

Task-sensitivity of unconscious word processing in spatial neglect

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ABSTRACT

Neuropsychological studies of spatial neglect have shown that ignored visual stimuli can produce measurable behavioral changes without eliciting subjective perceptual experience. However, such non-conscious, implicit cognitive processing may not be fully automatic but rather could be influenced by the patients' voluntary behavioral control. Using a hemifield priming paradigm with two different task instructions, we studied spatial neglect patients to assess whether non-conscious processing of ignored words is modulated by behavioral task requirements. In each trial, participants named or categorized a centrally presented target following a masked prime flashed to the left or right hemifield. By delivering equally invisible stimuli to both hemifields, this design allowed rigorous testing of the impact of task instructions on non-conscious processing in neglect patients and control participants. We observed that neglect patients showed slightly different patterns of masked priming from those obtained in healthy and right-hemisphere control patients. Importantly, however, all these three groups showed strong sensitivity to task contexts during the unconscious processing of masked words. The present results provide neuropsychological evidence that robust task-sensitive neural pathways are covertly operating on weak and normally imperceptible visual stimuli even when visuospatial attention is severely compromised.

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1. Introduction

Spatial neglect is a common neurological disorder typically caused by right frontoparietal damage and characterized by a lateralized disruption of spatial awareness for the contralesional space (Mesulam, 1999). It has been known that visual stimuli presented in the neglected hemispace can produce a measurable impact on patients' behavior despite the severe loss of conscious awareness. Specifically, neuropsychological studies of neglect patients suggest that neglected stimuli give rise to behavioral priming effects not only at the visuospatial level (Kristjansson, Vuilleumier, Malhotra, Husain, & Driver, 2005; Saevarsson, Joelsdottir, Hjaltason, & Kristjansson, 2008; Vuilleumier, Schwartz, Clarke, Husain, & Driver, 2002) but also at more abstract representational levels, such as lexico-semantic and numerical memory (Cappelletti & Cipolotti, 2006; Forti & Humphreys, 2007; Ladavas, Paladini, & Cubelli, 1993; McGlinchey-Berroth, Milberg, Verfaellie, Alexander, & Kilduff, 1993; Rusconi, Priftis, Rusconi, & Umiltà, 2006; Sackur

et al., 2008; Schweinberger & Stief, 2001). These observations are generally taken as indicating that ignored visual stimuli can reach higher-order cognitive processing systems, which operate covertly even when neglect patients have no subjective perceptual experience.

In the present study, we further studied spatial neglect patients with right-hemisphere damage to assess whether the non-conscious processing of ignored stimuli is modulated by the patients' voluntary behavior. Such top-down influence over non-conscious cognitive processing is proposed by a neurocognitive model of consciousness (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006 for review) and supported by behavioral studies with normal (e.g., Carr & Dagenbach, 1990; Dagenbach, Carr, & Wilhelmsen, 1989; Naccache, Blandin, & Dehaene, 2002) and brain-damaged subjects (Kentridge, Heywood, & Weiskrantz, 1999). Functional brain imaging data further show that behavioral task contexts exert a differential biasing influence over subliminal word processing by changing inter-regional connectivity between different neural components (Nakamura et al., 2006). This dynamic configuration of task-relevant neural networks is in accord with several other brain imaging data showing that the functional connectivity of the cerebral language network changes with task requirements (Bokde, Tagamets, Friedman, & Horwitz, 2001; Horwitz, Rumsey, & Donohue, 1998; Mechelli et al., 2005).

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However, for spatial neglect, it remains unclear whether such endogenous and goal-directed network is effectively configured in the generation of those behavioral effects reported in the existing literature. This is especially because visual attention per se may constitute a pivotal component of the goal-directed network (Chun, Golomb, & Turk-Browne, 2011; Dehaene et al., 2006; Horwitz et al., 1998), whereas this particular system is severely compromised in spatial neglect patients (Mesulam, 1999). Rather, those known effects might be largely attributed to bottom-up neural activations driven by external stimuli, since most previous work used non-degraded, clearly visible stimuli, which would induce fully conscious perception in normal people. Such visual stimuli with strong physical energy can induce evidence accumulation at multiple neural levels, thereby yielding various behavioral effects irrespective of the viewers' neurocognitive states (Dehaene et al., 2006).

Indeed, a recent study by Forti and Humphreys (2007) suggests that the neural processing stream for object recognition is weakly configured in neglect patients such that ignored stimuli can generate only transient and shallow-level representations, which decay more quickly than consciously perceived stimuli. Moreover, Vuilleumier et al. (2002) showed that the magnitude of long-term priming, or a behavioral index of implicit cognitive processing, did not change with the type of cognitive tasks engaged by neglect patients. Therefore, these observations seem to suggest that covert processing of ignored stimuli is mainly produced by strong stimulus-driven activations, rather than by effectively orchestrated neural systems. Conversely, if a goal-directed processing stream is indeed functioning in the non-conscious processing of neglected stimuli, it is predicted that (1) a brief presentation of masked words in the neglected hemifield will produce similar priming effects in neglect patients as in healthy control participants, and that (2) these effects will not generalize across different tasks but rather will change with the processing demands of tasks.

The present study tested these predictions by using a masked priming paradigm (Fig. 1) in spatial neglect patients. The visual masking procedure enabled us to restrict the physical strength of external stimuli and thereby investigate early-stage neurocognitive processes prior to strategic or attentional amplifications during visual object recognition (Forster, Mohan, & Hector, 2003; Dehaene & Naccache, 2001). Here we focused on masked "syllabic priming", a behavioral effect that is known to change with cognitive task requirements. Specifically, the visual recognition of a written word target is known to slow down when it is preceded by a prime word sharing the same syllable at the initial segment (Carreiras & Perea, 2002; Nakamura et al., 2012). Interestingly, however, the priming effect of syllabic overlap is reversed when participants read aloud written targets, i.e., reading latency is shortened when primes and targets have overlapping syllables at word-onset (Schiller, 2004). We used this task-related change of priming effects as a behavioral index for testing the task-sensitivity of unconscious word processing. These two types of priming each are thought to arise from different cognitive components of reading, e.g., lexical memory for word recognition (Carreiras & Perea, 2002) and speech-planning stage for word naming (Kinoshita, 2003), which probably rely on distinct task-specific neural pathways in the left-hemisphere reading network (see Section 4).

