain, but Figure 3 shows there was a SIRE effect for SR participants, who were more accurate following saccades than fixation. The reverse pattern occurred for nSR participants, who were less accurate following saccades than fixation. The pretest activity × handedness interaction was significant, $F(1, 62) = 4.32$, $p = .042$, $\eta_p^2 = .07$. Collapsing across face type, the saccade-induced increase in accuracy for SR participants fell just short of significance, $t(31) = 2.03$, $p = .051$, but, because it is critical to know whether the effect was specific to famous faces, we further tested the effect of pretest activity on each face type individually. For famous faces, saccades increased SR participants' accuracy ($M = 0.76$) only non-significantly over fixation ($M = 0.75$), $t(31) = .48$, $p = .633$. For novel faces, however, saccades significantly increased accuracy ($M = 0.86$) over fixation ($M = 0.83$), $t(31) = 2.64$, $p = .013$. For nSR participants, accuracy for both face types was non-significantly lower following saccades ($M_{famous} = 0.79$, $M_{novel} = 0.89$) than fixation ($M_{famous} = 0.81$, $M_{novel} = 0.90$), largest $t(31) = .63$, $p = .533$.

Response time (RT)

Bilateral gain. Figure 4 shows we obtained bilateral gain for famous faces, which were correctly recognised faster when presented bilaterally ($M = 830.16$ ms) versus unilaterally in either visual field ($M_{left} = 851.47$ ms, $M_{right} = 849.25$ ms). In contrast, RT for correct identification of novel faces given bilateral presentation ($M = 861.38$ ms), although faster than given unilateral-right presentation ($M = 876.03$ ms), was about the same as given unilateral-left presentation ($M = 863.80$ ms). The face type × visual field interaction was significant, $F(2, 124) = 3.83$, $p = .024$, $\eta_p^2 = .058$, as was the gain from presenting famous faces bilaterally versus in either visual field individually, smallest $t(63) = 3.14$, $p = .003$. For novel-face identification, bilateral and unilateral-left presentation both produced significantly faster correct classification than unilateral-right presentation, smallest $t(63) = 2.57$, $p = .012$, but RT did not differ significantly between the bilateral and unilateral-left conditions, $t(63) = .55$, $p = .585$.

No higher-order interactions involving face type and visual field were significant (smallest $p = .48$), suggesting that neither handedness nor pretest activity affected the size of the bilateral

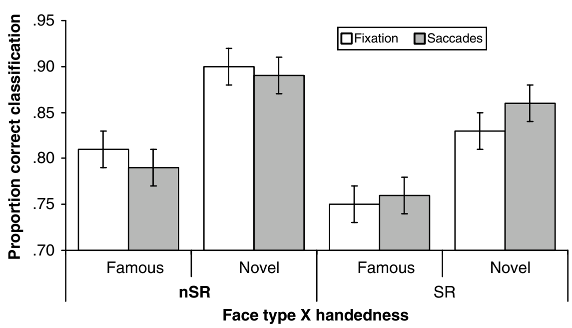

Figure 3. Mean proportion correct face-classification responses as a function of handedness, pretest activity, and face type. Errors bars indicate ±1 *SEM*.

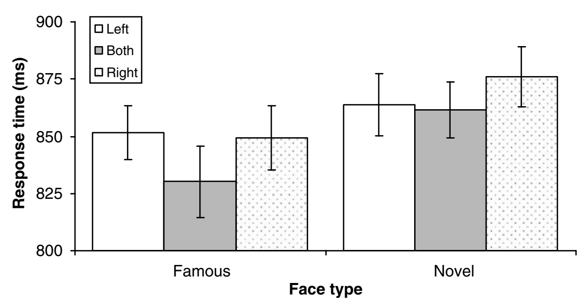

Figure 4. Mean response time for correct face-classification responses as a function of face type and visual field. Errors bars are 95% within-participants confidence intervals (Cousineau, 2005).

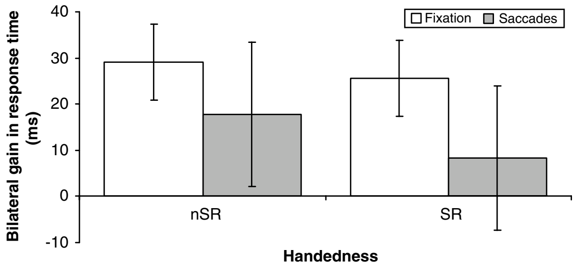

Figure 5. Mean bilateral gain in response time when correctly recognising famous faces as a function of handedness and pretest activity. Each participant's bilateral gain was calculated as mean response time across left and right unilateral trials minus mean response time on bilateral trials. Errors bars indicate ± 1 *SEM*.

gain effect. To confirm this, we directly examined the magnitude of bilateral gain (for famous faces only) by subtracting each participant's mean RT in the bilateral condition from the participant's RT averaged across the unilateral conditions. The larger this difference score, the greater the bilateral gain. We analysed these difference scores in the same manner as those for accuracy. Mean gain, overall, was 20.20 ms and, as depicted in Figure 5, this did not vary significantly by handedness, pretest activity, or their interaction (smallest $p = .30$).

