Visual recognition of mirrored letters and the right hemisphere advantage for mirror-invariant object recognition

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Published online: 1 May 2018
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Abstract

Unlike most objects, letter recognition is closely tied to orientation and mirroring, which in some cases (e.g., *b* and *d*), defines letter identity altogether. We combined a divided field paradigm with a negative priming procedure to examine the relationship between mirror generalization, its suppression during letter recognition, and language-related visual processing in the left hemisphere. In our main experiment, observers performed a centrally viewed letter-recognition task, followed by an object-recognition task performed in either the right or the left visual hemifield. The results show clear evidence of inhibition of mirror generalization for objects viewed in either hemifield but a right hemisphere advantage for visual recognition of mirrored and repeated objects. Our findings are consistent with an opponent relationship between symmetry-related visual processing in the right hemisphere and neurally recycled mechanisms in the left hemisphere used for visual processing of written language stimuli.

Keywords Mirror generalization · Cerebral laterality · Object recognition · Symmetry perception · Visual perception

Unlike most objects, letters and words have a canonical orientation. Mirror-reversed letters and words are especially difficult to recognize (Erlikhman, Strother, Barzakov, & Caplovitz, 2017), and in some cases, mirror reversal changes the identity of a letter. Whereas the silhouettes and are seen as mirror-reversed versions of the same object, orientation is the only discriminating property of letter identity for reversible letters (e.g. *b* and *d*). Left-right mirror reversals are the most common orientation error observed in early readers (Cairns & Steward, 1970; Cornell, 1985; Davidson, 1935; Fischer & Koch, 2016). Such errors are normal and disappear during the course of developing reading expertise. Some have even hypothesized that the unlearning of *mirror generalization* (i.e., = ; also called *mirror-invariant* object recognition) is the mechanism by which expert readers avoid mirror reversal errors (Dehaene, Cohen, Sigman, & Vinckier, 2005; Lachmann & van Leeuwen, 2007).

Interestingly, even expert readers do not automatically suppress mirror generalization of reversible letters (Ahr, Houdé, & Borst, 2016; Borst, Ahr, Roell, & Houdé, 2014; Brault Foisy, Ahr, Masson, Houdé, & Borst, 2017; Perea, Moret-Tatay, & Panadero, 2011), meaning that mirror generalization during letter recognition is not completely unlearned. Using a negative priming paradigm, in which observers made sequential judgments of letter pairs (primes) and animal pairs (probes), Borst et al. (2014) found that unlearning of mirror generalization is incomplete in expert readers. Specifically, they showed a negative priming effect of judging mirrored reversible letters (e.g., *b* and *d*) as “different” on a subsequent judgment of mirrored animal drawings (e.g., and) as “same.” The authors interpreted this effect as evidence of delayed reactivation of mirror generalization during the probe judgment, which resulted from active inhibition of mirror generalization during the prime judgment (also see Ahr, Houdé, & Borst, 2016, 2017; Brault Foisy et al., 2017).

In the present study, we partially replicated and adapted the method of Borst et al. (2014) to a *divided visual field paradigm*, commonly used to assess cerebral laterality of visual processing (Bourne, 2006). Of particular interest was the relationship between left-lateralized processing of written language and potentially opposite lateralization of mirror-invariant object recognition, and the role of symmetry in object recognition more generally.

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Experiments 1 and 2

Method

Participants A total of 170 volunteers participated in two experiments, run in parallel: Experiment 1 (140 total, 108 female, mean age = 21.61 years), the main divided visual field experiment; and Experiment 2 (30 total, 18 female, mean age = 20.78 years), a partial replication of Borst et al. (2014). All observers were naïve to the underlying aims of the experiments and reported normal or corrected-to-normal vision. All participants were graduate and undergraduate students at the University of Nevada, Reno. Undergraduate volunteers were given course credit for participation. The experimental protocol adhered to the Declaration of Helsinki, and prior to participating, each observer provided informed consent according to the guidelines of the Department of Psychology and the Institutional Review Board of the University of Nevada, Reno.