Several previous behavioral studies used similar priming paradigms to assess implicit cognitive processes in spatial neglect (Cappelletti & Cipolotti, 2006; Forti & Humphreys, 2007; Ladavas et al., 1993; McGlinchey-Berroth et al., 1993; Rusconi et al., 2006; Sackur et al., 2008; Schweinberger & Stief, 2001). We investigated unconscious cognitive processing in those patients more rigorously by delivering masked and thus equally invisible prime stimuli to the intact and neglected hemifields. This is important because the asymmetric visual awareness between the left and right hemifields

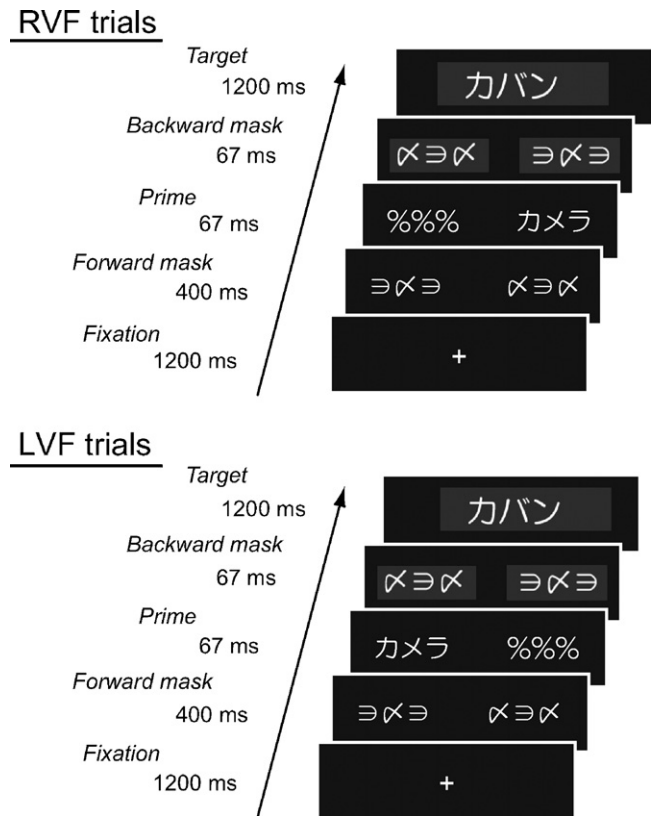


Fig. 1. Behavioral paradigm. Each trial consisted of a masked prime flashed to the left or right hemifield and a visible target displayed on the center of the screen for 1200 ms. Primes and targets were separated by a 67 ms of backward mask and thus presented with 134 ms stimulus onset asynchrony. Prime-target pairs either shared the first syllables or had mutually different syllables at the word onset. Participants either named visible targets or made natural/artificial judgment about them according to pre-specified instructions.

may confound the behavioral measurement of priming in neglect patients. That is, since the conscious perception of written words is known to induce a strong top-down amplification of the posterior reading systems (Dehaene et al., 2006), non-masked, consciously visible primes should exert much greater top-down modulation on early, bottom-up neural activation when presented to the intact hemisphere than when presented to the neglected hemifield.

2. Materials and methods

2.1. Participants

We examined 26 healthy control participants without neurological signs or symptoms (Experiment 1; 15 females; age range 20–76 years) to verify the masked priming effects during semantic categorization and those during word naming. Sampling control participants from the broad range of age groups allowed us to further assess possible age-related changes in these priming effects. In Experiment 2, we examined 14 spatial neglect patients with right-hemisphere damage (five females; mean age = 59.9 years, range = 32–76 years). Demographic and neurological data of these patients are summarized in Table 1. All patients had CT/MRI-identified vascular or neoplastic lesions in the right frontoparietal or subcortical structures, which spared the bilateral occipitotemporal cortex and the posterior corpus callosum. None of them had overt visual field defect on confrontation testing. The presence of left unilateral neglect was assessed with clinical pencil-and-paper testing, including standard line-bisection, letter cancellation and figure copying subtests of Behavioral Inattention Test (Wilson, Cockburn, & Halligan, 1987). All those patients exhibited >5 mm of rightward deviation in bisection and one or more omissions of left-sided elements in copying. Eleven of them showed >55% left-sided omissions relative to all omissions in cancellation. In addition, all of them showed one or more typical clinical signs of spatial neglect in everyday life situation, such as neglect of left limbs, left-sided collisions and neglect in dressing and eating (Azouvi et al., 2002). None of them had other cognitive or language deficit in routine neuropsychological assessment.

Table 1

Demographic and neurological data of spatial neglect (N1–N14) and control (C1–C12) patients. All these participants had focal brain damage in the right hemisphere. 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. Line bisection: rightward deviations (mm) from the midpoint of a 20-cm line, Letter cancellation: # omission errors (L/R, 57 lines for each side).

Patient	Age	Sex	Lesion site	Lesion etiology	Neurological deficit		Line bisection	Letter cancellation
					Somato-sensory	Motor		
N1	68	M	Frontal subcortical region	Ischemic	–	+	8	13/10
N2	55	F	Frontoparietal region	Ischemic	+	+	5	8/5
N3	71	M	Frontoparietal region	Ischemic	+	+	12	16/0
N4	64	M	Frontoparietal region	Ischemic	+	+	9	13/9
N5	45	M	Frontoparietal region	Ischemic	–	+	12	6/2
N6	76	F	Lateral prefrontal region	Ischemic	+	+	12	25/14
N7	61	M	Frontoparietal white matter	Ischemic	–	+	9	23/14
N8	49	F	Basal ganglia	Hemorrhagic	±*	±	8	22/17
N9	67	M	Basal ganglia	Hemorrhagic	–	+	16	11/12
N10	46	M	Basal ganglia	Hemorrhagic	±	+	10	16/0
N11	32	M	Basal ganglia	Hemorrhagic	+	+	10	19/19
N12	70	M	Posterior parietal region	Hemorrhagic	±*	±*	7	8/0
N13	64	F	Posterior parietal region	Hemorrhagic	–	+	10	3/0
N14	70	F	Superior parietal region	Ischemic	+	+	9	11/13
C1	68	M	Frontal subcortical region	Hemorrhagic	+	+	3	0/0
C2	56	F	Frontal white matter	Ischemic	–	+	2	1/2
C3	71	F	Frontoparietal region	Hemorrhagic	–	±	0	1/1
C4	68	M	Frontoparietal region	Ischemic	±	+	1	1/0
C5	60	M	Frontoparietal region	Hemorrhagic	±	+	2	4/4
C6	74	M	Frontoparietal white matter	Ischemic	–	+	0	0/2
C7	48	M	Internal capsule–frontoparietal white matter	Ischemic	±*	+	–1	4/5
C8	59	M	Basal ganglia	Ischemic	±	+	1	3/2
C9	63	M	Internal capsule	Ischemic	+	+	1	0/0
C10	63	M	Basal ganglia	Ischemic	+	+	3	0/0
C11	84	F	Parietal white matter	Ischemic	–	+	–2	0/0
C12	54	M	Parietal subcortical	Ischemic	+	+	–2	3/3

