Spatial and temporal influences on extinction

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Abstract

This study investigated the spatial and temporal characteristics of the attentional deficit in patients exhibiting extinction to determine the extent to which these characteristics can be explained by a theory of an underlying gradient resulting from the differential contribution of interacting cell populations. The paradigm required the identification of two letters whose spatial location was varied both within and across hemifields. Additionally, the interval between the appearances of the two stimuli was manipulated by changing the stimulus onset asynchrony (SOA). A final variable, that of expectancy, was introduced by making the stimulus location more or less predictable and examining the effect of this top–down contingency on performance. The findings were consistent across two patients and indicated the joint contribution of both spatial and temporal factors: the contralesional stimulus was maximally extinguished when it was preceded by the ipsilesional stimulus by 300–900 ms, but this extinction was reduced when the stimuli appeared further ipsilesionally. Interestingly, there was increased extinction of the contralesional stimulus when location was predictable. These findings support the hypothesis that the attentional deficit in extinction patients arises from a contralesional-to-ipsilesional gradient of cell populations that interact in a mutually inhibitory manner.
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1. Introduction

Hemispatial neglect, a deficit in which patients fail to detect or report information from the side of space contralateral to the damaged hemisphere, has been interpreted as arising from an underlying spatial impairment. Specifically, it has been suggested that this neuropsychological disorder emerges from a gradient of attention or spatial representation such that the further information appears contralaterally, the more poorly it is processed. Theories that describe neglect as a purely spatial deficit are no longer sufficient, however, since several recent studies have identified a clear deficit in these patients in the time course of processing information that appears to occur independently of the spatial impairment. The goal of the current paper is to examine how one might reconcile the seemingly disparate spatial and temporal influences on the behavior of patients with hemispatial neglect. We will argue that both the spatial and temporal dimensions can be explained by a unitary theoretical account in which competition between stimuli is determined both by the extent of the activation afforded by stimulus position and by the activation or rise time of the stimulus.

We first review the findings that support a spatial account of neglect and then present an overview of the studies that examine the temporal dimensions of the deficit. Thereafter, we present data from several studies of our own in which we orthogonally manipulate the spatial and temporal parameters concurrently.

1.1. Spatial account of neglect

A recurring theme in many theories of neglect is that a spatial gradient, with greater ipsilateral than contralateral weighting, mediates the pattern of impairment. Thus, following a right hemisphere lesion, information on the relative left of space is more poorly processed than the corresponding information on the right. What remains largely unspecified in these theories is how the neural substrate gives rise to this gradient. One obvious explanation for the underlying spatial gradient is that it emerges from the differential receptive field distribution across space. Rizzolatti et al. [24], in their study of visual receptive fields of cells in nonhuman primates, have delineated a neuronal imbalance that may serve as the basis for the gradient. The critical finding was that while 68% of cells had bilateral receptive fields, there were many more cells with exclusively contralateral receptive fields (29%) compared to those with solely ipsilateral

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receptive fields (3%). This distribution implies an overrepresentation of contralateral space. If one hemisphere were damaged, there would be an attentional deficit for the whole of visual space, but the severity of the deficit would follow an ipsilesional-to-contralesional gradient, with the deficit being most profound at contralesional regions. Although Rizzolatti's investigations of the neuronal imbalance were conducted in monkey postarcuate cortex, a similar imbalance may be mirrored in the visual areas of parietal cortex. Ben Hamed and Duhamel [3] have recently reported that the receptive fields of neurons in monkey posterior parietal (PP) cortex (area VIP) follow an ipsilateral-to-contralateral gradient similar to the one proposed by Rizzolatti et al.

In addition to this receptive field imbalance, Rizzolatti et al. further suggested that there was likely to be some cerebral asymmetry in humans such that the disparity between the representation of contralateral and ipsilateral space in the right hemisphere might be steeper than the one in the left hemisphere [25]. This arrangement would lead to severe under-representation of leftward regions if the right hemisphere were lesioned, but milder problems for rightward regions if the left hemisphere were lesioned. This speculation fits with the observation that left neglect (resulting from right hemisphere lesions) is more common than right neglect from left hemisphere lesions [4].

