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Research report

Symmetrical hemispheric priming in spatial neglect: A hyperactive left-hemisphere phenomenon?

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ABSTRACT

Hemispheric rivalry models of spatial neglect suggest that the left hemisphere becomes hyperactive following right-hemisphere lesions since the two hemispheres normally exert an inhibitory influence on each other via callosal connections. Using a masked hemifield priming paradigm, we investigated whether the putative change in hemispheric balance involves other, higher-order abstract representational systems in spatial neglect. Participants consisted of 12 neglect patients with right-hemisphere damage and three groups of control participants, i.e., 12 young healthy controls, 10 age-matched healthy controls and 10 right-hemisphere patients without spatial neglect. In each trial, participants made semantic categorization about a centrally presented target word which was preceded by a masked prime flashed either to the left or right visual field. All three control groups exhibited strong left-hemisphere advantage in inhibitory syllabic priming, consistent with the known left-hemisphere dominance in lexical inhibition during reading. By contrast, neglect patients exhibited a symmetrical pattern of priming between the left and right visual fields. These results suggest that (1) the neglected hemifield can rapidly extract abstract information even from weak and normally non-perceptible visual stimuli, but that (2) the normal left hemispheric dominance in reading is absent in neglect patients probably because of the generalized hyperactivity of the left hemisphere. Our results demonstrate a covert behavioral change in spatial neglect which may reflect the altered inter-hemispheric balance in the bilateral word recognition system encompassing lexico-semantic memory.

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1. Introduction

Spatial neglect is a common neuropsychological syndrome characterized by a lateralized disruption of spatial awareness

for contralesional space. Neuropsychological studies with neglect patients have suggested that this attentional bias is caused by a loss of inter-hemispheric balance after right-hemisphere lesions (Driver et al., 1997; e.g., Kinsbourne, 1977).

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Namely, these hemispheric rivalry models propose that the left hemisphere becomes hyperactive after right-hemisphere damage and inhibits visual recognition in the contralesional space since the two hemispheres normally exert an inhibitory influence on each other via callosal connections. Indeed, functional brain imaging and transcranial magnetic stimulation (TMS) studies with neglect patients have supported the putative hemispheric competition mechanism by showing that transcallosal inhibition operates between homotopic regions in two hemispheres, with increased excitability of the intact left hemisphere, at least for early visual and somatosensory systems (Fink et al., 2000; Forss et al., 1999; Koch et al., 2008; Oliveri et al., 1999).

However, little is known about whether lesion-induced changes in hemispheric balance affect other higher-order representational systems, such as lexico-semantic and numerical memory. That is, behavioral studies with normal people have shown that the two hemispheres each enfold a separate word recognition system showing hemispheric dominance at different stages of word processing, i.e., left-hemisphere advantage at lexical selection (Perea et al., 2008) and right-hemisphere advantage at coarse semantic encoding (Beeman et al., 1994). At the neural level, the lexico-semantic system involved in reading has been shown to be represented by the posterior occipitotemporal cortex in each hemisphere (Chertkow et al., 1997; Nakamura et al., 2007; Tyler et al., 2003). Importantly, a recent TMS study with normal people showed that the left occipitotemporal cortex and its right homotopic area exert the similar callosal inhibition during visual word recognition (Ueki et al., 2006). It is thus possible that hemispheric dominance in lexico-semantic memory is altered in spatial neglect after lateralized brain damage.

We addressed the question by using a hemifield phonological priming paradigm with visual masking (Fig. 1A). That is, the visual recognition of a target word is known to be inhibited after a brief exposure to another word (or primes) sharing the same first syllable with the target (Carreiras and Perea, 2002). Recent behavioral evidence from normal people has shown that such inhibitory regulation occurs at the lexical level during visual word recognition and reflects a bottom-up, lateral inhibition mediated by the left-hemisphere reading system (Perea et al., 2008). By manipulating the prime-target syllabic overlap, we tested whether the left-hemisphere dominance in inhibitory priming differed between neglect patients and control participants. Given the known role of the ventral visual system in word recognition (Dehaene et al., 2005), we selected only those neglect patients with focal right-hemisphere damage outside the bilateral occipitotemporal lobe and the posterior corpus callosum (see Methods).

