Support for distinct subcomponents of spatial working memory: A double dissociation between spatial-simultaneous and spatial-sequential performance in unilateral neglect

Murielle Wansard[1], Paolo Bartolomeo[2,3], Christine Bastin[4], Fermín Segovia[4], Sophie Gillet[1], Christophe Duret[5], and Thierry Meulemans[1]

[1] Department of Psychology, Behavior and Cognition, University of Liège, Liège, Belgium
[2]INSERM-UPMC UMRS 1127, Brain and Spine Institute, Groupe Hospitalier Pitié-Salpêtrière, Paris, France
[3]Department of Psychology, Catholic University, Milan, Italy
[4]Cyclotron Research Centre, University of Liège, Liège, Belgium
[5] Service de Médecine Physique et Réadaptation, Unité de Rééducation Neurologique, CRF "Les trois soleils", Boissise le Roi, France

Correspondence concerning this article should be addressed to:
Murielle Wansard
Department of Psychology: Cognition & Behaviour
Boulevard du Rectorat, B33
B-4000 Liège (Belgium)
Phone: +32 (0)4 366 47 19
Fax: +32 (0)4 366.28.75
E-mail: m.wansard@ulg.ac.be

Abstract

Over the last decade, many studies have demonstrated that visuo-spatial working memory (VSWM) can be divided into separate subsystems dedicated to the retention of visual patterns and their serial order. Impaired VSWM has been suggested to exacerbate left visual neglect in right-brain damaged individuals. The aim of this study was to investigate the segregation between spatial-sequential and spatial-simultaneous working memory in individuals with neglect. We demonstrated that patterns of results on these VSWM tasks can be dissociated. Spatial-simultaneous and sequential aspects of VSWM can be selectively impaired in unilateral neglect. Our results support the hypothesis of multiple VSWM subsystems, which should be taken into account to better understand neglect-related deficits.

Keywords: Unilateral neglect, visuo-spatial working memory, spatial cognition

Introduction

Working memory is defined as the “moment-to-moment monitoring, processing, and maintenance of information” (Baddeley & Logie, 1999, p. 28). According to Baddeley’s conception, working memory includes at least three distinct components: two slave systems—a phonological loop for the storage of verbal information, and a visuospatial sketchpad for the storage of visual and spatial information—and the central executive, which controls and regulates the activities of the two subsidiary systems (Baddeley & Hitch, 2007). Although the model originally included visuo-spatial working memory (VSWM) as a unitary component, a growing literature in cognitive neuroscience (Logie & Marchetti, 1991), neuropsychology (Carlesimo, Perri, Turriziani, Tomaiuolo, & Caltagirone, 2001; Darling, Della Sala, & Logie, 2007; Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999), child development (Logie & Pearson, 1997; Mammarella et al., 2006), and neuroimaging (Broggard, Allain, Aubin, & Le Gall, 2007) suggests that VSWM can be divided into two memory subsystems: a visual cache for the retention of the visual appearance of scenes or objects (attributes such as color, contrast, texture, and shape), and a spatial system for retaining pathways and sequences of movements (Logie, 1995, 2003; Logie & Della Sala, 2005; see Repovs & Baddeley, 2006, for a review).

However, as already outlined by Rudkin, Pearson, and Logie (2007), the majority of studies evaluating the segregation of VSWM have used two types of tasks: on the one hand, a task involving memory for sequences of spatial locations (Corsi blocks test: Milner, 1971), and on the other hand, a task involving memory for the visual appearance of abstract patterns (Visual Pattern Test: Della Sala et al., 1999). These two tasks, which evaluate spatial and visual working memory respectively, differ in at least two respects: the nature of the visuo-spatial information that has to be processed (sequence of locations vs. appearance of stimuli) and the presentation mode (simultaneous vs. sequential; Logie, 2011). It is thus difficult to say whether the fundamental distinction between spatial and visual working memory rests on the "static" (simultaneous) versus "dynamic" (sequential) character of the stimuli, or rather on the type of information to be stored (object vs. location). Thus far, a clear and consensual definition of the term "spatial" has not yet been reached. Logie (2011) points out that the word "spatial" could refer to (1) the relative locations of several different objects in an array, (2) the locations of individual features within an object, (3) the serial order in which locations were presented, and (4) a series of arm or body movements. In order to clarify the characteristics of the different components of VSWM, Mammarella, Pazzaglia, and Cornoldi (2008) proposed a distinction based on the nature of the recall material and the mode of presentation: spatial-sequential (Corsi blocks test: Milner, 1971), spatial-simultaneous (Visual pattern test, including spatial location of items: Della Sala et al., 1999), and visual (appearance of objects, such as shape, color, and texture; see also Lecerf & de Ribaupierre, 2005).

In individuals with right brain damage and left visual neglect related to dysfunction of fronto-parietal networks (Bartolomeo, Thiebaut de Schotten, & Doricchi, 2007), additional deficits of spatial working memory may contribute to individuals' impaired performance (e.g., Kristjánsson & Vuilleumier, 2010; Malhotra, Mannan, Driver, & Husain, 2004; Pisella, Berberovic, & Mattingley, 2004), and especially to the tendency to repeatedly return to the same items located on the right side of space during search (Husain et al., 2001; Mannan et al., 2005). Several functional imaging studies in healthy subjects support the idea that the right posterior parietal cortex, which is frequently damaged in spatial neglect and is known to be related to attentional networks (Bartolomeo, 2014), is important in tasks requiring spatial working memory (Awh & Jonides 2001; Corbetta & Shulman 2011). In keeping with this hypothesis, Malhotra et al. (2004, 2005) observed that individuals with neglect were impaired when asked to recall a sequence of presented locations in the correct order, or to judge whether a specific presented location was part of the sequence. In addition, this VSWM impairment may increase the severity of neglect (see also Husain et al., 2001). Moreover, recent evidence suggests that the recall of serial order may be closely linked to spatial representation (Fischer-Baum & Benjamin, 2014) and spatial attention (van Dijck, Abrahamse, Majerus, & Fias, 2013). In a recent study, Saj, Fuhrman, Vuilleumier, and Boroditsky (2014) demonstrated that individuals with neglect have impairments not only in processing one half of space, but also in processing half of a mental timeline when asked to represent the past and the future, suggesting that intact spatial representation is necessary for a least some types of temporal representations (for a review, see Bonato, Zorzi, & Umiltà, 2012).