We further recruited 12 age-matched right-hemisphere (RH) patients without spatial neglect (three females; mean age = 64.0 years, range = 48–84 years, see Table 1 for further details). These patients had only mild left sensorimotor deficit after cortical or subcortical damage sparing the occipitotemporal cortex and the corpus callosum. None of them had overt visual field defect on confrontation testing. Neglect and non-neglect control patients were tested between 1 and 3 months after disease onset. The experimental session was performed individually for each participant. All participants in Experiments 1 and 2 were right-handed native speakers of Japanese and had received at least 12 years 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

For masked primes, we used 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. For each prime, we prepared two different types of targets matched in frequency and word length by manipulating a syllabic overlap between primes and targets. The first type of targets shared the first syllable with their respective primes (e.g., prime = 'ka-me-ra' (camera)/target = 'ka-ba-n' (bag)), whereas the second type of targets had different onset syllables (e.g., prime = 'ka-me-ra' (camera)/target = 'bi-de-o' (video)). Masked primes always belonged to the same semantic category as visible targets. 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). A prime and a perceptual foil ("%%") were displayed simultaneously for 67 ms in either LVF or RVF with a probability of 50% and followed by a visible target appearing on the center of the screen for 1200 ms. The forward and backward masks were an alternating pair of strings of letter-like symbols ("X ⊃ X" and "X ⊃ X") assigned pseudo-randomly to the left visual field (LVF) and right visual field (RVF). 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°. Visible targets each subtended with a visual angle of ~4.7° and always appeared on the center of the screen. Using the same set of stimulus materials, we also assessed the perceptual discriminability of masked primes and confirmed that the visual awareness of primes decreased with age and that the visibility level in itself was not correlated with the magnitude of masked priming (Nakamura et al., 2012).

Word naming and semantic categorization tasks were performed in two separate sessions, each including 240 trials and lasting approximately 20 min. In each trial, participants either named target words or made natural/artificial judgment about them by pressing a key with their right index and middle fingers. Participants were requested to respond as quickly and as accurately as possible and were not informed about the nature of masks or the existence of primes. The order of

two tasks was counterbalanced across participants. A part of the present semantic decision data was used in our recent work (Nakamura et al., 2012).

3. Results

3.1. Experiment 1

We first tested 26 healthy control participants without neurological deficit to verify syllabic priming effects during semantic categorization and word naming. Participants performed both tasks with few errors, irrespective of whether masked primes were presented in the left or right visual fields (mean error rates (SD) = 4.55 (7.23)% for LVF and 4.84 (7.98)% for RVF in categorization and 0.48 (1.41)% for LVF and 0.61 (1.93)% for RVF in word naming, respectively).

We then assessed reaction time data to determine the overall priming patterns for each task. Mean reaction times for correct responses (Fig. 2A) were submitted to repeated-measures ANOVA treating syllabic overlap (shared and non-shared), task (categorization and naming), and prime hemifield (LVF and RVF) as within-participant factors. Normal participants overall responded 194 ms faster in naming than in categorization ($F(1,25) = 175.36, p < 0.001$). The main effect of syllabic overlap did not reach significance ($F(1,25) = 1.25, p > 0.2$) but interacted with task ($F(1,25) = 39.57, p < 0.001$), suggesting that semantic categorization and word naming produced different patterns of syllabic priming from each other. The effect of prime hemifield and other interactions were all non-significant ($p > 0.05$).

When the analysis was restricted to RVF trials, word naming latency was 7 ms faster when primes and targets shared onset syllables than otherwise ($F(1,25) = 4.80, p < 0.04$). By contrast, syllabic overlap slowed down participants' response by 20 ms during semantic categorization ($F(1,25) = 17.71, p < 0.001$). This differential, task-sensitive change of syllabic priming was confirmed by a significant interaction between task and syllabic overlap ($F(1,25) = 25.14, p < 0.001$).