This gradient account is particularly appealing as it is based on a clear neurophysiological mechanism, the differential organization of neurons with contralateral and ipsilateral receptive fields, and explains both within- as well as between-hemifield neglect. Indeed, one of the more intriguing and perhaps perplexing symptoms of neglect is that even the leftmost of two stimuli that appear within the same visual hemifield can be neglected [18]. Assuming that damage to the right PP lobe leaves a patient with only the graded representation of the left PP lobe, then a stimulus to the relative left, regardless of its absolute position in the visual field, would activate fewer PP cells than a stimulus on the relative right.

But relative spatial position does not explain one paradoxical but well-established finding and that is that stimuli on the relative right appear to be disproportionately salient for neglect patients; even in comparison with normal subjects, these patients show better performance for stimuli at greater eccentricities on the right [2,20,29]. This advantage for right stimuli suggests a competitive account in which, under normal conditions, the two hemispheres keep each other in check. As elaborated by Kinsbourne's account of mutual inhibition of attentional orienting [18], the two cerebral hemispheres compete to orient attention in opposite directions, to objects anywhere in the entire visual field. Furthermore, a study by Karnath and Fetter [17] suggests that it is not necessary to have objects present in the visual field to instigate this competition. Patients in this study were biased in directing their gaze to the right even when searching for a target (that was not actually present) in a darkened room. When the right hemisphere is damaged, the competition is

biased in one direction, and thus objects towards the left suffer and those towards the right should benefit.

A model demonstrating the behavior of a competitive mechanism such as that proposed by Kinsbourne [18] has been implemented by Cohen et al. [8]. In this model, distinct groups of parietal units represent different spatial locations. Units within a group are mutually excitatory, and a group of units feeds excitatory activation to units responsible for sensory processing of stimuli that appear at the locations corresponding to that group. Separate groups of parietal units mutually inhibit each other. When a group of parietal units is inhibited, it gives less support to its associated sensory units, and stimuli are processed more slowly, resulting in an increase in time before they are perceived. The model simulates neglect when one group of parietal units (corresponding to the right hemisphere) is "lesioned", that is, it is allotted fewer units compared to the group corresponding to the left hemisphere. Since this lesioned right hemisphere group has fewer parietal units, it is prone to be inhibited by the left hemisphere group. The right hemisphere group also builds up activation more slowly, since its fewer units produce less within-group mutual excitation. The strength of this model is that it describes neglect as the result of competitive interactions that can take place anywhere in the visual field, an idea that helps to account for many phenomena. A limitation, however, is that it does not account for the well-known asymmetry in the distribution of attention (and subsequent incidence of neglect). Many studies have shown that the two parietal hemispheres do not play equal roles in visual tasks, as suggested by the mutual inhibition view, with the right parietal lobe mediating attention across both visual fields and the left parietal only mediating attention to the right visual field (RVF) [9,14,32].

In summary, we think that an explanation of neglect as the result of competition along a gradient, reflecting the differential distribution of contra- and ipsilateral neurons, provides a reasonably good account of the spatial deficit in neglect.

1.2. Temporal accounts

Theories that describe neglect as a purely spatial deficit, although increasingly well articulated, are no longer sufficient, since several recent studies have identified a clear temporal aspect of the deficit as well. For example, Husain et al. [16] found abnormally long and severe attentional blink effects in neglect patients. The attentional blink is a reduction in the ability to identify the second of two target letters that appear in a rapid serial visual presentation (RSVP) display, having reported the first letter correctly. The decrement for the second letter is especially evident at time lags of about 100–600 ms and the claim is that this interval reflects the period during which the attentional processing of the first target interferes with processing of the second target [6]. Although normal subjects show this second-letter decrement, Husain et al. found that the temporal interval for the decrement was

three times longer in neglect patients than in normal controls. The severity of the deficit was also greater for the patients than for the controls. Importantly, in this experiment, all the stimuli were presented centered over fixation. That the patients require a longer temporal interval than normals for correct second-letter report suggests that there is a temporal dimension to the neglect deficit that is independent of any spatial dimension. This result is easily reconciled with a gradient account of neglect if one accepts the view that damage to the right hemisphere will reduce performance for the whole visual field so that, even at fixation, the activation of visual stimuli can be slowed relative to normal subjects.