Unlike in accuracy, there were no significant effects involving handedness or pretest activity in the initial analysis of RT (smallest $p = .44$), indicating no inconsistent-handedness advantage or SIRE on this measure.

Other effects

Figure 1 shows that classification accuracy was lower for famous faces ($M = 0.78$) than novel ones ($M = 0.87$), but Figure 4 shows that, when classification *was* accurate, mean RT was faster for famous ($M = 843.63$ ms) than novel faces ($M = 867.07$ ms). The main effect of face type was significant for accuracy, $F(1, 62) = 23.31$, $p < .001$, $\eta_p^2 = .273$, and approached significance for RT, $F(1, 62) = 3.85$, $p = .054$, $\eta_p^2 = .058$.

DISCUSSION

As in prior studies (Baird & Burton, 2008; Mohr et al., 2002; Schweinberger et al., 2003), we found bilateral gain for famous-face recognition, but not novel-face identification, indicating that famous-face recognition benefited from interhemispheric interaction, but novel-face identification did not. Therefore, if inconsistent handedness and saccade execution are associated with increased interhemispheric interaction and enhance memory via that mechanism (Christman et al., 2003, 2004), then both factors should have increased the size of the bilateral gain effect and enhanced famous-face recognition, without affecting novel-face identification. These predictions were not borne out. First, neither factor increased bilateral gain (Figures 2 and 5). Second, nSR participants (henceforth, inconsistent-handers) were more accurate than SR participants (henceforth, consistent-handers) at both recognising famous faces *and* identifying novel faces, and, in fact, their advantage was larger for identifying novel faces (Figure 3), and individually significant only for novel faces. Third, saccade execution increased both famous-face recognition *and* novel-face identification, and, in fact, the increase was larger for novel faces (Figure 3), and individually significant only for novel faces (Figure 3). In sum, both inconsistent handedness and saccade execution benefited memory, but not in a way unequivocally supporting the idea that they affect memory by increasing interhemispheric interaction.

One could possibly argue that the interhemispheric interaction account was partially supported by the finding that both inconsistent handedness and saccade execution were associated with superior face classification. The effects of handedness and (for consistent-handers) pretest activity on face classification accuracy did not interact significantly with face type (famous or novel), and so it could be argued that inconsistency and saccades increased famous-face recognition by increasing interhemispheric interaction while they increased novel-face identification via some other, as-yet unknown mechanism or mechanisms. This argument is undercut, however, by two other findings from the present study. First, the effects of handedness and pretest activity on famous-face recognition were, at best, weak, with neither being conventionally significant. Second, neither inconsistency nor saccades increased the size of bilateral gain, which was the other measure of degree of interhemispheric interaction. Hence, the more parsimonious argument would seem to be that neither inconsistency nor saccades increase interhemispheric interaction, but nevertheless they both enhance face classification, and perhaps especially novel-face identification, by some other mechanism or mechanisms.

Empirically, the effects of inconsistent handedness and saccade execution on face memory resemble their effects on memory for other stimuli. Both factors significantly increased correct identification of novel faces. Increases in correct responses to novel faces represent *reductions* in false recognition, because erroneous responses to novel faces are instances in which never-been-seen individuals were falsely identified as famous, or previously encountered. Inconsistent handedness (Christman et al., 2004; Lyle & Jacobs, 2010; Lyle, Logan, et al., 2008; Propper et al., 2005) and saccade execution (Brunyé et al., 2009; Christman et al., 2004; Lyle, Logan, et al., 2008; Parker & Dagnall, 2007; Parker et al., 2008) have previously been found to reduce false retrieval of various non-face stimuli. These benefits have come without reduction (and sometimes with significant increases) in correct retrieval, and the same was true here: Both factors were associated with numerically, but non-significantly, greater correct recognition of famous faces. Hence our findings further support and generalise inconsistent handedness and saccade execution as a potent predictor and enhancer, respectively, of resistance to false retrieval.

The presently obtained SIRE effect, described above, also resembles prior ones in being specific to consistent-handers. Inconsistent-handers had numerically more false recognition of novel faces and less correct recognition of famous faces following saccades versus fixation. Null effects (Brunyé et al., 2009), and even significant negative effects (Lyle et al., 2010, Lyle, Logan, et al., 2008, Lyle et al., in press), of saccade execution on inconsistent-handers' memory (and creativity; Shobe et al., 2009) have been documented, and actually outnumber cases in which saccades have benefited inconsistent-handers' memory (Christman et al., 2006; Lyle & Jacobs, 2010). In contrast, consistent-handers have benefited from saccades in every published report. The present study supports the conclusion that SIRE is a more robust phenomenon among consistent-handers than inconsistent-handers, and points to the importance of assessing handedness consistency in all future SIRE studies (cf. Parker, Buckley, et al., 2008; Parker & Dagnall, 2007, Parker & Dagnall, 2010; Parker, Relph, et al., 2008).