Together, these different studies suggest that individuals with neglect may have difficulty processing serial order in a spatial working memory task such as the Corsi block test, since this ability relies on spatial attention.

By contrast to its spatial subcomponent, the “visual” aspect of working memory has received limited attention in unilateral neglect. Contrasting individuals’ performance on a same-different judgment with an immediate visual memory task using similar items, D'Erme and Bartolomeo (1997) found evidence suggesting a lateralized visual memory deficit in neglect. Pisella et al. (2004) described impaired memory for changes in spatial location, but not for color or shape, in eight individuals with neglect.

However, no study has compared performance of individuals with unilateral neglect on tests tapping spatial and visual memory as two separate cognitive subsystems.

Here, we focused on possible dissociations in performance between spatial-sequential and spatial-simultaneous subcomponents of working memory in individuals with left neglect. Because neglect patients have deficits in spatial attention/representation, if the ability to process serial order information relies on spatial attention/representation, then individuals with neglect should have difficulty with the spatial-sequential task. On the other hand, if the spatial-sequential and spatial-simultaneous components reflect two separable subsystems of working memory, we might observe individuals with neglect who present specific alterations affecting one, the other, or both of these subsystems.

In addition, we predicted that individuals whose primary deficit is in the maintenance of temporal order information (spatial-sequential task) should make more errors related to order than location, while individuals whose primary deficit is in the processing of spatial configuration should not have particular difficulty with order processing, but should make location errors as well as omitting items in both tasks.

Method

Participants

Twelve right brain-damaged individuals suffering from left spatial neglect (5 women and 7 men) were recruited from hospitals in Paris (France) and in the French-speaking part of Belgium. Unilateral neglect was diagnosed by impaired performance on at least two tests of the Batterie d'Evaluation de la Négligence (BEN; Azouvi et al., 2002). Exclusion criteria were bilateral lesions or premorbid history of major psychiatric or neurological diseases. Participants had no known history of other medical diseases such as dementia at the time of testing. As an indicator of neglect severity, the proportion of scores impaired on the BEN is reported in Table 3.

The mean time interval between stroke onset and experimental testing was 169.08 days (range: 29-409 days). Individuals with neglect were aged from 43 to 88 years (mean age = 62.08, SD = 12.29), and had 6 to 17 years of education. Table 1 shows the demographic and clinical data for the individuals with neglect.

Twelve healthy elderly controls matched with neglect participants for age (mean age = 62.42, SD = 8.73) and educational level (mean = 11.25, SD = 3.08) were also tested as controls. Controls did not differ from the neglect group in terms of age, $t(22) = -.08$, $p = .94$, or educational level, $t(22) = -.05$, $p = .96$. The study was approved by the local research ethics committee. All participants gave their written informed consent prior to their inclusion in this study.

== INSERT TABLE 1 HERE ==

Procedure

Spatial-sequential and spatial-simultaneous working memory were assessed by means of computerized tasks developed with the Toolbook software (Version 9.0) and presented on a touchscreen (Shuttle X50V2; 32.7 x 39.1 cm) at a viewing distance of approximately 50 cm. All participants were seated comfortably in front of the computer screen, with their body midline approximately aligned with the vertical midline of the screen. Each trial started with the presentation of a matrix pattern to be memorized, which progressed in size from the smallest (with two filled cells) to the largest (with 16 filled cells) over the course of the task. To avoid neglect-related laterality effects, we kept the horizontal axis of the grid constant, while the vertical size varied (see Husain et al., 2001). The aim of this manipulation was to increase the complexity of the pattern and the resulting working memory load while limiting the impact of visual neglect on the participant's score. Each level of complexity was made up of four trials in which half of the square cells were filled in black, equivalently distributed in the left and the right halves of the screen over the four trials. After each trial, an empty matrix appeared on the screen for free recall, which involved the participant touching the cells that he/she remembered as being filled on the empty matrix displayed on the screen. The squares selected by the participant were visually marked on the screen. The task ended when the participant was no longer able to improve his/her performance: i.e., when the number of items correctly recalled did not increase from one level of difficulty to the next. The subject's score (memory span) corresponded to the highest score obtained at least three times out of all trials (see below for details).

In the *spatial-sequential* working memory task, a sequence of squares—one square per second, with an inter-stimulus interval of one second—was presented in a specific serial order, similar to the Corsi test (Milner, 1971). After each trial, a beep prompted the participant to recall the sequence by touching the squares in the correct order on the screen. To estimate spatial-sequential working memory capacity as precisely as possible, we based our scoring procedure on the maximal number of items per trial that the participant was able to recall in the correct relative order. As depicted in Figure 1, for the presented sequence 1-2-3-4-5, if the participant answered 1-3-4-6 or 1-5-3-4-2, the score would be 3 in both cases: in each case, the locations 1, 3, and 4 are reproduced in the correct order (in the first case, with an omission between 1 and 3 and a location error between 4 and 5, and in the second case, with an inversion between locations 2 and 5). Our aim with this procedure was to avoid underestimating the neglect participants' score because of their difficulty processing the stimuli presented on the left side.

== INSERT FIGURE 1 HERE ==

The procedure for the *spatial-simultaneous* working memory task was very similar to the visual pattern span task (Della Sala et al., 1999). The entire visual pattern was presented simultaneously for two seconds; afterwards, the empty matrix appeared on the screen for recall. The subject had to remember the locations of the squares that had been filled in with black, and respond by touching the corresponding locations on the screen. Scoring was based on the number of correct stimulus locations.

Following Bartolomeo, D'Erme, Perri, and Gainotti (1998), we administered separate tasks in which no manual motor response was required, in order to control for possible difficulties in programming leftward hand movements. In these tasks, after having seen the visual pattern or the sequence (depending on the task), the participants were presented an empty grid, containing digits randomly placed in the cells. In this condition, rather than touching the cells in the matrix, they instead responded by pronouncing the digits corresponding to the pattern or sequence.

Results

Span scores

We performed a repeated measures analysis of variance (ANOVA) on the memory span scores with group (controls vs. individuals with neglect) as a between-subjects variable, and task type (sequential vs. simultaneous) as repeated measure. There was a main effect of group, $F(1,22) = 29.84$, $p < .001$, MSE = 63.02, $\eta^2 p = .57$. There was also an effect of task type, with better performance on the spatial-simultaneous task, $F(1,22) = 73.99$, $p < .001$, MSE = 67.69, $\eta^2 p = .77$ for all participants. There was an interaction between group and task type, $F(1,22) = 5.12$, $p = .03$, MSE = 4.69, $\eta^2 p = .19$. Planned comparisons showed that controls achieved better performance than neglect participants both on the spatial-simultaneous working memory task, $F(1,22) = 20.04$, $p < .001$, and on the spatial-sequential task, $F(1,22) = 20.71$, $p < .001$.