Materials Both experiments used letters as prime stimuli and animal silhouettes as probes. Prime stimuli (eight possible letters in total) consisted of two pairs of letters that had a lateral mirror-image counterpart (p|q and b|d) two pairs that did not (a|h and f|t) and could appear as mirror symmetric image pairs, nonmirrored image pairs, or pairs of the same letter (e.g., d|d or a|a). All were in lowercase Arial font, approximately $2^\circ \times 3.2^\circ$ of visual angle. Probe stimuli (eight possible animals in total) were pairs of solid black animal silhouettes; all silhouettes were $\sim 3.3^\circ \times 3.6^\circ$ of visual angle and could face either to the left or right. Probes were either pairs of different animal silhouettes (e.g., |) , pairs of identical animal silhouettes facing the same direction (e.g., |) , or mirror-symmetric silhouettes of the same animal, facing different directions (e.g., |). Our use of silhouettes instead of line drawings is the only difference in our stimuli as compared to those of Borst et al. (2014). Stimuli were presented on a Dell Precision T1650 (Intel Xeon E3 3.5 GHz), with a 24-inch display, and 1920×1200 resolution. The stimuli were created and presented with the Psychophysics Toolbox Version 3.0.10 (Brainard, 1997) for MATLAB (MathWorks Inc., Natick, MA).

Procedure Participants viewed the stimuli from 57 cm using a chin rest. As shown in Fig. 1, trials begin with a central fixation cross (500 ms) replaced by the prime (250 ms), followed by a blank screen for up to 2,500 ms, or until a response was recorded, than another fixation cross (500 ms), followed by the probe (250 ms) in either the LVF or the RVF, and another blank screen for up to 2,500 ms or until a response is recorded. As in Borst et al. (2014), participants were instructed to respond via key press (f/key or j/key) whether the pairs of images that appeared onscreen were the same or different,

counterbalanced between f/j and j/f for same/different. Pairs of the same animal were to be identified as “same” regardless of their relative orientation. The prime-probe conditions of interest identified in Borst et al. were the “negative prime” condition, in which mirror-image letter primes (e.g., b|d) preceded mirror image animal probes (e.g., |) , and the “no prime” condition, in which non-mirror-image different-letter primes (e.g., a|h) preceded mirror-image probes (e.g., |).

Prime pairs were presented centrally in both experiments, with each letter in the pair centered 2.5° to either side of fixation. In Experiment 1, animal silhouette probes appeared in either the left visual field (LVF) or right visual field (RVF), centered 5° from fixation, with each probe 2.5° from the center of the pair. The same prime-probe sequences occurred for each hemifield condition, and trial sequence was randomized for each participant. In Experiment 2, animal silhouette probes were presented centrally, with one stimulus centered 2.5° to the left and one 2.5° to the right of fixation.

Participants performed 20 practice trials of primes and probes randomly sampled from the experimental conditions. They then completed 392 trials in which half of the stimuli pairs were the same and half were different, with each combination of correct responses appearing equally often.

Results

Both of our experiments were designed to elicit negative priming for judgments of mirror-image probes preceded by mirrored reversible letters (i.e., b|d $\rightarrow$ |), which Borst et al. (2014) showed were delayed relative to the probe judgments preceded by nonmirrored letters (i.e., a|h $\rightarrow$ |). Like Borst et al., we performed analyses of response times (RTs) on correct responses to mirrored probes, but we also include additional analyses of other relevant probe conditions. Response accuracy was also analyzed, and abnormally short RTs (less than 200 ms) and outliers (defined as RTs more than two standard deviations from the individual mean of each participant), were excluded from analysis (3.8% of the RTs).

Primes Table 1 shows mean RTs for mirror-image primes (or *mirr*, e.g., b|d) and non-mirror-image primes (or *non*, e.g., a|h). Prime RT and accuracy data for Experiment 1 was analyzed using 2 (type of prime: *mirr* or *non*) $\times 2$ (probe hemifield: LVF or RVF) repeated-measures ANOVAs. Consistent with Borst et al. (2014), who showed better performance for nonmirrored versus mirrored letters ($RT_{\text{mirr}} > RT_{\text{non}}$ and $accuracy_{\text{mirr}} < accuracy_{\text{non}}$), our analysis revealed that participants were slower and less accurate responding to *mirr* primes than to *non* primes, $F(1, 139) = 44.70$, $p < .001$, $\eta_p^2 = .24$, for RT; $F(1, 139) = 8.85$, $p = .003$, $\eta_p^2 = .06$, for accuracy. Prime responses were the same for both probe hemifield locations, $F(1, 139) = .34$, $p = .56$, for RT; $F(1, 139) = .13$, $p = .72$ for