Drawing on the interhemispheric interaction account, Lyle, Logan, et al. (2008) suggested SIRE may be less reliable for inconsistent-handers because a greater baseline level of interhemispheric interaction gives them smaller margins for saccade-induced increases (see also Brunyé et al., 2009; Shobe et al., 2009). The present findings undermine that explanation, however: Inconsistent-handers did not exhibit SIRE, even though SIRE in consistent-handers was unrelated to increased interhemispheric interaction.

There is one respect in which the inconsistent-handedness memory advantage obtained here might be seen to conflict with a prior report. Here, inconsistent-handers were more likely than consistent-handers to correctly identify novel faces, but Lyle, McCabe, et al. (2008) found no inconsistent-handedness advantage on a face recognition test consisting of once-seen targets and novel lures. Both procedures required identifying novel faces as novel, but inconsistent-handers were only advantaged in this study. However, the procedures differed markedly in several ways, such as the ''background'' against which novel faces were judged (famous versus once-seen targets) and the test presentation duration (150 ms versus unlimited). Future research could investigate whether an inconsistent-handedness advantage in face memory depends on these factors or others.

Theoretically, the present results substantially advance ideas introduced in Lyle and Martin (2010). Regarding saccade execution, Lyle and Martin argued that saccade execution does not increase interhemispheric interaction and, accordingly, that increased interaction does not cause SIRE. However, Lyle and Martin did not test for SIRE itself. Here, finding that saccade execution did not increase bilateral gain, which depends on interhemispheric interaction, strengthens the claim that saccade execution does not increase interhemispheric interaction, and finding a SIRE effect that closely resembles prior ones confirms the idea that SIRE is not caused by increased interhemispheric interaction.

The above conclusions—that saccades do not increase interhemispheric interaction and SIRE is not caused by increased interhemispheric interaction—also follow from a recent study of electroencephalography (EEG) coherence, which is an electrophysiological measure of hemispheric functional connectivity (Samara, Elzinga, Slagter, & Nieuwenhuis, 2011). The authors of that study argued that EEG coherence might be taken to index interhemispheric interaction, with greater coherence indicating greater interaction (see also Propper, Pierce, Geisler, Christman, & Bellorado, 2007). Samara et al. measured EEG coherence and memory for words following saccades or fixation and found SIRE without a concomitant increase in coherence.

If saccade execution does not increase interhemispheric interaction, then why did it enhance retrieval for consistent-handers in this study? As described in the Introduction, Lyle and Martin (2010) reasoned that the saccade activity in SIRE studies likely engages the intraparietal sulcus, as have similar activities examined with fMRI (de Haan, Morgan, & Rorden, 2008; Ettinger et al., 2008; Petit, Clark, Ingeholm, & Haxby, 1997). The intraparietal sulcus is often characterised in the most general terms as involved in top-down attentional control (e.g., Cabeza, 2008; Ciaramelli et al., 2008; Corbetta & Shulman, 2002; Yantis, 2008), and, more specifically, some have suggested the region modulates the activation level of neural representations to either bring task-relevant information into conscious focus, or maintain it in focus (Majerus et al., 2006; Roth, Johnson, Raye, & Constable, 2009). Accurate classification of briefly presented faces in the present procedure presumably required maintaining high-fidelity representations of the faces after the visual offset of the faces, because, as shown in Figure 4, mean classification RT far exceeded faces' 150 ms presentation duration. If, as assumed, pretest saccade execution engaged the intraparietal sulcus, it may have promoted or increased the region's subsequent contribution to maintaining face representations, upon which classification decisions were based. This would benefit face classification generally, but would especially benefit novel-face classification, which took longer than famous-face classification (again, see Figure 4). Hence this account can accommodate the finding that saccades enhanced novel-face classification more robustly than famous-face classification. Whether this account can also accommodate all previously documented SIRE effects (and other saccade-induced cognitive enhancements; Lyle & Martin, 2010; Shobe et al., 2009) is beyond the scope of this paper, but modulating the activation level of neural representations in accordance with current agendas is, theoretically, critical to many cognitive tasks. As such, it is possible to envision explanations for numerous enhancement phenomena in terms of this mechanism. The account also generates novel testable hypotheses. One such hypothesis is that saccade execution should affect tasks that are more purely attentional in nature than any previously studied. Indeed, Edlin and Lyle (2010) recently evaluated the effect of saccade execution on the revised attention network test (Fan et al., 2009) and found that it increased scores specifically on the executive control component.