To determine whether difficulties in programming leftward hand movements influenced performance in our experimental tasks, separate *t* tests for paired samples between experimental tasks and the control task (in which no manual motor response was required) were performed. Neglect participants' performance on the control task without motor response was similar to their performance on the motor task both for the spatial-sequential working memory, $t(10) = -.43$, $p = .68$, and for spatial-simultaneous working memory, $t(11) = .29$, $p = .78$.

In order to explore possible deficits in spatial-sequential and spatial-simultaneous working memory tasks and uncover dissociations in performance between the two types of task, we selected as a first step neglect participants who performed two standard deviations below the control mean in at least one working memory task, either visual or spatial. To establish with more certainty that the performance of the neglect participants who were included in the dissociation was in fact impaired, a final series of four trials (corresponding to the next level of difficulty) was administered to determine whether they were able to improve (or normalize) their performance. Out of the seven patients who were initially included, five failed to increase their performance and therefore were included in the supplementary analyses. We used a modified one-tailed *t*-test to compare each of these five neglect participants' individual scores to those of a new small normative sample matched for age and educational level[1] (n = 8; Crawford & Howell, 1998). In addition, the Revised Standardized Difference Test (RSDT; Crawford & Garthwaite, 2005) was used to evaluate whether the difference between a patient's scores in the two tasks was significantly different from controls. As suggested by Crawford, Garthwaite, and Porter (2010), we also report effect size (as point estimates) obtained (see Z-cc and Z-dd, Table 2). Performance was considered as impaired when a patient scored lower than the matched control group with an alpha level set at .05. Three different patterns of impairment emerged (Figure 2). Three individuals with neglect showed generalized difficulties, performing poorly both on spatial-sequential and spatial-simultaneous tasks, while two

---

[1] Each of these five neglect participants is compared to a specific control group matched for age and educational level.

other showed a double dissociation in performance, with a selective deficit either on the spatial-sequential task or the spatial-simultaneous task (Table 2). The neglect participants with impaired VSWM did not differ in age, $t(10) = .34$, $p = .74$, educational level, $t(10) = .76$, $p = .46$, or time since stroke, $t(10) = 1.13$, $p = .28$ from the neglect participants with unimpaired working memory; these variables are thus unlikely to account for their different patterns of performance. The individuals with impaired VSWM showed more severe neglect than the other neglect participants, $t(10) = -3.02$, $p = .01$.

Otherwise, we observed that the severity of neglect affected performance on the sequential task, $r(12) = -.71$, $p = .01$, but not on the simultaneous task, $r(12) = -.34$, $p = .28$.

== INSERT FIGURE 2 AND TABLE 2 HERE ==

Pattern of errors

Error rates and left-right distribution of errors (omissions and errors of location or serial order) for the two tasks were determined for each individual (see Table 3). Given the heterogeneity of our participants' cognitive profiles, we only examined the types and rates of errors of two individuals: one with a selective impairment in the spatial-sequential task (P3) and one with a selective impairment in the spatial-simultaneous task (P9).

Regarding our predictions, we observed that P3 made more serial order (63%) than location errors (37%) in the spatial-sequential task. Participant P9 also made more serial order errors (47%) than location errors (13%). However, while P3 did not make any omissions, patient P9 also made a considerable number of omissions (40%), at almost the same rate as location errors. In the spatial-simultaneous task, P3's errors were almost exclusively location errors (94%), while P9 primarily made omissions (64%), but also location errors (36%).

Participant P9's high proportion of omissions is striking in both tasks not only relative to P3, but also, for the right side, relative to all other neglect participants.

Anatomical Correlates

The volume and the location of the cerebral lesion were determined for each pattern of impairment. For each neglect participant, MRI or CT scans (available for 11 out of the 12 individuals with neglect) were first spatially normalized to MNI space using an MR or CT template specifically optimized for individuals in the age range at which strokes commonly occur, from the Clinical Toolbox in SPM8 (Rorden, Bonilha, Fridriksson, Bender, & Karnath, 2012). We used SPM8 normalization routines with lesion cost function masking (Brett, Leff, Rorden, & Ashburner, 2001) in order to ensure that non-linear spatial transformations did not shrink the size of the brain lesion or distort the local healthy tissue. Next, areas of lesion were manually traced on the normalized structural image of the brain using the PMOD software (http://www.pmod.com/technologies/index.html). As expected, neglect participants with generalized VSWM impairment (P6, P7, and P10) had larger lesions compared to the neglect participants with selective impairments (see lesion volumes, Table 1). Figure 3A shows the lesion overlap for neglect participants with generalized deficits. All these individuals with neglect had damage to the posterior insula. The individual with a selective spatial-sequential deficit had damage affecting the putamen and insula (Figure 3B). The participant with a selective deficit on the spatial-simultaneous task had damage to the caudate nucleus, basal ganglia and surrounding white matter (Figure 3C). Thus, in this limited sample, damage to the posterior insula was present in all individuals with a spatial-sequential deficit, whether or not it was accompanied by a spatial-simultaneous impairment. Among individuals without impairment, there was no area that was consistently damaged, reflecting the neuroanatomical heterogeneity of the damage that can lead to spatial neglect. Of note, with the exception of the common posterior insula damage in patients with generalized deficits and patients with spatial-sequential deficits, no other similarity in lesion site was observed between groups. However, it must be recalled that there are several important problems with lesion overlap when addressing network-based functions such as attention or VSWM (see Bartolomeo, 2011). The present observations should thus be confirmed in larger groups of individuals with neglect and complemented by the study of structural connectivity.

== INSERT FIGURE 3 HERE ==

Discussion

Until now, research on working memory in visual neglect has mostly focused on spatial-sequential working memory (e.g., Husain et al., 2001; Malhotra et al., 2004; 2005), without considering the other subcomponents of VSWM (Logie, 1995; 2003). And yet, evidence is accumulating that VSWM may be separated into a number of subcomponents (e.g., static vs. dynamic, appearance vs. location; Darling et al., 2007; Mammarella et al., 2006; Broggard et al., 2007). The purpose of the present study was to explore VSWM deficits in a group of individuals with neglect. More specifically, our aim was to determine whether a dissociation between spatial-sequential and spatial-simultaneous subcomponents of working memory might be observed in left neglect individuals.