Fig. 1 Trial sequence used in Experiment 1. Experiment 2 sequence was identical, but animal silhouette probes occurred centered on fixation rather than in the left visual field (LVF) or right visual field (RVF)

accuracy, and there was no interaction between prime type and probe hemifield, $F(1, 139) = .86, p = .36$, for RT; $F(1, 139) = .88, p = .35$, for accuracy. Thus, any differences in probe RTs could not be due to hemifield differences in prime RTs (recall that primes were always viewed centrally).

Based on separate Bonferroni-corrected planned comparisons ($\alpha = .025$) of prime RTs for the two probe locations (see Table 1), we confirmed consistency of effect sizes between our prime RTs, LVF: $t(139) = 7.36, p < .001, d = .42$; RVF: $t(139) = 4.30, p < .001, d = .31$, and those of Borst et al. ($d = .46$; this and all subsequent effect sizes for Borst et al., differ from what they reported because we computed effect sizes, and recomputed theirs, without correction for within-subjects correlation because we are comparing two within-subjects experiments). Prime response accuracy in each hemifield was similar to that reported by Borst et al. (~95% accuracy), and it was consistent with RT (i.e., higher RTs were

associated with lower accuracy, and therefore showed no evidence of speed–accuracy trade-off). Prime response results for Experiment 2 (both RT and accuracy, including effect size for RT), $t(30) = 6.26, p < .001, d = .51$, were consistent with those in Experiment 1 and those of Borst et al.

Probes Table 1 shows mean RTs for mirror-image probes following *mirr* primes (i.e., $b|d \rightarrow \text{animal}| \text{animal}$) and mirror-image probes following *non* primes (i.e., $a|h \rightarrow \text{animal}| \text{animal}$) for probes viewed in the LVF or RVF (Experiment 1) or viewed centrally (Experiment 2). Borst et al. (2014) interpreted greater RTs to mirror-image probes following *mirr* primes than mirror-image probes following *non* primes ($RT_{\text{mirr}} > RT_{\text{non}}$) as delayed reactivation of mirror generalization following mirror letter discrimination. For Experiment 1, a 2 (type of prime: *mirr* or *non*) $\times$ 2 (probe hemifield: LVF or RVF) repeated-measures ANOVAs on response RT and accuracy data for mirror-image

Table 1 Response times (ms) and accuracies (%) in the two types of prime (letters without versus with mirror-image counterparts) and the two types of probe (preceded by letters without vs. with mirror-image

counterpart primes) in the left visual field (LVF) and right visual field (RVF) conditions of Experiment 1, and centrally in Experiment 2.

Prime	RT		Accuracy		RT Center	Accuracy Center
	LVF	RVF	LVF	RVF		
ah fg (non)	653 (119)	659 (129)	97.1 (5.3)	97.6 (4.9)	651 (135)	96.6 (5.5)
bd pq (mirr)	690 (121)	689 (128)	96 (5.6)	95.8 (6.7)	727 (163)	92.6 (12)
Probe						
non $\rightarrow \text{animal} \text{animal}$	718 (127)	732 (127)	87.9 (11.9)	86.1 (12.7)	654 (137)	92.6 (7.3)
mirr $\rightarrow \text{animal} \text{animal}$	722 (122)	744 (136)	87 (11)	85.1 (12.9)	678 (131)	91.3 (7.6)
Negative Priming	4 (57)	12 (60)	-0.9 (10.8)	-3.1 (11.6)	24 (41)	-1.3 (8.2)

Note. Standard deviations appear in parentheses. Negative priming reflects the difference in performance on probe responses between the two priming conditions (in bold). Planned t-tests showed significant negative priming for RVF and Center ($p < .05$) but not for LVF ($p = .34$)

probes revealed slower responses for probes following *mirr* primes than *non* primes, $F(1, 139) = 5.03, p = .027, \eta_p^2 = .035$, and slower responses in the RVF than in the LVF, $F(1, 139) = 17.06, p < .001, \eta_p^2 = .109$. There was no main effect of prime type on probe response accuracy, $F(1, 139) = 2.01, p = .15$, but there was a main effect of hemifield, with lower response accuracy for probes in the RVF than in the LVF, $F(1, 139) = 4.60, p = .034, \eta_p^2 = .032$. No interaction between prime type and hemifield was observed in either RT, $F(1, 139) = 1.48, p = .23$, or accuracy, $F(1, 139) = .001, p = .98$.