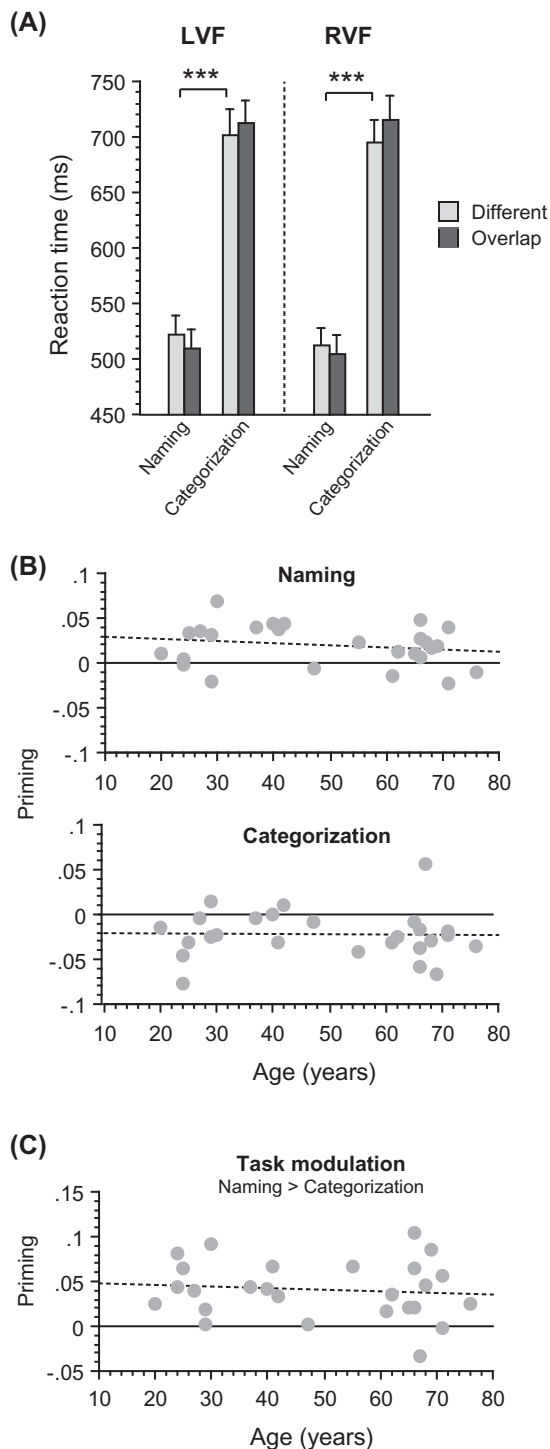


Fig. 2. Task-dependent changes of syllabic priming in healthy control participants. (A) Mean reaction times during semantic categorization and word naming. In RVF trials, semantic categorization time was prolonged when masked primes shared onset syllables with targets than when otherwise ($p < 0.001$). However, the priming effect of onset syllables was reversed when participants read aloud targets, i.e., word naming latency was shortened when primes and targets shared onset syllables ($p < 0.04$). This task-dependent change of syllabic priming was confirmed by a significant interaction between syllabic priming and task ($***p < 0.001$ for RVF). As for LVF trials, the effect of response inhibition during categorization was non-significant ($p = 0.10$), whereas response facilitation during naming was significant ($p < 0.005$) and did not differ from RVF trials ($p > 0.4$). This again produced a significant interaction between syllabic priming and task ($**p < 0.001$ for LVF). (B) Effects of age on the amount of priming during categorization and naming. For each participant, the priming index, or the individual-level magnitude of priming, was calculated as $(RT_{\text{different trials}} - RT_{\text{shared trials}}) / (RT_{\text{different trials}})$ and plotted in the ordinate for each task (positive values represent positive effects of priming).

Table 2

Mean error rate (SD) during semantic categorization and word naming (%) in RH-controls and neglect patients.

	RH control	Neglect
Categorization		
LVF	6.32 (7.07)	10.83 (8.87)
RVF	6.18 (6.64)	11.19 (7.62)
Naming		
LVF	1.81 (4.74)	2.02 (2.65)
RVF	2.50 (5.58)	1.90 (2.71)

On the other hand, a slightly different pattern of syllabic priming was observed for LVF trials. Like RVF trials, syllabic overlap facilitated naming response by 12 ms ($F(1,25) = 21.97$, $p < 0.001$). For categorization, however, the inhibitory effect of syllabic overlap was found only as a non-significant trend (9 ms; $F(1,25) = 2.88$, $p = 0.10$). This between-task difference still created a significant interaction between task and syllabic overlap ($F(1,25) = 12.83$, $p = 0.001$). In summary, these results confirmed that the patterns of masked syllabic priming changed as a function of task requirements.

Next, we assessed whether the observed effects of masked syllabic priming changed with age. To this end, we calculated the strength of correlation between the magnitude of priming and age across participants (Fig. 2B). A simple regression analysis with age as a predictor variable revealed no trend of age-dependent change in priming, either in categorization or in word naming ($p > 0.3$ for both). In Fig. 2C, we further examined whether the magnitude of task modulation in priming, i.e., the difference in priming effect-size between categorization and naming, was correlated with age. Again this analysis revealed no correlation between the two variables ($p > 0.5$), suggesting that the task-related change in priming was also highly constant across different age groups.

3.2. Experiment 2

We next collected behavioral data from 14 spatial neglect patients and 12 RH-control patients using the same semantic categorization and word naming tasks as Experiment 1. Mean error rates for each task for each group are presented in Table 2. Since neglect patients tended to be more error-prone than RH-controls, we first examined the error rates using repeated-measures ANOVA treating syllabic overlap (shared and non-shared), task (categorization and naming), prime hemifield (LVF and RVF) as within-participant factors and group (patients and controls) as a between-participants factor. This analysis revealed that the overall error rate was higher in categorization than in naming ($F(1,24) = 17.83$, $p < 0.001$) but did not differ between the two groups ($F(1,24) = 2.13$, $p > 0.15$). The error rate was slightly but significantly higher when primes and targets shared onset syllables than otherwise (effect-size = 1.70%, $F(1,24) = 13.11$, $p = 0.001$), whereas this inhibitory effect of syllabic overlap was greater in categorization than in naming ($F(1,24) = 7.79$, $p < 0.02$). Other effects and interactions were all non-significant ($p > 0.05$).

We then assessed reaction time data for correct responses (Fig. 3) using repeated-measures ANOVA including syllabic overlap (shared and non-shared), task (categorization and naming),

Simple regression analysis revealed no significant correlation between age and priming index, either for categorization or naming ($r^2 = 0.001$, $p > 0.5$ for categorization and $r^2 = 0.039$, $p > 0.3$ for naming), suggesting that masked priming effects were highly constant across different age groups. (C) Effects of age on task-modulation of priming. For each participant, the individual-level task-effect on priming, calculated as the priming index for naming minus the priming index for categorization, was plotted against age. Here again no correlation was found between these two variables ($r^2 = 0.014$, $p > 0.5$), suggesting that the task-dependent modulation on priming was constant across participants of different age groups.