Our results show a double dissociation in performance on the two tasks (Crawford, Garthwaite, & Gray, 2003): individuals with neglect may present VSWM alterations specifically affecting one, the other, or both of these subsystems (the administration of control tasks confirmed that performance in the experimental tasks was not influenced by difficulties in programming leftward hand movements).

In addition, the observed patterns of errors of participants P3 and P9 diverged in ways that reinforce the distinction between their forms of impairment.

Confirming our hypothesis, P3 demonstrated clear evidence of a selective serial order processing deficit in the spatial-sequential task. By contrast, P9 made almost as many omissions (40%) as serial order errors (47%). In the spatial-simultaneous task, it appears that P3 made mainly location errors (94%, vs. 6% omissions), unlike P9 who made more omissions (64%) than location errors (36%). In other words, it appeared that neglect participant P3 had difficulty with serial order processing in the spatial-sequential task, while the deficit of neglect participant P9 was more related to the processing of spatial configurations, leading to a high rate of omissions, particularly on the spatial-simultaneous working memory task.

The neuropsychological evaluation, as well as the type of neglect of the five neglect participants included in the double dissociation, did not reveal any specific pattern of impairment or neglect type in comparison to the other individuals with neglect. Consistently with previous studies, we observed that individuals with impaired VSWM showed more severe neglect than those without VSWM impairment (Husain et al., 2001; Malhotra et al., 2005). While VSWM deficits are not necessarily specific to the neglect syndrome, our findings are in agreement with the recent proposal that impairment of VSWM can contribute to and exacerbate neglect symptoms (Husain & Rorden, 2003, Robertson, 2001). However, the double dissociation highlighted here cannot be related to lateralized neglect severity, since observation of error patterns demonstrated that neither P3 (on the spatial sequential task) nor P9 (on the spatial-simultaneous task) left out more items on the left side than individuals with a generalized VSWM deficit (see Table 3).

Although attentional deficits appear to be prominent in neglect (see for example, Bartolomeo, Thiebaut de Schotten, & Chica, 2012), our results confirm that VSWM deficits can also occur

(Husain et al., 2001; Malhotra et al., 2005), and additionally suggest that spatial-sequential and spatial-simultaneous aspects can have different weights in different individuals.

Nevertheless, in the case of double dissociations, it is always important to consider more parsimonious alternatives to the hypothesis of two independent subsystems. In the present case, dissociations in performance between spatial-sequential and spatial-simultaneous working memory tasks might simply be related to differences in the relative difficulty of the tasks, or in their attentional demands. For example, Rudkin et al. (2007) suggested that spatial-sequential working memory tasks—requiring the recall of the positions and order of stimuli—recruit more attentional resources than the recall of locations that are presented simultaneously. Using a dual-task paradigm, they observed that performance on tasks involving temporal order processing was disrupted by a concurrent random digit generation task (requiring attentional resources), while the simultaneous task was not. So, the recruitment of attentional processes may be substantial when memory for temporal order is required (Avons & Mason, 1999; McAfoose & Baune, 2009; Smyth et al., 2005).

In our study, performance on the sequential task was always worse than on the simultaneous task: this is consistent with the idea that the need to handle temporal information in the sequential task created additional attentional demands. In agreement with this proposal, we observed that the severity of neglect influenced performance only on the sequential task ($r = -.71$, $p = .01$). This might raise the concern that individual P3 could show a selective spatial-sequential deficit simply because this task requires more attentional or general memory resources. However, the observation of a selective impairment in the simultaneous condition seems to be incompatible with this hypothesis: if it were true, we should have observed a significant change on the sequential task as well, which is considered to be more complex (requiring the recall of both location and serial order).

Another possibility is that the impairment of individual P9 on the simultaneous task was the result of an issue with perceptual encoding: due to her neglect, this individual might have particular difficulty perceiving the stimuli in the simultaneous condition. But this possibility can be rejected: this individual showed no sign of visual extinction[2] in the simultaneous task. Moreover, the severity of spatial neglect also does not explain this pattern of results: if the only relevant difference between the two tasks was their complexity (and therefore their attentional demands), then the individuals with less severe neglect (such as P9) should have shown difficulties only in the more complex task, whereas the individuals with more severe neglect would have been expected to show difficulties in both tasks, which was not the case (such as P3).

Keeping in mind the existence of other hypotheses concerning the mechanisms that sustain the memory for serial order, we investigated the alternative possibility that non-specialized memory resources might be dedicated to the processing of serial order. Segregation between memory encoding for serial order and item representation has already been proposed in the verbal domain (Majerus, Poncelet, Elsen, & Van der Linden, 2006). Some studies have presented evidence that verbal and visuo-spatial working memory may share a common system for the representation of serial order, in the form of cross-modal interference effects (Depoorter & Vandierendonck, 2009; Zimmer & Heinrich, 2011) and shared neural correlates (Majerus et al., 2010; see also Hurlstone, Hitch, & Baddeley, 2014, for a review).

In our sample, three participants (P6, P7, P10) showed impairments in all the administered VSWM tasks, while showing no specific difficulty in processing serial order, either in the spatial or the

---

[2] The number of omissions on the simultaneous task was strictly the same on the left (32%) and the right (32%) sides. In addition, P9 showed no sign of visual extinction in the finger confrontation test (Azouvi et al., 2002).

verbal modality. The only participant who showed clear evidence of a selective serial order processing deficit was P3, whose lack of impairment in the simultaneous task suggests that his deficit does not reflect a more general VSWM impairment. The observation that this participant also had difficulties in the digit span task (see Table 1) is consistent with the idea that the same system underlies memory for serial order in both verbal and VSWM tasks.

In light of these considerations, it seems likely that our results can be better accounted for by a multi-component conception of VSWM, with different VSWM subsystems for retaining location (spatial configuration) and serial order, the latter being shared with the verbal subsystem (Logie, 2011; Pickering, Gathercole, Hall, & Lloyd, 2001; but see also Majerus et al., 2010; Hurlstone, Hitch, & Baddeley, 2014).