This temporal interference is also evident when stimuli appear in opposite hemifields. In one such 'prior entry' study with left neglect patients, Rorden et al. [27] presented stimuli (horizontal line segments) to the left or the right side of a fixation cross, separated in time by a range of stimulus onset asynchronies (SOAs). Subjects were asked to judge which stimulus had appeared first. The critical measure was the SOA at which patients' judgments crossed over from reporting the left to reporting the right stimulus as first. Whereas for control subjects the critical time was 0 ms SOA (when the stimuli appeared simultaneously), the neglect patients required a 200 ms lead by the left stimulus to make this judgment. This result is especially notable because it shows that even when there is no deficit in (eventually) reporting the stimulus, performance is still shown to be impaired in the temporal dimension, relative to the control subjects. Furthermore, this facet of the deficit presumably has nothing to do with impaired orienting of attention, since the patients' problem was exhibited for contralesional stimuli that preceded the ipsilesional stimuli by 200 ms. It was not the case that the patients were distracted by the ipsilesional stimulus, since it was not yet present and suggests, instead, that the rise time of the left stimulus is slowed. Of special note is the fact that this deficit can be ameliorated if an auditory signal alerts patients to the onset of the visual stimuli. Robertson et al. [26] found that regardless of its spatial source, a phasic warning tone removed the deficit in temporal order judgments found in the above study, and cited this as evidence in favor of Kinsbourne's hypoarousal account.

di Pellegrino et al. [10] found similar and perhaps even more dramatic temporal effects, by showing a decrement in reporting a contralesional letter across substantial time lags. The patient's task was to identify two letters presented bilaterally. When the two letters were separated by a long time lag (1000 ms SOA), the patient correctly identified the left letter in nearly all trials, regardless of which letter appeared first. In accordance with previous studies, the patient was unable to identify the left letters when both appeared simultaneously (0 s SOA). Intermediate SOAs (100–600 ms) resulted in levels of performance that fell in between those obtained in the 1000 and 0 ms SOA conditions; the shorter the SOA, the worse the performance on the left letter. Most importantly, the decrement for reporting the left letter was unaffected by order of appearance of the letters; the patient

was equally impaired in reporting the left letter if it appeared first or if it was preceded by the right letter.

An important point from di Pellegrino et al.'s study is that extinction is not an all-or-none phenomenon, but manifests in a temporally graded fashion across SOA. Extinction cannot be merely the failure to detect a contralesional stimulus in the presence of an ipsilesional one but, rather, reflects the inhibition of the contralesional stimulus by the ipsilesional stimulus. This inhibition was maximal when the stimuli appeared simultaneously, but was even present over intervals spanning hundreds of milliseconds.

di Pellegrino et al. followed up this study with another experiment with the same patient, FB [11]. This experiment compared the processing time necessary to identify a letter in either the left visual field (LVF) or the right visual field (RVF). The task was essentially an attentional blink task that required FB to identify two letters that appeared in the same location, separated by various SOAs. The SOA necessary for FB to report both stimuli was twice as long in the LVF than in the RVF. This experiment showed a direct relationship between the time course of processing a stimulus and the ability of a stimulus to compete for selection: LVF stimuli require a longer time course of processing and also tend to be extinguished by RVF stimuli.

1.3. Aims of the present study

Studies investigating the temporal dimension emphasize the competitive aspect of neglect, but have so far not addressed the problem of relative spatial location and the question of a within-hemifield gradient. All investigations of the temporal dimension were performed with stimuli presented either centrally (as in the Husain et al. study) or bilaterally. If extinction depends both on the location of the stimuli and the time course of attentional processing, what relationship is there between these spatial and temporal dimensions?

We hypothesize that the spatial and temporal dimensions of these patients' deficits emerge from the same underlying cause, a pathological gradient of attentional ability. If there are fewer neurons representing a leftward location, this could result in both a weakened ability to compete with rightward stimuli as well as a longer time course of processing. Furthermore, this suggests that for tasks that require attending to two stimuli, a change in the spatial location of the stimuli will also produce a change in the temporal pattern of the deficit. If neglect is the result of a contralesional-to-ipsilesional gradient of representation, then presenting pairs of stimuli more ipsilesionally should (1) reduce the severity of the deficit for the left stimulus and (2) alter the time course of the deficit, measured by left stimulus performance for various SOAs. To fully examine how these interactions are manifested within and across the visual fields, we conducted two series of experiments: in the first, pairs of stimuli appeared only within the RVF (Experiments 1–3), and in the second, pairs of stimuli could appear within either hemifield or bilaterally (Experiments 4 and 5).