Several past studies used similar priming techniques to demonstrate that neglect patients have implicit, non-conscious recognition of ignored visual stimuli even without perceptual awareness (Cappelletti and Cipolotti, 2006; Forti and Humphreys, 2007; Ladavas et al., 1993; Rusconi et al., 2006; Schweinberger and Stief, 2001). However, we assessed the functional state of the hemispheric reading systems more rigorously by delivering masked and invisible prime stimuli equally to both the intact and neglected hemifields. This masked priming paradigm enabled us to stimulate each hemispheric system separately, because weak

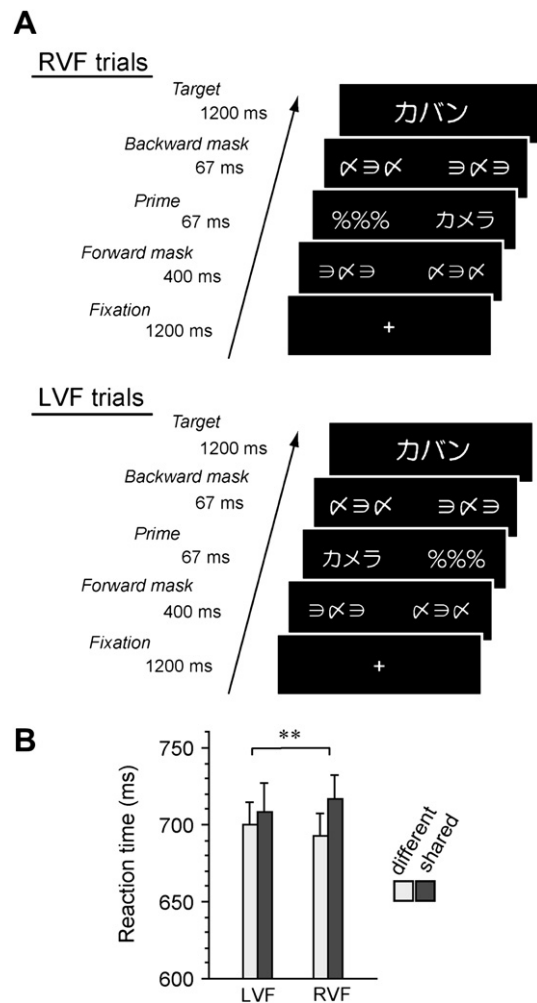


Fig. 1 – Behavioral paradigm and asymmetric syllabic priming in normal participants. (A) Each target appeared on the center of the screen for 1200 msec, following a masked prime presented briefly either in the left or right hemifield. Primes and targets either shared the first syllable or had mutually different onset syllables. Participants made natural/artificial judgment about visible targets. **(B)** Young control participants responded to target words more slowly when masked primes sharing syllabic overlap with targets appeared in the RVF, whereas no such response inhibition occurred when those primes appeared in the LVF. This lateralized effect of inhibitory priming was confirmed as a significant interaction between syllabic overlap and prime-hemifield (** $p < .005$).

lexico-semantic activation induced by subliminal primes is shown to occur only within each hemisphere and does not spread across hemispheres (Reynvoet and Ratinckx, 2004). For testing neglect patients, moreover, the visual masking procedure provided an additional advantage by eliminating behavioral effects associated with the asymmetric visual awareness between the left and right hemifields. This is important because the conscious perception of written words is known to exert strong top-down amplification of the posterior reading systems (Dehaene et al., 2006). Thus, given

that visual stimuli presented in the neglected hemifield do not yield conscious perceptual experience, non-masked, consciously visible words should induce much greater top-down modulation when presented to the intact hemisphere, which may strongly bias the behavioral measurement of hemispheric dominance in word recognition.