Nevertheless, these findings should be treated with caution, because in our study only five out of 12 individuals with neglect were impaired on at least one spatial working memory task (i.e., seven individuals did not show any VSWM deficit). This suggests that spatial-sequential and spatial-simultaneous working memory deficits cannot be considered as a primary feature of neglect syndrome, but could instead be the consequence of a specific brain lesion characteristic that individuals may present in some cases (either in terms of lesion volume or in terms of the involvement of particular brain regions, such as the insula). According to some authors, attentional disturbances as well as VSWM deficits can play a major role in left neglect (e.g., Bartolomeo et al., 2012; Corbetta & Shulman, 2011). Some studies have reported that attentional deficits can impair encoding in VSWM (Fukuda & Vogel, 2011; Gmeindl & Courtney, 2011). These systems could be in close interaction and thus influence each other. For example, performance impairment on the sequential task could result from difficulty in shifting attention to each of the sequentially presented stimuli and/or from difficulty in remembering the temporal order of stimuli, while performance impairment on the simultaneous task could result from difficulty in remembering the particular location of the marked squares and/or difficulty in grouping them into a geometrical shape to reduce memory load.

Our results highlight the heterogeneous nature of spatial neglect: while neglect was always associated to attentional deficits, it was not necessarily accompanied by an inability to process serial order information. However, further studies will be needed to investigate these complex relationships between attention, VSWM and visual neglect.

One may wonder what the behavioral impact of these specific impairments in neglect individuals is, for example in their pathological patterns of visual search. Re-exploration behavior in neglect has often been related to spatial working memory impairment (e.g., Husain et al., 2001; Mannan et al., 2005; Parton et al., 2006; Wojciulik, Husain, Clarke, & Driver, 2001). However, in these studies, no direct evaluation of spatial working memory was carried out, since it was the re-cancellation behavior itself that was considered as a measure of impaired spatial working memory. Others have called into question this interpretation, and claimed that impaired spatial working memory cannot fully account for re-cancellation behaviors (Olk & Harvey, 2006; Ronchi, Posteraro, Fortis, Bricolo, & Vallar, 2009; Wansard et al., 2014). Recently, Emrich, Al-Aidroos, Pratt, and Ferber (2010) suggested that visual and spatial working memory may play different but complementary roles during visual search. While both spatial and visual working memory could play a role in the inhibition of previously searched items (Woodman, Vogel, & Luck, 2001), visual working memory might be responsible for storing already searched information, whereas spatial working memory might contribute to the planning of upcoming saccades (Peterson, Kramer, Wang, Irwin, & McCarley, 2001). These suggestions provide a plausible alternative explanation for the apparent lack of relationship between spatial working memory and re-exploration behaviors in unilateral neglect found in some studies. A systematic evaluation of the visual and spatial subcomponents of working memory in neglect individuals, in relation to their performance in visual search tasks, should provide insights into the relationship between spatial and/or visual working memory impairment and re-cancellation behaviors in individuals with neglect.

In conclusion, despite the relatively small number of individuals with neglect included in the present study, our results indicate that sequential and simultaneous spatial working memory can be selectively impaired in unilateral neglect. Attentional disturbances alone cannot explain the differential patterns of our neglect participants' deficits in the retention of spatial information. Further studies will be needed to explore more precisely the dissociation between memory for features of objects' appearance (color, texture, and contrast) and for their location in space, the possible dissociation in the recall of serial order between spatial and verbal working memory, as well as the functional impact of these deficits on individuals' everyday life, especially in connection to the role of these specific aspects of VSWM in spatial exploration.

References

Avons, S. E., & Mason, A. (1999). Effects of visual similarity on serial report and item recognition. *The Quarterly Journal of Experimental Psychology, 52A*(1), 217-240.

Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences, 5*(3), 119-126.

Azouvi, P., Samuel, C., Louis-Dreyfus, A., Bernati, T., Bartolomeo, P., Beis, J.-M., . . . Rousseaux, M. (2002). Sensitivity of clinical and behavioral tests of spatial neglect after right hemisphere stroke. *Journal of Neurology Neurosurgery and Psychiatry, 73*, 160-166.

Baddeley, A. D., & Hitch, G. J. (2007). Working memory: Past, present…and future? . In N. Osaka, R. H. Logie & M. D'Esposito (Eds.), *The cognitive neuroscience of working memory* (pp. 1-20). New York, NY: Oxford University Press.

Baddeley, A. D., & Logie, R. H. (1999). Working memory: The Multiple-Component Model. In A. Miyake & P. Shah (Eds.), *Models of Working Memory: mechanisms of active maintenance and executive control*. Cambridge: University Press.

Bartolomeo, P. (2014). Attention disorders after right brain damage: Linving in halved world. London: Springer-Verlag.

Bartolomeo, P., D'Erme, P., Perri, R., & Gainotti, G. (1998). Perception and action in hemispatial neglect. *Neuropsychologia, 36*(3), 227-237.

Bartolomeo, P., Thiebaut de Schotten, M., & Chica, A. B. (2012). Brain networks of visuospatial attention and their disruption in visual neglect. *Frontiers in human neuroscience, 6*, 110. doi: 10.3389/fnhum.2012.00110

Bartolomeo, P., Thiebaut de Schotten, M., & Doricchi, F. (2007). Left unilateral neglect as a disconnection syndrome. *Cerebral Cortex, 17*(11), 2479-2490.

Bartolomeo, P. (2011). The quest for the ‘critical lesion site’ in cognitive deficits : Problems and perspectives. *Cortex, 47*, 1010-1012.

Bonato, M., Zorzi, M., & Umiltà, C. (2012). When time is space: Evidence for a mental time line. *Neuroscience and Biobehavioral Reviews, 36,* 2257-2273. doi: 10.1016/j.neubiorev.2012.08.007

Brett, M., Leff, A.P., Rorden, C., & Ashburner, J. (2001). Spatial normalization of brain images with focal lesions using cost function masking. *NeuroImage, 14*, 486–500.

Broggard, H., Allain, P., Aubin, G., & Le Gall, D. (2007). Mémoire de travail et contrôle attentionnel. In G. Aubin, F. Coyette, P. Pradat-Diehl & C. Vallat-Azouvi (Eds.), *Neuropsychologie de la mémoire de travail* (pp. 135-166). Marseille: Solal.