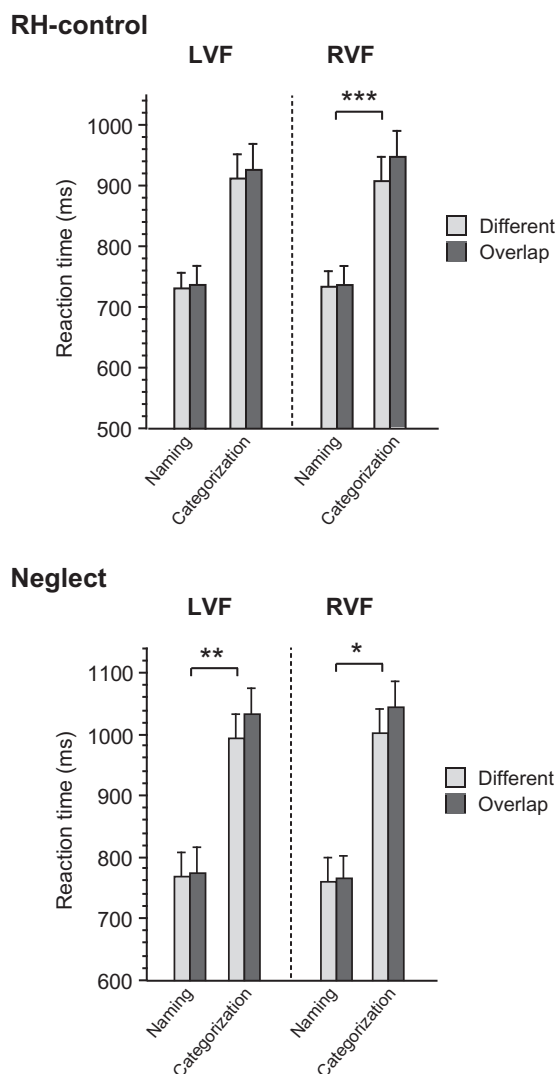


Figure 3

Fig. 3. Syllabic priming effects in RH-control and neglect patients. (Top) Like healthy participants in Experiment 1, RH-controls showed an asymmetric pattern of inhibitory syllabic priming during categorization, with the effect-size being significant for RVF trials ($p < 0.001$) but not for LVF trials ($p < 0.06$), creating a significant priming-by-hemifield interaction ($p = 0.002$). By contrast, these patients showed neither facilitatory nor inhibitory priming during word naming, irrespective of whether primes appeared in the LVF or in the RVF ($p > 0.1$ for both). For RVF trials, however, there was a significant interaction between priming and task ($***p < 0.001$). (Bottom) Unlike healthy participants and RH-control patients, neglect patients showed inhibitory priming during categorization regardless of the prime hemifield ($p < 0.02$ for RVF and $p = 0.001$ for LVF). In contrast, syllabic overlap produced no priming during word naming ($p > 0.2$ for both hemifields). These priming patterns created a symmetrical pattern of priming-by-task interaction significant for both hemifields ($**p < 0.005$ for LVF and $*p < 0.05$ for RVF). In addition, a between-hemifield comparison restricted to the categorization task revealed no significant difference between RVF and LVF ($F < 1$).

prime hemifield (LVF and RVF) as within-participant factors and group (patients and controls) as a between-participants factor. Both groups responded faster in word naming than in categorization ($F(1,24) = 96.37$, $p < 0.001$). Unlike the healthy control participants in Experiment 1, prime-target syllabic overlap globally slowed down behavioral response by 20 ms ($F(1,24) = 32.10$, $p < 0.001$). However, this inhibitory effect of syllabic overlap interacted with task ($F(1,24) = 33.98$, $p < 0.001$), suggesting that syllabic

priming was again sensitive to task requirements. The effect of prime hemifield was not significant ($F < 1$) but interacted with task ($F(1,24) = 5.07$, $p < 0.04$). Importantly, none of these effects and interactions differed in effect-size between two groups, because the main effect of group neither reached significance ($F(1,24) = 1.69$, $p > 0.2$) nor interacted with any other effects ($p > 0.15$ for all). This finding therefore suggests that neglect patients and RH controls showed the similar pattern of priming and its task-related modulations.

Based on the task-sensitive patterns of syllabic priming observed in Experiment 1, we further examined the priming $\times$ task interaction more closely for each group. As for RH-controls, the inhibitory effect of syllabic overlap was overall significant (effect-size = 16 ms, $F(1,11) = 12.49$, $p < 0.005$) and greater in categorization relative to naming ($F(1,11) = 11.46$, $p < 0.01$) and in RVF trials relative to LVF trials ($F(1,11) = 4.74$, $p = 0.05$). When the analysis was restricted to RVF trials, significant interaction was observed between priming and task ($F(1,11) = 25.98$, $p < 0.001$), suggesting that masked syllabic priming in RVF trials was modulated by task contexts. Indeed, additional analysis for RVF trials confirmed significant effect of priming during categorization ($p < 0.001$) but not during word naming ($F < 1$).

For LVF trials, syllabic priming was non-significant for naming ($F < 1$) but was seen as a non-significant trend for categorization ($p < 0.06$), resulting in no significant priming $\times$ task interaction ($F < 1$). Therefore, the impact of tasks on syllabic priming apparently differed between RH-controls and normal controls, because the critical priming $\times$ task interaction was significant for LVF in Experiment 1. To address this point, we additionally compared the magnitude of priming $\times$ task interaction for each hemifield between healthy controls in Experiment 1 and RH-controls in Experiment 2. However, this analysis revealed no significant difference between two groups, either for LVF or for RVF ($p > 0.15$ for both).

Neglect patients also showed a negative effect of syllabic priming (overall effect-size = 15 ms, $F(1,13) = 19.64$, $p < 0.001$), whereas its magnitude was greater in categorization than in naming ($F(1,13) = 22.57$, $p < 0.001$). Interestingly, the magnitude of priming did not differ between LVF and RVF ($F < 1$). Moreover, the critical priming-by-task interaction was significant for both RVF ($F(1,13) = 6.62$, $p = 0.02$) and LVF ($F(1,13) = 11.21$, $p = 0.005$), suggesting that the task-dependent influence over syllabic priming was symmetrical in neglect patients. Indeed, syllabic priming during categorization was significant for both RVF (42 ms, $p < 0.02$) and LVF (39 ms, $p = 0.001$), whereas syllabic priming during naming did not approach significance for either hemifield ($F < 1$ for both). Taken together, these results suggest that top-down, strategic behavior modulates the amount of masked priming effects not only in RH-controls but also in neglect patients.