2. Methods

2.1. Participants

We first conducted a pilot study with 12 young control participants without neurological signs or symptoms (Experiment 1; eight females; age range 24–42 years) to verify the hemispheric effects on masked syllabic priming in normal people. In Experiment 2, we examined 12 spatial neglect patients with right-hemisphere damage (three females; mean age = 63.6 years, range = 46–71 years). Demographic and neurological data of these patients are summarized in Table 1. All of them had CT/MRI-identified cerebrovascular lesions in the right frontoparietal or subcortical structures which spared the bilateral occipitotemporal cortex and the posterior corpus callosum. The presence of left unilateral neglect was determined using clinical pencil-and-paper tests including line bisection and object copying. All neglect patients exhibited 10–15 mm of rightward deviation in a standard line-bisection test with a 200-mm horizontal line. None of them had other cognitive or language deficit in routine neuropsychological assessment. We further recruited 10 age-matched healthy control participants without known neurological disorder

(seven females; mean age = 59.3 years, range = 55–71 years) and 10 right-hemisphere (RH) patients without spatial neglect (two females; mean age = 62.3 years, range = 46–74 years, see Table 1). The latter, RH-control patients had only mild left sensorimotor deficit after cortical or subcortical stroke sparing the occipitotemporal cortex and the corpus callosum. Neglect and non-neglect control patients were tested between 1 and 3 months after stroke onset. The experimental session was performed individually for each participant. All participants were right-handed native speakers of Japanese and had received 12 years or more of formal education. Informed consent was obtained from all participants prior to the experiment. The protocol of this study was approved by the ethical committee of the Toranomon Hospital and the hospital committee of the Yokohama Stroke Center.

2.2. Behavioral paradigm

Target words consisted of 30 medium-to-high frequency nouns (3–4 characters in length) written in a Japanese syllabic script (katakana). Half of them represented natural objects, while the other half artifacts. By manipulating a syllabic overlap with these targets, we prepared two different types of primes matched in frequency and word length. The first type of primes shared the first syllable with their respective targets [e.g., prime = ‘ka-ba-n’ (bag)/target = ‘ka-me-ra’ (camera)], whereas the second type of primes had different onset syllables [e.g., prime = ‘bi-de-o’(video)/prime = ‘ka-me-ra’ (camera)]. Masked primes always belonged to the same semantic category as visible targets.

Table 1 – Demographic and neurological data of spatial neglect and control patients.

Patient	Age	Sex	Lesion site	Lesion etiology	Neurological deficit		
					Spatial neglect	Somatosensory	Motor
N1	68	M	R frontal subcortical area	Ischemic	+	–	+
N2	55	F	R basal ganglia	Hemorrhagic	+	+	+
N3	71	M	R frontoparietal region	Hemorrhagic	+	+	+
N4	70	M	R posterior parietal region	Hemorrhagic	+	+	+
N5	46	M	R basal ganglia – frontoparietal junction	Hemorrhagic	+	±	+
N6	64	F	R posterior parietal region	Hemorrhagic	+	–	±
N7	49	F	R basal ganglia	Hemorrhagic	+	±*	±
N8	48	M	R basal ganglia	Ischemic	+	+	±
N9	67	M	R basal ganglia – frontoparietal junction	Hemorrhagic	+	–	+
N10	53	M	R frontoparietal region	Ischemic	+	±	+
N11	60	M	R posterior parietal region	Hemorrhagic	+	±	+
N12	61	M	R frontoparietal region	Ischemic	+	–	+
C1	46	M	R basal ganglia	Hemorrhagic	–	+	+
C2	63	M	R basal ganglia	Ischemic	–	+	+
C3	68	M	R frontal subcortical area	Hemorrhagic	–	±	+
C4	67	M	R internal capsule	Ischemic	–	–	+
C5	56	F	R frontoparietal region	Ischemic	–	–	+
C6	67	M	R frontoparietal region	Ischemic	–	–	+
C7	74	M	R basal ganglia	Hemorrhagic	–	–	+
C8	59	F	R basal ganglia	Ischemic	–	±	+
C9	69	M	R basal ganglia	Ischemic	–	–	+
C10	54	M	R parietal subcortical area	Ischemic	–	+	+

N: neglect patients, C: control patients without neglect, Neurological deficits on the contralesional side: + present, – absent, ± transient or equivocal, * present only in the upper limbs.