In addition to the primary conditions of interest (mirror-image probes preceded by *mirr* primes or *non* primes) for Experiment 1, we ran two additional 2 (type of prime: *mirr* or *non*) $\times$ 2 (probe hemifield: LVF or RVF) repeated-measures ANOVAs on response RT and accuracy data for *same* image probes (e.g.,) and *different* image probes (e.g.,) preceded by *mirr* primes or *non* primes. For *same* image probes, analysis of RT data found no main effect of prime, $F(1, 139) = .19, p = .67$, a main effect of hemifield (slower responses in the RVF than in the LVF), $F(1, 139) = 10.90, p = .001, \eta_p^2 = .073$, and no interaction between prime type and hemifield, $F(1, 139) = .96, p = .33$. For *different* image probes, RT data analysis revealed no main effect of prime, $F(1, 139) = .25, p = .61$; no main effect of hemifield, $F(1, 139) = .11, p = .74$; and no interaction, $F(1, 139) = 1.99, p = .16$. For both *same* image probes and *different* image probes, accuracy data showed the same pattern of results. Mean RTs to the three probe types (*mirror*, *same*, and *different*), collapsed across prime and hemifield conditions, were compared using a one-way repeated-measures ANOVA with a Greenhouse–Geisser correction, which revealed a significant difference between probe types, $F(1.49, 206.67) = 90.41, p < .001, \eta_p^2 = .39$. Post hoc tests with Bonferroni correction found RTs to *same* image probes ($M = 694, SD = 122$) were faster than *mirror* image probes ($M = 729, SD = 120$), $t(139) = 9.18, p < .001, d = .28$, and RTs to *mirror* image probes were faster than *different* image probes ($M = 774, SD = 132$), $t(139) = 6.79, p < .001, d = .36$.

In Experiment 2, we were interested in confirming negative priming for centrally viewed probes and the degree to which RTs differed from those in Experiment 1. A Bonferroni-corrected planned comparison ($\alpha = .025$) revealed that $RT_{\text{mirr}} > RT_{\text{non}}$ for centrally viewed probes, $t(30) = 3.25, p = .003, d = .18$.

To compare negative priming effects between experiments, planned comparison tests were also conducted on RTs for mirror-image probes in the LVF and RVF (Experiment 1). For probes in the RVF, $t(139) = 2.42, p = .017, d = .10$, and for probes in the LVF, $t(139) = .85, p = .34, d = .03$. The corresponding effect size in Experiment 2 ($d = .18$) was larger than those in Experiment 1, but smaller than that of Borst et al. ($d = .26$). Accuracy was similar ($\sim 90\%$) in both of our experiments and in Borst et al.'s.

Discussion

Here, we tested for possible relationships between visual object recognition and known cerebral asymmetries for visual processing of written language, including left-lateralized neural mechanisms “recycled” (Dehaene & Cohen, 2007) for visual recognition of letters and words. Consistent with the results of Borst and colleagues (Ahr, Houdé, & Borst, 2016, 2017; Borst et al., 2014; Brault Foisy et al., 2017), we observed negative priming of mirrored reversible letters (e.g., *b* and *d*) on mirrored animal images (e.g., and). We also observed a clear right hemisphere (RH) advantage for object recognition (performance on the probe task irrespective of prime type). Interestingly, however, we did not observe a clear relationship between the RH advantage for object recognition and negative priming.