In Fig. 4, we further visualized the individual-level priming pattern across different participant groups in Experiments 1 and 2. It can be seen that most participants in the healthy control group showed positive priming effects in naming and negative priming effects in categorization, for both RVF and LVF trials. By contrast, individual-level priming for RH-controls and neglect patients was overall negative in categorization and distributed around zero in naming, whereas this task-related change was especially pronounced for RVF trials. However, it is of note that most of these patients showed the similar downward pattern of task modulation in priming as the one observed in normal controls.

For neglect patients, we additionally looked at whether the amount of task effects on masked priming differed between patients with frontal lesions ($N = 7$) and those with non-frontal lesions ($N = 7$). That is, it is possible that the strength of top-down modulation of masked priming might be greater in non-frontal

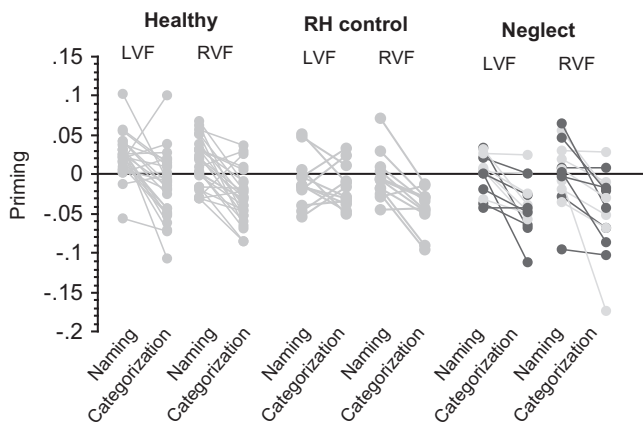


Fig. 4. Individual-level priming patterns in neglect patients and control participants. The priming index in the ordinate was calculated for each participant in Experiments 1 and 2 in the same way as in Fig. 2. Here the task modulation of priming for each participant is represented by the slopes between the two tasks. Most participants showed the similar downward slopes from naming to categorization across all three groups, especially in RVF trials. For neglect patients, dark gray and light gray dots each represent patients with frontal and non-frontal lesions, respectively. However, these two subgroups were almost indistinguishable in terms of the pattern and amount of priming effects (see Section 3).

patients, because the frontal lobe is thought to exert top-down biasing influence on posterior brain regions involved in the non-conscious processing of incoming stimuli (e.g., Dehaene & Naccache, 2001). We assessed the impact of frontal damage using ANOVA with syllabic overlap (shared and non-shared), task (categorization and naming), prime hemifield (LVF and RVF) as within-participant factors as within-participant factors and frontal damage (with and without) as a between-participants factor. However, the effect of frontal damage neither reached significance ($F(1,12)=1.75, p>0.2$) nor interacted with the effect of syllabic overlap ($F(1,12)=1.80, p>0.2$). The critical three-way interaction between task, syllabic overlap and frontal damage never approached statistical significance ($F<1$). These results therefore suggest that the magnitude of priming and its task modulation did not differ between frontal and non-frontal patients. Other interactions were all non-significant ($p>0.05$).

4. Discussion

Our results from healthy control participants (Experiment 1) showed that syllabic overlap between primes and targets produced inhibitory priming effects during the semantic categorization task. This syllabic priming showed a known pattern of hemispheric asymmetry, with its effect-size being greater for RVF primes than LVF primes as observed previously (Nakamura et al., 2012). On the other hand, the same syllabic overlap facilitated spoken response during word naming irrespective of the prime hemifield. This task-related reversal of priming direction produced a significant priming-by-task interaction, not only for the RVF but also for the LVF, indicating that masked priming effects are modulated by behavioral task requirements. The observed task-sensitivity in masked priming is interpreted as reflecting a context-dependent selective activation of reading pathways according to the observers' conscious task-setting (e.g., Nakamura, Dehaene, Jobert, Le Bihan, & Kouider, 2007), and is thus distinct from more global effects of priming during conscious word recognition, which can generalize across different behavioral tasks (e.g., Monsell, 1985; Scarborough, Gerard, & Cortese, 1979).

4.1. Neurocognitive loci of syllabic priming and their task-related activations

The observed task-related change of syllabic priming can be attributed to different neurocognitive components of reading. For word naming, a similar facilitatory priming by shared word-onsets is thought to rely on several different cognitive processes, such as grapheme-to-phoneme mapping (Forster & Davis, 1991) and speech planning stages (Malouf & Kinoshita, 2006). At the neural level, the neural substrate of these onset priming effects probably includes the left inferior parietal cortex previously associated with print-to-sound conversion (Price, 2000), the left ventral premotor cortex involved in speech planning (Eickhoff, Heim, Zilles, & Amunts, 2009; Wise, Greene, Buchel, & Scott, 1999), and further more downstream motor components, such as the primary motor cortex (Dehaene et al., 1998), ventral premotor cortex (Nakamura et al., 2007) and basal ganglia (Aron et al., 2003; Eimer & Schlaghecken, 1998).

On the other hand, negative priming during visual word recognition is known to occur when high-frequency primes share overlapping sublexical elements with word targets, either at orthographic (Davis & Lupker, 2006) or syllabic (Carreiras & Perea, 2002; Matheya, Zagarb, Doignonb, & Seigneuric, 2006) levels. Such inhibitory modulation by onset-sharing primes is thought to reflect a lateral inhibition of lexical competitors, because those primes simultaneously activate other lexical codes sharing overlapping sublexical elements with targets, which needs to be suppressed by target codes during word identification. Consistent with the lateralized effect of syllabic priming during categorization in the present study, recent work by Perea, Acha, and Fraga (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. In addition, it is of note that the similar competitive interaction could also occur at the post-lexical semantic stage, i.e., selective activation of target codes and lateral inhibition of related codes stored nearby in the semantic system (Carr & Dagenbach, 1990; Dagenbach et al., 1989).

Given that the observed syllabic effect reflects the fast lateral inhibition of potential lexical or semantic neighbors, the most likely neural correlate of such bottom-up cognitive processing is the left posterior temporal cortex involved in lexico-semantic memory. Indeed, functional brain imaging and magnetic stimulation studies converge to suggest that the left ventral occipitotemporal cortex enfold a whole word-recognition system for high-frequency words (Glezer, Jiang, & Riesenhuber, 2009; Nakamura et al., 2006, 2010; Vinckier et al., 2007). Recent lesion analysis data further showed that the adjacent posterior temporal region is involved in lexical activation and postlexical form-to-meaning mapping (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004; Vandenbulcke, Peeters, Dupont, Van Hecke, & Vandenberghe, 2007).