Each trial included a four-field sequence of a forward mask, a prime word with a visual foil, a backward mask and a target word (Fig. 1). The forward and backward masks were an alternating pair of strings of letter-like symbols (“ $\propto \ni \propto$ ” and “ $\ni \propto \ni$ ”) assigned pseudo-randomly to the left visual field (LVF) and right visual field (RVF). A prime and a perceptual foil (“%%”) appeared simultaneously for 67 msec either in the LVF or in the RVF with a probability of 50%. The forward masks, primes, foils and backward masks were all centered at 2.7° left or right of the fixation, whereas their overall visual length was 2.5°. Each target, subtending with a visual angle of 4.7°, was displayed for 1200 msec on the center of the screen. Each target was presented eight times throughout the experiment, while prime items never appeared as a consciously visible word. Participants made natural/artificial judgment about visible targets by pressing a key with their right index and middle fingers as quickly and accurately as possible. Each participant received a single session including 240 trials and lasting ~20 min.

We assessed the perceptual discriminability of masked primes in a separate session with 12 young and 10 age-matched healthy participants and eight RH-control patients. In addition, we collected data from eight of our neglect patients. In this forced-choice test, each trial started with the same sequence of masks and words as the main experiment, followed by an additional word on the center of the screen. Participants were asked to determine whether or not this last word was same as the preceding prime without time pressure (80 trials). For each participant, we computed a prime-discriminability index (d') for each hemifield by treating the “same” trials as signal and “different” trials as noise, respectively.

3. Results

3.1. Experiment 1

We first investigated the hemispheric effects on masked syllabic priming in young control participants without neurological deficit. A post-session debriefing revealed that half of these participants noticed the existence of primes and could occasionally identify them during the experiment. All of them performed the semantic categorization task with few errors, irrespective of whether masked primes were presented in the LVF (mean error rate (\pm SD) = 3.82 (\pm 1.83)%) or in the RVF (mean error rate (\pm SD) = 3.89 (\pm 2.31)%).

We then examined mean reaction time for correct responses (Fig. 1B) using 2×2 repeated-measure analysis of variance (ANOVA) treating participants as a random variable and prime-target syllabic overlap (shared and different) and prime-hemifield (LVF and RVF) as within-participant factors. The main effect of prime-hemifield never approached significance ($F < 1$), suggesting that participants responded to centrally presented targets equally fast, irrespective of whether masked primes appeared in the LVF or in the RVF. On the other hand, participants overall responded 17 msec more slowly when primes and targets shared the first syllables than when they had no syllabic overlap at word onset. This inhibitory priming of syllabic overlap was significant [$F(1, 11) = 5.127, p < .05$] but interacted with prime-hemifield [$F(1, 11) = 13.90, p = .003$], suggesting hemispheric asymmetry in syllabic

priming. Indeed, additional pairwise comparisons for each hemifield revealed a strong left-hemisphere dominance in syllabic priming, with a robust inhibitory effect for the RVF [$F(1, 11) = 14.74, p = .003$] but not for the LVF [$F(1, 11) = 1.04, p > .3$]. These findings replicate the previously known effect of negative syllabic priming (Carreiras and Perea, 2002) and also fit with the recent behavioral evidence showing that lexical-level inhibition by orthographic neighbors is enhanced in the left hemisphere (Perea et al., 2008).

In the prime visibility test, the overall mean (\pm SD) of d' scores was .98 (\pm .78) for the LVF and 1.27 (\pm .74) for the RVF, respectively. This behavioral index was significantly greater than zero, both for the LVF ($p < .005$) and the RVF ($p < .001$), with no between-hemifield difference ($p > .3$). This finding suggests that young control participants were at least partially aware of the identity of masked primes.