One possibility is that our divided field negative priming method was insufficiently sensitive to reveal cerebral asymmetries of delayed reactivation of mirror generalization. Consistent with this possibility, the negative priming effect was decreased for probes viewed in the periphery (Experiment 1) relative to those viewed centrally (Experiment 2), despite equivalent accuracies in the two experiments, and the main effect of hemifield on the probe task was actually greater than that of prime type. This means that if hemispheric differences exist with respect to inhibition of mirror generalization during letter recognition, then such differences are relatively small with respect to object recognition performance more generally.

Despite an absence of clear hemifield differences in negative priming, our results demonstrate for the first time that, like other priming studies of object recognition (e.g., Stankiewicz & Hummel, 2002), delayed reactivation of mirror generalization occurs for peripherally viewed probes. This is important because it implies that the mirror generalization mechanism reactivated in the probe task (with primes viewed in a different retinal location than the probes) is *location invariant*, and possibly located in high-tier visual cortex (Cohen et al., 2002; Grill-Spector et al., 1999; Strother, Aldcroft, Lavell, & Vilis, 2010).

In addition to our finding of negative priming, and the lack of interaction with hemifield, our finding of an LVF/RH advantage for perception of symmetric object pairs is important in its own right for several reasons. First, behavioral and neuroimaging studies (Burgund & Marsolek, 2000; Marsolek, 1999; Vuilleumier, Henson, Driver, & Dolan, 2002) have shown that viewpoint invariance is associated with relatively “abstract” representation in the left hemisphere (LH) and viewpoint-dependent representation in the right (RH). However, in contrast to our experiments, these studies presented object pairs sequentially, which highlights the distinction between single object viewing as opposed to simultaneously viewing object pairs.

Our results showed that, for object pairs, repeated objects (same animal probes) are more efficiently processed than are mirrored object pairs (mirrored animal probes), and both are more efficiently processed than different objects are (different animal probes). Additionally, mirrored and repeated object pairs showed an RH advantage, whereas pairs of different objects do not. Taken together, our results are consistent with those of previous studies showing an advantage for repetition (translation) detection versus mirror symmetry detection in the context of object pairs, and the opposite for single objects (Baylis & Driver, 2001; Bertamini, Friedenberg, & Kubovy, 1997; Corballis & Roldan, 1974; Koning & Wagemans, 2009). Furthermore, our results suggest greater RH involvement in recognizing both mirrored and repeated (translated) objects. This is consistent with the existence of extrastriate visual cortical mechanisms involved in both mirror generalization and symmetry detection (Bona, Cattaneo, & Silvanto, 2016; Bona, Herbert, Toneatto, Silvanto, & Cattaneo, 2014; Kietzmann et al., 2015; Pegado, Nakamura, Cohen, & Dehaene, 2011; Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005). To our knowledge, our finding of an RH advantage for mirrored and repeated object pairs is the first of its kind (for a recent and fairly exhaustive review of symmetry and object recognition, see Bertamini, Silvanto, Norcia, Makin, & Wagemans, 2018). We propose that neural mechanisms underlying visual processing of symmetric stimuli are compromised in the LH due to recycling for purposes of word recognition. Verma, Van Der Haegen, and Brysbaert (2013) made a closely related proposal based on single-object symmetry results.

In conclusion, the fact that subjects were, for the most part, very accurate on the task, even though it was performed in the periphery, is important in its own right. Indeed, this was a primary motivation for the classic study by Corballis and Roldan (1974), and many subsequent studies (Verma et al., 2013; Wright, Makin, & Bertamini, 2017). Our results show that, like symmetry detection, mirror-generalized object recognition might be accomplished by independent mechanisms in each hemisphere (Wright et al., 2017) and does not require callosal transfer (Herbert & Humphrey, 1996). Our results also support and extend the observation of delayed reactivation of mirror generalization reported by Borst and colleagues (Ahr et al., 2016, 2017; Borst et al., 2014; Brault Foisy et al., 2017). It is important to note that Borst and colleagues did not claim that the inhibition of mirror generalization is limited to one hemisphere or the other. Others studies, however, suggest that mirror inhibition during visual recognition of letters and words is automatic and occurs in neurally recycled mechanisms in the left occipitotemporal cortex (Dehaene et al., 2010; Pegado et al., 2011). Our results show that active inhibition of mirror generalization occurs in both hemispheres, and that it is related to but distinct from the RH advantage for recognizing mirrored or repeated objects as being the same.

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