4.2. Task-sensitivity of syllabic priming in spatial neglect

In Experiment 2, RH-control patients exhibited the similar asymmetric pattern of syllabic priming during semantic categorization as the one seen in healthy controls, with the significant hemifield advantage for the RVF. By contrast, these patients showed no syllabic priming during word naming and hence acted differently from healthy controls regardless of the prime hemifield. Consequently, RH-controls showed a lateralized pattern of task-by-priming interaction, significant only in the RVF and not in the LVF, because of the left-right asymmetry in inhibitory priming during categorization and the total lack of facilitatory priming during naming. However, this finding does not immediately

suggest the absence of top-down influence over masked priming in the LVF, because the magnitude of task-by-priming interaction in itself differed neither between healthy controls and RH-controls nor between the LVF and the RVF in Experiment 2 (see below for further discussion).

Next, we observed that neglect patients exhibited the symmetrical pattern of inhibitory priming between RVF and LVF during semantic categorization, as reported previously (Nakamura et al., 2012). This finding at least suggests that the neglected hemifield extracts task-relevant information from normally imperceptible stimuli as effectively as the intact hemifield. By contrast, like RH-controls, neglect patients showed no significant syllabic priming during word naming irrespective of the prime hemifield. Importantly, however, a significant interaction between task and priming was obtained in those neglect patients, suggesting that the effect of syllabic priming itself remained sensitive to task contexts even in the neglected hemifield. Given that the two types of masked priming each rely on distinct neurocognitive components of visual word processing as argued above, these results suggest that a robust task-relevant neural pathway is covertly assembled for neglected stimuli outside the main field of visuospatial attention.

In addition, we found that the facilitatory syllabic priming during word naming was absent in both the RH-control and neglect patients. Although rather unexpected, this finding can be attributed to the fact that many of these patients suffered from frontoparietal or basal ganglia lesions (see Table 1), which clearly overlaps the speech production system in the left and right hemispheres (Fiez & Petersen, 1998; Price, 2010), which comprises the putative neural correlates of the syllabic priming during word naming (see above). These structures are anatomically and functionally distinct from the left occipitotemporal lobe, i.e., the neural locus of inhibitory syllabic priming during semantic categorization as mentioned above. Since the left and right occipitotemporal cortex was intact in both groups of patients, this spatial distribution of brain lesions probably accounts for the observed task-specific pattern of priming effects.

To summarize, the robust effects of masked priming in the neglected hemifield are in good accordance with the current cognitive model of consciousness that weak stimulus-driven activation can reach distant brain areas without perceptual awareness when visual stimuli are attended by observers (Dehaene et al., 2006). In the present study, moreover, the observed task-sensitivity in neglect patients suggests that task-specific neurocognitive components of reading are assembled effectively as a goal-directed endogenous processing stream even when the visual attention system is severely compromised. It can be therefore concluded that the behavioral response generated from non-conscious visual stimuli in the neglected hemifield strongly relies on a dynamic and task-specific configuration of the relevant neural components, rather than on automatic neural activations triggered by those external stimuli.

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References

- Aron, A. R., Schlaghecken, F., Fletcher, P. C., Bullmore, E. T., Eimer, M., Barker, R., et al. (2003). Inhibition of subliminally primed responses is mediated by the caudate and thalamus: Evidence from functional MRI and Huntington's disease. *Brain*, 126, 713–723.
- Azouvi, P., Samuel, C., Louis-Dreyfus, A., Bernati, T., Bartolomeo, P., Beis, J. M., et al. (2002). Sensitivity of clinical and behavioural tests of spatial neglect after right hemisphere stroke. *Journal of Neurology, Neurosurgery and Psychiatry*, 73, 160–166.
- Bokde, A. L., Tagamets, M. A., Friedman, R. B., & Horwitz, B. (2001). Functional interactions of the inferior frontal cortex during the processing of words and word-like stimuli. *Neuron*, 30, 609–617.
- Cappelletti, M., & Cipolletti, L. (2006). Unconscious processing of Arabic numerals in unilateral neglect. *Neuropsychologia*, 44, 1999–2006.
- Carr, T. H., & Dagenbach, D. (1990). Semantic priming and repetition priming from masked words: Evidence for a center-surround attentional mechanism in perceptual recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 16, 341–350.
- Carreiras, M., & Perea, M. (2002). Masked priming effects with syllabic neighbors in a lexical decision task. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 1228–1242.
- Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A taxonomy of external and internal attention. *Annual Review of Psychology*, 62, 73–101.
- Dagenbach, D., Carr, T. H., & Wilhelmsen, A. (1989). Task-induced strategies and near-threshold priming: Conscious influences on unconscious perception. *Journal of Memory and Language*, 28, 412–443.
- Davis, C. J., & Lupker, S. J. (2006). Masked inhibitory priming in English: Evidence for lexical inhibition. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 668–687.
- Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends in Cognitive Sciences*, 10, 204–211.
- Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition*, 79, 1–37.
- Dehaene, S., Naccache, L., Le Clec, H. G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., et al. (1998). Imaging unconscious semantic priming. *Nature*, 395, 597–600.
- Dronkers, N. F., Wilkins, D. P., Van Valin, R. D., Jr., Redfern, B. B., & Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition*, 92, 145–177.
- Eickhoff, S. B., Heim, S., Zilles, K., & Amunts, K. (2009). A systems perspective on the effective connectivity of overt speech production. *Philosophical Transactions: Series A, Mathematical, Physical, and Engineering Sciences*, 367, 2399–2421.
- Eimer, M., & Schlaghecken, F. (1998). Effects of masked stimuli on motor activation: Behavioral and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 1737–1747.
- Fiez, J. A., & Petersen, S. E. (1998). Neuroimaging studies of word reading. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 914–921.
- Forster, K. I., & Davis, C. (1991). The density constraint on form-priming in the naming task: Interference effects from a masked prime. *Journal of Memory and Language*, 30, 1–25.
- Forster, K. I., Mohan, K., & Hector, J. (2003). The mechanics of masked priming. In K. Kinoshita, & S. J. Lupker (Eds.), *Masked priming: State of the art* (pp. 3–37). Hove: Psychology Press.
- Forti, S., & Humphreys, G. W. (2007). The representation of unseen objects in visual neglect: Effects of view and object identity. *Cognitive Neuropsychology*, 24, 661–680.
- Glezer, L. S., Jiang, X., & Riesenhuber, M. (2009). Evidence for highly selective neuronal tuning to whole words in the visual word form area. *Neuron*, 62, 199–204.
- Horwitz, B., Rumsey, J. M., & Donohue, B. C. (1998). Functional connectivity of the angular gyrus in normal reading and dyslexia. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 8939–8944.
- Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (1999). Attention without awareness in blindsight. *Proceedings: Biological sciences, The Royal Society*, 266, 1805–1811.
- Kinoshita, S. (2003). The nature of masked onset priming effects in naming: A review. In S. Kinoshita, & S. J. Lupker (Eds.), *Masked priming: The state of the art*. New York: Psychology Press.
- Kristjansson, A., Vuilleumier, P., Malhotra, P., Husain, M., & Driver, J. (2005). Priming of color and position during visual search in unilateral spatial neglect. *Journal of Cognitive Neuroscience*, 17, 859–873.
- Ladavas, E., Paladini, R., & Cubelli, R. (1993). Implicit associative priming in a patient with left visual neglect. *Neuropsychologia*, 31, 1307–1320.
- Malouf, T., & Kinoshita, S. (2006). Masked onset priming effect for high-frequency words: Further support for the speech-planning account. *The Quarterly Journal of Experimental Psychology*, 60, 1155–1167.
- Matheya, S., Zagarb, D., Doignon, N., & Seigneure, A. (2006). The nature of the syllabic neighbourhood effect in French. *Acta Psychologica*, 123, 372–393.
- McGlinchey-Berroth, R., Milberg, W. P., Verfaellie, M., Alexander, M., & Kilduff, P. (1993). Semantic priming in the neglected field: Evidence from a lexical decision task. *Cognitive Neuropsychology*, 10, 79–108.
- Monsell, S. (1985). Repetition and the lexicon. In A. W. Ellis (Ed.), *Progress in the psychology of language* (pp. 147–195). London: Erlbaum.
- Mechelli, A., Crinion, J. T., Long, S., Friston, K. J., Lambon Ralph, M. A., Patterson, K., et al. (2005). Dissociating reading processes on the basis of neuronal interactions. *Journal of Cognitive Neuroscience*, 17, 1753–1765.
- Mesulam, M. M. (1999). Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences*, 354, 1325–1346.
- Naccache, L., Blandin, E., & Dehaene, S. (2002). Unconscious masked priming depends on temporal attention. *Psychological Science*, 13, 416–424.
- Nakamura, K., Dehaene, S., Jobert, A., Le Bihan, D., & Kouider, S. (2007). Task-specific change of unconscious neural priming in the cerebral language network. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 19643–19648.