3.2. Experiment 2

3.2.1. Masked syllabic priming effects

Neglect patients, RH-control patients and age-matched normal participants performed the same semantic categorization task with high accuracy (Table 2). In a post-session debriefing, only two control participants occasionally noticed the existence of primes but reported being unable to identify them during the experiment. For error rates, we ran repeated-measure ANOVA with prime-hemifield (LVF and RVF) as within-participant factor and group (neglect, RH-control and normal) as a between-participant factor. The overall error rate neither differed across the three groups nor changed with prime-hemifield (both $F_s < 1$). These main effects did not interact with each other ($F < 1$). Thus, errors were distributed equally across groups and not systematically affected by prime-hemifield.

We next examined mean reaction times for correct responses (Fig. 2) with $2 \times 2 \times 3$ repeated-measures ANOVA treating syllabic overlap (shared and different), prime-hemifield (LVF and RVF) as within-participant factors and group (neglect, RH-control and normal) as a between-participant factor. There was a significant inhibitory effect of syllabic overlap [$F(1, 21) = 32.25, p < .001$]. The main effect of prime-hemifield never approached significance ($F < 1$). In contrast, we found a significant effect of group [$F(2, 29) = 4.74, p = .02$] and a non-significant trend of group \times hemifield interaction [$F(1, 21) = 3.59, p = .07$]. Moreover, these factors showed significant triple interaction [$F(2, 29) = 5.53, p = .009$], suggesting that the degree of hemispheric asymmetry in syllabic priming differed across the three groups (see below for further analysis). All other interactions were non-significant (all $F_s < 1$).

Table 2 – Mean error rate (\pm SD) during semantic categorization (%).

Group	Prime-hemifield	
	LVF	RVF
Neglect	7.85 (\pm 6.28)	8.13 (\pm 5.45)
RH control	7.17 (\pm 6.66)	7.83 (\pm 7.05)
Normal	5.25 (\pm 3.38)	4.75 (\pm 3.12)

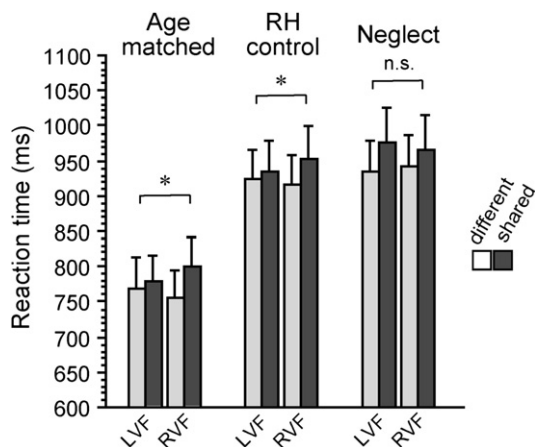


Fig. 2 – Syllabic priming in neglect patients and control participants. Age-matched normal participants and non-neglect RH-control patients showed the same lateralized effect of inhibitory syllabic priming as young controls in Experiment 1 ($p < .05$). By contrast, this normal hemispheric dominance in syllabic priming was not found in neglect patients (see Results).

When the analysis was restricted to normal controls, we found a significant effect only for syllabic overlap [$F(1, 9) = 39.81, p < .001$] and not for hemifield ($F < 1$). These effects interacted with each other [$F(1, 9) = 6.65, p = .03$]. Further posthoc analysis for each hemifield revealed a robust inhibitory effect for the RVF [$F(1, 9) = 116.84, p < .001$] but not for the LVF ($F < 1$). On the other hand, RH-controls also showed a significant effect of syllabic priming [$F(1, 9) = 11.99, p = .007$]. Again, the effect of hemifield was non-significant ($F < 1$) and interacted with syllabic overlap [$F(1, 9) = 17.53, p = .02$]. Pair-wise comparison for each hemifield confirmed a significant inhibitory effect for the RVF [$F(1, 9) = 17.73, p = .002$] and not for the LVF [$F(1,9) = 2.53, p = .15$]. Note that this asymmetric hemispheric priming in the two control groups replicates the left-hemisphere dominance observed with the younger participants in Experiment 1.