Carlesimo, G.A., Perri, R., Turriziani, P., Tomaiuolo, F., & Caltagirone, C. (2001). Remembering What But Not Where: Independence of Spatial and Visual Working Memory in the Human Brain. *Cortex, 37*(4), 519-534. doi: 10.1016/s0010-9452(08)70591-4

Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. *Annual Review of Neuroscience, 34*, 569-599. doi: 10.1146/annurev-neuro-061010-113731

Crawford, J.R., & Garthwaite, P.H. (2005). Testing for suspected impairments and dissociations in single-case studies in neuropsychology: Evaluation of alternatives using Monte Carlo simulations and revised tests for dissociations. *Neuropsychology, 19*, 318-331

Crawford, J.R., Garthwaite, P.H., & Gray, C.D. (2003). Wanted: Fully operational definitions of dissociations in single-case studies. *Cortex, 39*, 357-370.

Crawford, J. R., & Howell, D. C. (1998). Comparing an individual's test score against norms derived from small samples. *Clinical Neuropsychologist, 12*(4), 482-486.

Crawford, J.R., Garthwaite, P.H., & Porter, S. (2010). Point and interval estimates of effect sizes for the case-controls design in neuropsychology: Rationale, methods, implementations, and proposed reporting standards. *Cognitive Neuropsychology, 25*(3), 245-260.

D'Erme, P., & Bartolomeo, P. (1997). A unilateral defect of short-term visual memory in left hemineglect. *European Journal of Neurology, 4*, 382-386.

Darling, S., Della Sala, S., & Logie, R. H. (2007). Behavioral evidence for separating components within visuo-spatial working memory. *Cognitive Processing, 8*(3), 175-181. doi: 10.1007/s10339-007-0171-1

Della Sala, S., Gray, C., Baddeley, A., Allamano, N., & Wilson, L. (1999). Pattern span: a tool for unwelding visuo-spatial memory. *Neuropsychologia, 37*(10), 1189-1199. doi: 10.1016/s0028-3932(98)00159-6

Depoorter, A., & Vandierendonck, A. (2009). Evidence for modality-independent order coding in working memory. *Quarterly Journal of Experimental Psychology, 62*(3), 531-549.

Emrich, S. M., Al-Aidroos, N., Pratt, J., & Ferber, S. (2010). Finding memory in search: the effect of visual working memory load on visual search. *Quarterly journal of experimental psychology, 63*(8), 1457-1466. doi: 10.1080/17470218.2010.483768

Fischer-Baum, S., & Benjamin, A.S. (2014). Time, space, and memory for order. *Psychonomic Bulletin and Review.* doi: 10.3758/s13423-014-0604-7

Fukuda, K., & Vogel, K. (2011). Individual differences in recovery time from attentional capture. *Psychological Science, 22*(3), 361-368. doi: 10.1177/0956797611398493

Gmeindl, L., & Courtney, S.M. (2012). Deconstructing spatial working memory and attention deficits in multiple sclerosis. *Neuropsychology, 26*(1), 57-70. doi: 10.1037/a0026213

Hurlstone, M.J., Hitch, G.J., & Baddeley, A. (2014). Memory for serial order across domains: An overview of the literature and directions for future research. *Psychological Bulletin, 140*(2), 339-373. doi: 10.1037/a0034221

Husain, M., Mannan, S., Hodgson, T., Wojciulik, E., Driver, J., & Kennard, C. (2001). Impaired spatial working memory across saccades contributes to abnormal search in parietal neglect. *Brain, 124*(5), 941-952. doi: http://dx.doi.org/10.1093/brain/124.5.941

Husain, M., & Rorden, C. (2003). Non-spatially lateralized mechanisms in hemispatial neglect. *Nature Reviews Neuroscience, 4,* 26-36.

Kristjánsson, Á., & Vuilleumier, P. (2010). Disruption of spatial memory in visual search in the left visual field in patients with hemispatial neglect. *Vision Research, 50*(14), 1426-1435. doi: 10.1016/j.visres.2010.03.001

Lecerf, T., & de Ribaupierre, A. (2005). Recognition in a visuospatial memory task: the effect of presentation. *European Journal of Cognitive Psychology, 17*, 47-75.

Logie, R. H. (1995). *Visuo-Spatial Working Memory*. Hove, UK: Lawrence Erlbaum.

Logie, R. H. (2003). Spatial and visual working memory: A mental workspace. *Psychology of Learning and Motivation, 42*, 37-78.

Logie, R. H. (2011). The visual and the spatial multicomponent working memory. In A. Vandierendonck & A. Szmalec (Eds.), *Spatial working memory* (pp. 19-45). Hove, UK: Psychology Press.

Logie, R. H., & Della Sala, S. (2005). Disorders of Visuospatial Working Memory. In P. Shah & A. Miyake (Eds.), *The Cambridge handbook of Visuospatial Thinking* (pp. 81-120). New York, NY: Cambridge University Press.

Logie, R. H., & Marchetti, C. (1991). Visuo-spatial working memory : Visual, spatial or central executive? In R. H. Logie & M. Denis (Eds.), *Mental Images in Human Cognition* (Vol. 80, pp. 105-115). Amsterdam: Elsevier Science Publishers.

Logie, R. H., & Pearson, D. G. (1997). The Inner Eye and the Inner Scribe of Visuo-spatial Working Memory: Evidence from Developmental Fractionation. *European Journal of Cognitive Psychology, 9*(3), 241-257.

Majerus, S., D'Argembeau, A., Martinez Perez, T., Belayachi, S., Van der Linden, M., Collette, F., Salmon, F., Seurinck, R., Fias, W., & Maquet, P. (2010). The commonality of neural networks for verbal and visual short-term memory. *Journal of Cognitive Neuroscience, 22*(11), 2570-2593. doi: 10.1162/jocn.2009.21378

Majerus, S., Poncelet, M., Elsen, B., & Van der Linden, M. (2006). Exploring the relationship between new word learning and short-term memory for serial order recall, item recall and item recognition. *European Journal of Cognitive Psychology, 18*(6), 848-873.

Malhotra, P., Jager, H., Parton, A., Greenwood, R., Playford, E., Brown, M. M., . . . Husain, M. (2005). Spatial working memory capacity in unilateral neglect. *Brain, 128*(2), 424-435. doi: http://dx.doi.org/10.1093/brain/awh372

Malhotra, P., Mannan, S., Driver, J., & Husain, M. (2004). Impaired Spatial Working Memory: One Component of the Visual Neglect Syndrome? *Cortex, 40*(4-5), 667-676. doi: 10.1016/s0010-9452(08)70163-1

Mammarella, I. C., Cornoldi, C., Pazzaglia, F., Toso, C., Grimoldi, M., & Vio, C. (2006). Evidence for a double dissociation between spatial-simultaneous and spatial-sequential working memory in visuospatial (nonverbal) learning disabled children. *Brain and cognition, 62*(1), 58-67. doi: 10.1016/j.bandc.2006.03.007

Mammarella, I. C., Pazzaglia, F., & Cornoldi, C. (2008). Evidence for different components in children's visuospatial working memory. *British Journal of Developmental Psychology, 26*(3), 337-355. doi: 10.1348/026151007x236061

Mannan, S., Dominic, M., Hodgson, T., Driver, J., Kennard, C., & Husain, M. (2005). Revisiting Previously Searched Locations in Visual Neglect: Role of Right Parietal and Frontal lesions in Misjudging Old Locations as New. *Journal of Cognitive Neuroscience, 17*(2), 340-354.