- Nakamura, K., Hara, N., Kouider, S., Takayama, Y., Hanajima, R., Sakai, K., et al. (2006). Task-guided selection of the dual neural pathways for reading. *Neuron*, 52, 557–564.
- Nakamura, K., Kouider, S., Makuuchi, M., Kuroki, C., Hanajima, R., Ugawa, Y., et al. (2010). Neural control of cross-language asymmetry in the bilingual brain. *Cerebral Cortex*, 20, 2244–2251.
- Nakamura, K., Oga, T., Takahashi, M., Kuribayashi, T., Kanamori, Y., Matsumiya, T., Maeno, Y., & Yamamoto, M. (2012). Symmetrical hemispheric priming in spatial neglect: A hyperactive left-hemisphere phenomenon? *Cortex*, 48, 421–428.
- Perea, M., Acha, J., & Fraga, I. (2008). Lexical competition is enhanced in the left hemisphere: Evidence from different types of orthographic neighbors. *Brain and Language*, 105, 199–210.
- Price, C. J. (2000). The anatomy of language: Contributions from functional neuroimaging. *Journal of Anatomy*, 197, 335–359.
- Price, C. J. (2010). The anatomy of language: A review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences*, 1191, 62–88.
- Rusconi, E., Priftis, K., Rusconi, M. L., & Umiltà, C. (2006). Arithmetic priming from neglected numbers. *Cognitive Neuropsychology*, 23, 227–239.
- Sackur, J., Naccache, L., Pradat-Diehl, P., Azouvi, P., Mazevet, D., Katz, R., et al. (2008). Semantic processing of neglected numbers. *Cortex*, 44, 673–682.
- Saevarsson, S., Joelsdottir, S., Hjaltason, H., & Kristjansson, A. (2008). Repetition of distractor sets improves visual search performance in hemispatial neglect. *Neuropsychologia*, 46, 1161–1169.
- Scarborough, D., Gerard, L., & Cortese, C. (1979). Accessing lexical memory: The transfer of word repetition effects across task and modality. *Memory and Cognition*, 7, 3–12.
- Schiller, N. O. (2004). The onset effect in word naming. *Journal of Memory and Language*, 50, 477–490.
- Schweinberger, S. R., & Stief, V. (2001). Implicit perception in patients with visual neglect: Lexical specificity in repetition priming. *Neuropsychologia*, 39, 420–429.
- Vandenbulcke, M., Peeters, R., Dupont, P., Van Hecke, P., & Vandenberghe, R. (2007). Word reading and posterior temporal dysfunction in amnesic mild cognitive impairment. *Cerebral Cortex*, 17, 542–551.
- Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigman, M., & Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: Dissecting the inner organization of the visual word-form system. *Neuron*, 55, 143–156.
- Vuilleumier, P., Schwartz, S., Clarke, K., Husain, M., & Driver, J. (2002). Testing memory for unseen visual stimuli in patients with extinction and spatial neglect. *Journal of Cognitive Neuroscience*, 14, 875–886.
- Wilson, B., Cockburn, J., & Halligan, P. (1987). Development of a behavioral test of visuospatial neglect. *Archives of Physical Medicine and Rehabilitation*, 68, 98–102.
- Wise, R. J., Greene, J., Buchel, C., & Scott, S. K. (1999). Brain regions involved in articulation. *Lancet*, 353, 1057–1061.