Neglect patients also showed a significant effect for syllabic overlap [$F(1, 11) = 15.05, p = .003$] and not for hemifield ($F < 1$). However, contrary to both control groups, no significant interaction was found between syllable overlap and hemifield [$F(1, 11) = 1.54, p > .2$]. Indeed, inhibitory syllabic priming was significant for both the RVF [$F(1, 11) = 5.22, p = .04$] and the LVF [$F(1, 11) = 16.53, p = .002$].

3.2.2. Between-group comparisons of syllabic priming effects
We further compared syllabic priming effects between age-matched normal participants, RH-control patients and neglect patients. Given the clear hemispheric asymmetry in syllabic priming in the two control groups, the critical question here is to determine whether the symmetrical priming effects in neglect patients substantially departed from these controls by testing three-way interactions between syllabic overlap, hemifield and group. We first compared syllabic priming effects between 10 age-matched normal controls and 10 RH-controls by treating group (normals and RH-controls) as

a between-participant factor. This analysis revealed that RH-controls overall responded 156 msec more slowly than normal controls [$F(1, 18) = 7.06, p = .02$]. However, hemispheric dominance in syllabic priming did not differ between the two groups, since there was no significant triple interaction between syllabic overlap, hemifield and group ($F < 1$).

We then compared 12 neglect patients with each of the two control groups. Compared to normal controls, neglect patients responded 179 msec more slowly [$F(1, 20) = 8.05, p = .01$]. Critically, between-group ANOVA revealed significant triple interaction between syllabic overlap, hemifield and group [$F(1, 20) = 7.39, p = .01$]. On the other hand, when compared with RH-controls, neglect patients were no slower to recognize visible targets ($F < 1$). However, the critical triple interaction was also significant in this between-group comparison [$F(1, 20) = 6.21, p = .02$].

To illustrate the overall distribution of hemifield priming effects across different participant groups, we collected reaction time data from Experiments 1 and 2 and plotted the magnitude of individual-level priming in Fig. 3. Note that neglect patients showed no left–right hemifield asymmetry whereas all three groups of control participants showed the RVF dominance in priming effects. Additionally, we compared reaction time data between age-matched normal controls and young participants to assess the possible effects of age on behavioral measures. This additional analysis showed that aged controls responded as quickly as younger participants since there was no significant effect of group [$F(1, 20) = 2.00, p = .1$]. The magnitude of syllabic priming neither differed between the two groups ($F < 1$). Other interactions were all non-significant ($p > .15$).

3.2.3. Prime discriminability

The overall mean (\pm SD) of d' scores in 10 age-matched healthy controls was .34 (\pm .56) for the RVF and .40 (\pm .60) for the LVF,

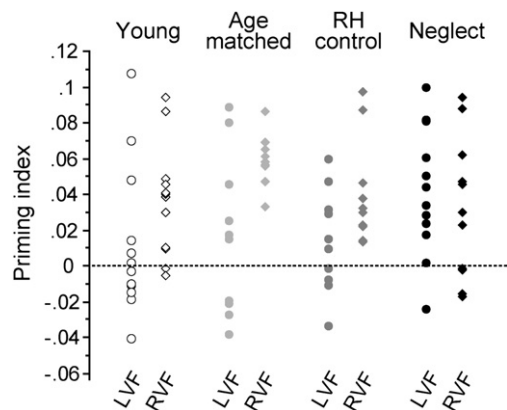


Fig. 3 – Overall distribution of syllabic priming effects in neglect and control groups. For each participant, the priming index in the ordinate was calculated as $(RT_{\text{different trials}} - RT_{\text{shared trials}}) / (RT_{\text{different trials}})$ and plotted for each hemifield (positive values represent positive effects of inhibitory priming). For young and age-matched normals and RH-control patients, this individual-level index of syllabic priming was overall clustered on the positive side for the RVF, but was distributed around zero for the LVF. In contrast, neglect patients showed no such left-right hemifield difference in priming index.