An alternative account of the finding that saccade execution increased novel-face identification more robustly than famous-face recognition was suggested by an anonymous reviewer, who posited that saccade execution (and also inconsistent handedness) might increase functional access to right hemisphere processing, rather than increase interhemispheric interaction per se. This account logically rests on the supposition that right hemisphere processing contributes more to novel-face identification than to famous-face recognition. A thorough evaluation of this supposition in light of the larger literature on face processing is beyond the scope of this article but, restricting ourselves to consideration of the present data only, we did find limited evidence that the right hemisphere contributes to novel-face identification in a way it does not contribute to famous-face recognition. Specifically, novel faces were identified more quickly when presented to the right hemisphere, either individually or simultaneous with presentation to the left hemisphere, than when presented to the left hemisphere alone. This hemispheric difference did not occur in famous-face recognition (see Figure 4). However, novel faces were *not* identified more accurately when processed by the right hemisphere versus the left hemisphere alone (see Figure 1). Hence, the right hemisphere may make a unique contribute to the speed, but not the accuracy, with which novel faces are processed. From this it follows that, if saccade execution increased functional access to right hemisphere processing, then it should have increased the speed with which novel faces were identified. However, this was not the case: There were no significant effects of pretest activity (or handedness) on RT.

Regarding handedness, the present findings both complicate and confirm ideas from Lyle and Martin (2010). There we suggested that inconsistent-handers experience greater interhemispheric interaction *and* superior intrahemispheric processing, and both may contribute to inconsistent-handers' memory advantages. Here a complicating finding was the lack of evidence of greater interhemispheric interaction among inconsistent-handers. How might the present and prior findings be reconciled? As Lyle and

Martin noted, interhemispheric interaction is not a monolithic construct. It may be that inconsistent-handers' superior interhemispheric processing is specific to only some types of operations, or operations involving only some types of information. This could be, if, as Christman et al. (2003, 2004); see also Propper et al., 2005) argued, inconsistent-handers' superior interhemispheric interaction is due to them having larger corpora callosa. Studies examining corpus callosum size as a function of consistency of handedness have yielded a complex and somewhat uncertain picture of the existence of differences (e.g., Cowell, Kertesz, & Denenberg, 1993; Habib et al., 1991; Welcome et al., 2009; Witelson, 1985), but it seems clear that, if inconsistent-handers do have any size advantages over consistent-handers, they are not structure-wide, but rather specific to certain sub-regions. Because different regions of the corpus callosum connect different cortical regions (Huang et al., 2005), and thus transmit different types of information, it follows that inconsistent-handers would exhibit greater interhemispheric processing on tasks requiring transmission of some types of information, but not others. A similar point was made by Potter and Graves (1988), who studied interhemispheric transfer of motor, tactile, and visual information in a sample of highly consistent right-handers and a sample of right- and left-handers who were, on average, more inconsistent. The more inconsistent group exhibited some evidence of greater interhemispheric transfer of motor and tactile information, but not visual information. Our research here and in Lyle and Martin has indicated an inconsistent-handedness advantage in the interhemispheric coordination of letter-identity information, which may be phonological in nature, but not visual information (about faces); the latter null effect accords with Potter and Graves.

If inconsistent-handers' advantage in interhemispheric processing is more modality- or operation-specific than originally conceptualised, it challenges superior interhemispheric interaction as a general mechanism to explain all inconsistent-handedness memory advantages. Strengthening this challenge is the current finding that inconsistent-handers, who did not exhibit superior interhemispheric interaction, nonetheless were advantaged on face memory, and especially on novel-face identification, which apparently does not depend on interhemispheric interaction in the first place. Clearly, then, superior interhemispheric interaction does not underlie *all* inconsistent-handedness memory advantages, and another mechanism, presumably more purely intrahemispheric in nature, must be at work, at least in some cases. This confirms Lyle and Martin's (2010) idea that superior intrahemispheric processing may contribute to inconsistent-handers' memory advantages. Additional research will be necessary to determine the extent to which an inconsistent-handedness memory advantage on any specific type of memory test is due to superior interhemispheric interaction, superior intrahemispheric processing, or some combination. Additional research is also needed to determine whether these processing differences interact with saccade execution in some way that causes inconsistent-handers to exhibit SIRE less reliably than consistent-handers.

Conclusion

This study further establishes inconsistent handedness as a predictor of superior memory and saccade execution as a memory enhancer, especially for consistent-handers, who need enhancement the most. However, the study indicates that the search for the cause of these potentially important effects should be broadened beyond interhemispheric interaction.

Manuscript received 17 November 2010
Manuscript accepted 26 May 2011

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