McAfoose, J., & Baune, B. T. (2009). Exploring visual-spatial working memory: a critical review of concepts and models. *Neuropsychology review, 19*(1), 130-142. doi: 10.1007/s11065-008-9063-0

Milner, B. (1971). Interhemispheric differences in the localization of psychological processes in man. *British Medical Bulletin, 27*, 272-277.

Olk, B., & Harvey, M. (2006). Characterizing exploration behavior in spatial neglect: omissions and repetitive search. *Brain Research, 1118*(1), 106-115. doi: 10.1016/j.brainres.2006.08.011

Parton, P., Malholtra, P., Nachev, P., Ames, D., Ball, J., Chataway, J., & Husain, M. (2006). Space re-exploration in hemispatial neglect. *Cognitive Neuroscience and Neuropsychology, 17*(8), 833-836.

Peterson, M. S., Kramer, A. F., Wang, R. F., Irwin, D. E., & McCarley, J. S. (2001). Visual Search has Memory. *Psychological Science, 12*(4), 287-292. doi: 10.1111/1467-9280.00353

Pickering, S. J., Gathercole, S. E., Hall, M., & Lloyd, S. A. (2001). Development of memory for pattern and path: Further evidence for the fractionation of visuo-spatial memory. *The*

Quarterly Journal of Experimental Psychology A, 54(2), 397-420. doi: 10.1080/02724980042000174

Pisella, L., Berberovic, N., & Mattingley, J. B. (2004). Impaired Working Memory for Location but not for Colour or Shape in Visual Neglect: a Comparison of Parietal and Non-Parietal Lesions. *Cortex, 40*(2), 379-390. doi: 10.1016/s0010-9452(08)70132-1

Repovs, G., & Baddeley, A. (2006). The multi-component model of working memory: explorations in experimental cognitive psychology. *Neuroscience, 139*(1), 5-21. doi: 10.1016/j.neuroscience.2005.12.061

Robertson, I.H. (2001). Do we need the "lateral" in unilateral neglect? Spatially nonselective attention deficits in unilateral neglect and their implications for rehabilitation. *NeuroImage,14,* 85-90.

Ronchi, R., Posteraro, L., Fortis, P., Bricolo, E., & Vallar, G. (2009). Perseveration in left spatial neglect: drawing and cancellation tasks. *Cortex, 45*(3), 300-312. doi: 10.1016/j.cortex.2008.03.012

Rorden, C., Bonilha, L., Fridriksson, J., Bender, B., & Karnath, H. O. (2012). Age-specific CT and MRI templates for spatial normalization. *NeuroImage, 61*(4), 957-965.

Rudkin, S. J., Pearson, G., & Logie, R. H. (2007). Executive processes in visual and spatial working memory tasks. *The Quarterly Journal of Experimental Psychology, 61*(1), 79-100.

Saj, A., Fuhrman, O., Vuilleumier, P., & Boroditsky, L. (2014). Patients with left spatial neglect also neglect the “left side” of time. *Psychological Science, 25*(1), 207-214. doi: 10.1177/0956797612475222

Smyth, M. M., Hay, D. C., Hitch, G. J., & Horton, N. J. (2005). Serial position memory in the visual-spatial domain: reconstructing sequences of unfamiliar faces. *The Quarterly Journal of Experimental Psychology, 58*(5), 909-930. doi: 10.1080/02724980443000412 van Dijck, J.P., Abrahamse, E.L., Majerus, S., & Fias, W. (2013). Spatial attention interacts with serial-order retrieval from verbal working memory. *Psychological Science, 24*(9), 1854-1859. doi: 10.1177/0956797613479610

Wansard, M., Meulemans, T., Gillet, S., Segovia, F., Bastin, C., Toba, M.N., & Bartolomeo, P. (2014). Visual neglect: Is there a relationship between impaired spatial working memory and re-cancellation? *Experimental Brain Research, 232*, 3333-3343. doi: 10.1007/s00221-014-4028-4

Wojciulik, E., Husain, M., Clarke, K., & Driver, J. (2001). Spatial working memory deficit in unilateral neglect. *Neuropsychologia, 39*(4), 390-396. doi: http://dx.doi.org/10.1016/S0028-3932%2800%2900131-7

Woodman, G. F., Vogel, E. K., & Luck, S. J. (2001). Visual search remains inefficient when visual working memory is full. *Psychological Science, 12*(3), 219-224.

Zimmer, H. D., & Heinrich, R. L. (2011). Spatial information in (visual) working memory. In A. Vandierendonck & A. Szmalec (Eds.), *Spatial Working memory*. New York: Psychology Press.

Table 1

Demographic, neurological and clinical data on neglect patients

Patient	Sex/Age/Education	Days post stroke onset	Etiology	Neglect severity	Lesion volume (cm^3/%)	Bells Cancellation (left/right found targets, max = 15/15)	Bells Cancellation (Time in seconds)	Letter cancellation (left/right found targets, max = 30/30)	Line bisection (mm of rightward deviation for 20 cm	Landscape drawing score	Reading (left/right words, max = 61/55)	Clock drawing	Digit span
P1	M/64/17	261	I/Ins (sylvian)	0.31	65.45/.045	12/14*	127	10/29*	+12*	1*	61/55	0	6
P2	F/53/15	409	H/Ic (sylvian)	0.29	9.57/.007	15/15	290*	30/30	+2.5	1*	61/55	1*	5
P3	M51/16	187	N/F	0.76	26.96/.019	14/14	272*	20/29*	-1.5	1*	NA	1*	2*
P4	M/43/14	34	I+H/PF (sylvian)	0.59	39.75/.027	1/14*	58	10/23*	-4.5	0	60/55*	0	6
P5	M/62/10	159	I/P Ins (sylvian)	0.31	69.48/.048	14/15	102	30/30	+15.5*	1*	60/55*	0	6
P6	F/53/6	78	I/P Ins (sylvian)	0.81	129.57/.089	0/5*	72	NA	+39*	4*	0/37*	1*	5
P7	F/54/10	106	I+H/T	0.41	29.51/.02	14/13	230*	30/30	+12.5*	1*	61/55	1*	4
P8	F/68/6	137	I/F Th	0.24	1.33/.001	10/14*	60	21/27*	-1	0	61/55	0	NA
P9	F/70/6	182	I/TP (sylvian)	0.38	6.292/.004	11/13	211*	NA	+9*	0	61/55	1*	5
P10	M/75/12	41	I/FP Bg ic	0.62	95.62/.066	0/13*	50	0/10*	+13.5*	NA	61/55	1*	6
P11	M/88/16	29	I+H/FO	0.25	15.83/.011	12/15*	159	24/29*	+1.5	0	61/55	0	4
P12	M/64/6	405	H/F	0.20	NA	15/14	252*	NA	-4.5	0	NA	1*	NA