respectively. This behavioral index did not depart significantly from zero, either for the RVF ($t = 1.93$, $p > .08$) or the LVF ($t = 2.11$, $p > .06$) and showed no significant difference between hemifields ($t = .19$). For RH-control participants, the average d' score was $.39 (\pm .64)$ for the RVF and $.32 (\pm .60)$ for the LVF, respectively. The prime visibility neither differed from zero ($p > .1$ for both hemifields) nor showed significant between-hemifield difference ($t = .35$). These findings therefore suggest that age-matched healthy controls and non-neglect RH patients were almost unable to report the identity of masked primes, irrespective of whether the stimuli appeared in the LVF or in the RVF. It is thus highly unlikely that our neglect patients had any more conscious perception of primes in the same stimulus sequence. Indeed, the mean d' score obtained from eight neglect patients did not exceed those of the control groups [$.24 (\pm .45)$ for the RVF and $.22 (\pm .39)$ for the LVF]. Like control participants, this visibility index was different neither from the chance-level ($p > .15$ for both hemifields) nor between hemifields ($t = .15$).

For normal controls, we additionally examined whether prime visibility changed with aging by contrasting age-matched participants and young participants in Experiment 1. Using a 2×2 ANOVA with prime-hemifield and group, we confirmed that young participants perceived masked primes more accurately than age-matched controls, irrespective of whether the stimuli appeared in the LVF or in the RVF [$F(1, 20) = 13.41$, $p < .005$]. We then assessed whether the individual-level priming index (see Fig. 3) was correlated with each participant's d' score and age. Indeed, this analysis revealed a significant negative correlation between prime visibility and age ($r = -.51$, $p < .001$). By contrast, priming index was neither correlated with visibility nor with age ($p > .5$ for both). To summarize, these findings suggest that (1) the perceptual awareness of primes decreased with age and that (2) this visibility level in itself was not directly correlated with the observed effect of syllabic priming. This is consistent with the finding that the magnitude of priming did not differ between young and age-matched normal controls (see above).

4. Discussion

Our results from Experiment 1 confirmed that masked syllabic priming has an inhibitory effect strongly lateralized to the left hemisphere. This same pattern of lateralized syllabic priming was also found in age-matched control participants. For normal readers, negative masked priming during visual word recognition is known to occur when high-frequency primes share overlapping sublexical elements with word targets, either at orthographic (Davis and Lupker, 2006) or syllabic (Carreiras and Perea, 2002; Matheya et al., 2006) levels. Such inhibitory modulation is thought to reflect lateral inhibition of lexical competitors during target identification, since those primes simultaneously activate other lexical codes having sublexical overlap with targets, which need to be suppressed by target codes during word identification. Recent work by Perea et al. (2008) further suggests that lexical inhibition is enhanced in the left hemisphere relative to the right hemisphere because orthographic encoding of written words operates differently between the left and right reading

systems. Our results from control participants therefore replicate those previous studies on negative orthographic/syllabic priming and support the inter-hemispheric asymmetry in lexical inhibition during reading. This inhibitory effect of priming was lateralized to RVF trials in our control participants, probably because visually degraded primes flashed to the right hemisphere cannot activate the left-hemisphere system effectively via long-distance callosal connections (see also Dehaene et al., 2006; Reynvoet and Ratinckx, 2004), thereby yielding only weak inhibitory effects in behavioral measures.

In Experiment 2, however, we found that neglect patients showed negative syllabic priming regardless of whether masked primes were presented to the LVF or RVF. This masked priming effect by LVF primes suggests that neglect patients can extract task-relevant abstract information even from weak and normally imperceptible stimuli in the neglect hemifield, and thus extends past-neuropsychological studies which obtained semantic or numerical priming by using non-degraded, stronger visual stimuli (Cappelletti and Cipolotti, 2006; Forti and Humphreys, 2007; Ladavas et al., 1993; Rusconi et al., 2006; Schweinberger and Stief, 2001). Interestingly, the present finding suggests that this fast word recognition in the neglected hemispace may operate effectively even at the leftmost part of visual stimuli in the object-centered space, since masked inhibitory priming effects occur only at the initial and leftmost segment of each word (Davis and Lupker, 2006).

Moreover, the significant triple interaction between syllabic overlap, prime-hemifield and group confirmed that the symmetrical pattern of hemispheric priming is distinct from the left-hemisphere dominance observed in control participants. Given that masked syllabic priming reflects lexical inhibition during visual word recognition, this finding suggests a covert lesion-induced change of hemispheric asymmetry in lexical memory in spatial neglect. In fact, in a previous study with neglect patients, Schweinberger and Stief (2001) reported a similar increase in repetition priming effect for LVF primes during lexical decision. This hyper-priming was also attributed to the lexical access stage of reading because response facilitation was found only for real words and not for pseudowords. This is therefore in good accord with the increased right-hemisphere priming observed in the present study, which is also likely to reflect lexical-level processing of written words.

At the neural level, the existing neuropsychological and functional brain imaging data converge to suggest that lexico-semantic memory involved in reading is represented in the left lateral temporal cortex (Chertkow et al., 1997; Devlin et al., 2004; Nakamura et al., 2007, 2006; Tyler et al., 2003). Recent lesion analysis data further showed that the adjacent posterior temporal region is involved in lexical access and form-to-meaning mapping (Dronkers et al., 2004; Vandenbulcke et al., 2007). As mentioned earlier, the same left occipitotemporal region is shown to exert reciprocal inhibitory interaction with its right homotopic area during visual word recognition in normal people (Ueki et al., 2006).

It is important to note that the damaged right hemisphere in itself is unlikely to produce the observed hyper-priming by LVF primes. This is especially because inhibitory syllabic priming is shown to rely on a fine-grained orthographic

encoding mechanism proper to the left-hemisphere visual system (Perea et al., 2008). In contrast, the right-hemisphere system is thought to encode written words at a coarser, multi-letter unit (e.g., bigram and trigram) and exert much weaker lateral inhibition among lexical competitors (Lavidor and Ellis, 2002). Importantly, this coarse input coding seems to reflect an intrinsic and probably innate property of the human right-hemispheric object recognition system that shows general advantage in holistic visual analysis (e.g., Fink et al., 1996). It is therefore unlikely that the visual encoding pattern of the right-hemisphere reading system drastically changed with acquired brain damage.

Another interesting possibility is that lateralized brain damage may affect hemispheric language dominance in the functional reorganization of the dominant and non-dominant hemispheres. For instance, several neuroimaging studies with aphasic patients have shown that the right inferior frontal cortex, or a right homolog of Broca's area, can play a compensatory role in lexical retrieval during language recovery (Blasi et al., 2002; Raboyeau et al., 2008; Saur et al., 2006). For the present study, however, the observed symmetrical effect of priming cannot be attributed to such localized change in hemispheric dominance between a damaged neural system in one hemisphere and its homotopic system in the other hemisphere. This is because the cortical substrate of visual word recognition is identified in a restricted part of the left occipitotemporal region (Dehaene et al., 2005) whereas this same area, its right-hemisphere homolog and their transcallosal connections are all intact in our neglect patients.

Rather, we propose that the symmetrical hemispheric priming in neglect patients reflects a more generalized hyperactivity of the intact hemisphere involving the entire task-relevant reading network. That is, because of this global change in hemispheric balance, the left-hemisphere word recognition system outside specific lesion sites may become hypersensitive and exert enhanced lexical inhibition even on weak transcallosal signals produced by LVF primes. Such generalized hyperactivity of the left hemisphere seems consistent with Kinsbourne's early hemispheric inhibition model (1977) and fits with the fact that spatial neglect affects the left-right balance in a broad range of human behavior, including visual, sensorimotor, imaginary, and even social interactions (Mesulam, 1999). In summary, our results suggest that, like those other neurocognitive systems, the visual word recognition system in spatial neglect operates with the different hemispheric bias from premorbid status. This lesion-induced change in hemispheric balance could be covert in nature without immediate impact at the clinical level, but may provide a novel insight into the cerebral architecture of reading.

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