I: ischemic; H: hemorrhagic; N: neoplastic; F: frontal; P: parietal; T: temporal; O: Occipital; Th: thalamus; Ins: insula; Bg: basal ganglia; ic: internal capsule.. Lesion volume %: Percentage of total cerebral volume that is damaged. For line bisection, positive values indicate rightward deviation, and negative values indicate leftward deviation. Score for landscape drawing indicates the number of omitted left-sided details. Score > 0 for clock drawing indicates left-sided details missing. Asterisks denote pathological performance. NA: not available.

Table 2

Scores on the spatial-sequential and spatial-simultaneous tasks

Patient	**Span Scores**		**One-tailed t-test**						**RSDT**		
	Sequential	***Simultaneous***	***Sequential***			***Simultaneous***					
			t	***p***	***Z-cc***	***t***	***p***	***Z-cc***	***t***	***p***	***Z-dd***
Sequential and simultaneous impairments											
P6	3 (5.29 ± 0.76)	3 (7.86 ± 0.69)	-2.83	.02*	-3.02	-5.23	<.001*	-5.59	1.60	.08	-1.90
P7	3 (5.25 ± 0.89)	5 (7.88 ± 0.99)	-2.39	.02*	-2.54	-2.74	.01*	-2.90	0.21	.42	-0.24
P10	3 (5 ± 0.76)	4 (7.63 ± 0.92)	-2.48	.02*	-2.65	-3.73	.004*	-3.96	0.89	.20	-1.04
Sequential impairment											
P3	3 (5.63 ± 0.52)	7 (8 ± 0.76)	-4.77	.001*	-5.06	-1.24	.13	-1.32	-2.75	.01*	3.33
Simultaneous impairment											
P9	4 (4.875 ± 0.64)	5 (7.5 ± 0.53)	-1.29	.12	-1.37	-4.41	.002*	-4.68	3.05	.009*	-3.83

Z-cc: effect size for simple *t*-test.
Z-dd: effect size for the RSDT.
* for significant results.
Means and standard deviation for the matched control group are reported in parentheses.

Table 3
Span scores and percentage of errors by side for neglect participants and controls.

	SPAN SCORES			**PATTERN OF ERRORS (%)**										
	Sequential	***Simultaneous***	***Neglect severity***	***Sequential***						***Simultaneous***				
				Location		***Order***		***Omission***		***Location***		***Omission***		
				L	***R***	***L***	***R***	***L***	***R***	***L***	***R***	***L***	***R***
P1	5	7	0.31	9	24	19	29	10	9	20	43	14	23
P2	4	7	0.29	25	29	21	25	0	0	24	76	0	0
P3	3	7	0.76	16	21	30	33	0	0	47	47	6	0
P4	4	8	0.59	21	8	46	25	0	0	50	50	0	0
P5	4	6	0.31	11	16	38	14	16	5	4	10	72	14
P6	3	4	0.81	26	15	11	26	22	0	3	12	73	12
P7	3	5	0.41	16	0	16	21	37	10	10	14	67	9
P8	4	7	0.24	4	18	55	23	0	0	31	69	0	0
P9	4	5	0.38	8	5	25	23	22	17	21	15	32	32
P10	3	4	0.62	23	23	15	12	18	9	19	31	36	14
P11	5	7	0.25	7	25	32	36	0	0	36	54	5	5
P12	4	6	0.20	12	16	44	28	0	0	26	63	0	11
C1	6	7		20	25	30	25	0	0	42	58	0	0
C2	6	8		29	18	18	35	0	0	67	33	0	0
C3	4	9		0	7	50	43	0	0	35	65	0	0
C4	5	8		13	31	31	25	0	0	53	41	0	6
C5	5	9		0	15	38	46	0	0	14	86	0	0
C6	5	8		5	24	38	33	0	0	36	64	0	0
C7	5	7		13	27	33	13	0	14	22	78	0	0
C8	6	8		23	15	35	19	4	4	38	55	0	7
C9	5	10		10	0	50	40	0	0	62	38	0	0
C10	4	8		24	28	20	28	0	0	36	55	0	9
C11	5	7		14	14	32	40	0	0	15	85	0	0
C12	6	9		8	0	48	40	4	0	0	63	12	25

Figure Captions

Figure 1. *Examples of scoring in the spatial-sequential task. The presented sequence is shown at the top of the figure. Example 1 represents a recalled sequence with an omission between 1 and 3 and a location error between 4 and 5. Example 2 represents a sequence with an inversion between locations 2 and 5 (see text for more details). Responses counting for one point are represented by a black square.*

Figure 2. *Patterns of impairments on VSWM tasks. (I) Individuals with neglect showing generalized difficulties on both spatial-sequential and spatial-simultaneous working memory tasks; (II) Selective deficit of the spatial-sequential subcomponent of VSWM; (III) Selective deficit of the spatial-simultaneous subcomponent of VSWM. The dashed line represents performance 2 SDs below the mean of controls.*

Figure 3. *Reconstruction of brain lesions in individuals with spatial neglect. Results are superimposed on slices of the Montreal Neurological Institute (MNI) standard brain for neglect participants with (A) generalized deficits, (B) selective spatial-sequential deficit, (C) selective spatial-simultaneous deficit, and (D) no impairment. The number of overlapping lesions in each subgroup is illustrated by different colors coding increasing frequencies, from cold colors (blue variant for 1 or 2 patients) to warm colors (yellow to orange for 3 to 5 patients).*