In addition to manipulating spatial and temporal parameters, we examined one further variable, known to influence the severity of PP patients' deficits and that is top–down attention. It is well known that neglect can be ameliorated by cueing or explicitly instructing the patient to attend to the left [22,23]. Allowing PP patients to covertly orient attention to a predictable location also improves detection performance [29]. It remains unclear, however, what the effects of top–down attention will be when the position of a *pair* of competing stimuli is predictable, given that attending to broader or narrower regions of space can enhance or impair performance in multiple targets tasks [19].

One possibility is that top–down signals may interact with the competitive mechanisms that we have described, potentially amplifying the inhibition between stimuli and augmenting the separation between the representation of a target and a distractor [5]. If so, this would magnify the competition and enhance the disparity between the right and left stimuli further especially under those conditions where the competition is already strong (short SOA, contralesional positions). Another possibility is that patients may be able to use this top–down signal in a positive fashion to orient more rapidly to the weaker left signal once its position is more predictable. This would then reduce extinction. To investigate the contribution of top–down attention on spatial and temporal competition, we conducted two versions of each experiment, one in which stimulus locations were blocked and predictable, and one in which stimulus locations varied randomly and were thus unpredictable.

2. Experiment 1

In this first experiment, we document the time course of a neglect patient's attentional deficit for stimuli that appear exclusively in the ipsilesional hemifield and across a wide range of SOAs.

2.1. Subject

LD is a 76-year-old right-handed native English-speaking male with a high school education. In October 1998, he suffered a right middle cerebral artery infarct that gave rise to a left hemianopia. A CT scan (see Fig. 1) revealed damage to the right temporoparietal junction and the right posterior frontal region. His performance on a battery of
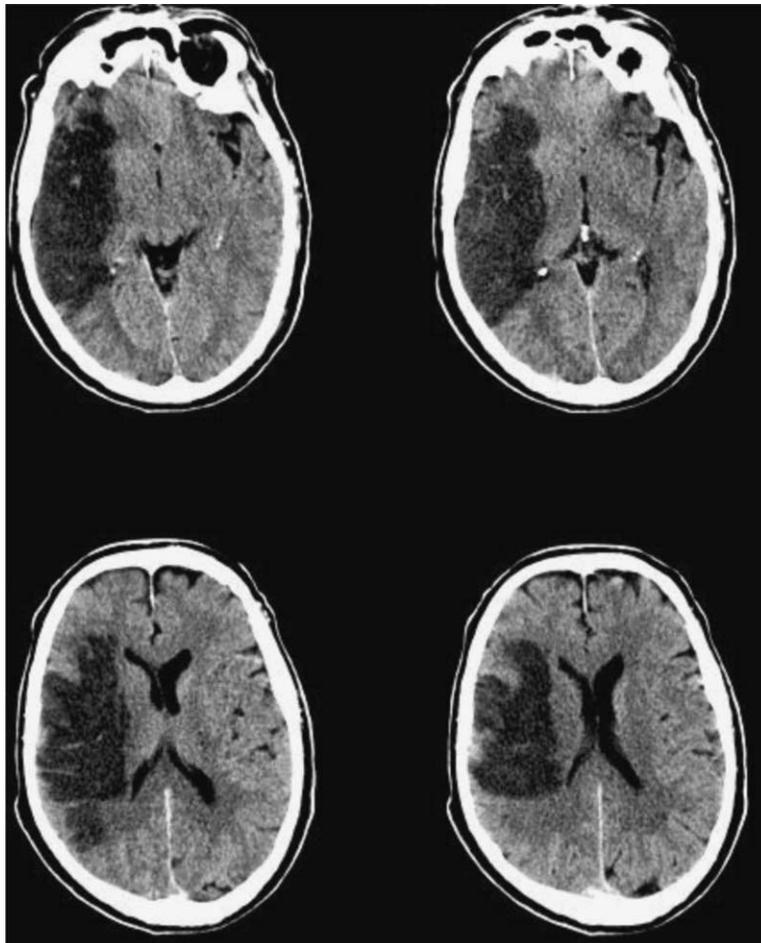
Fig. 1. CT scan for patient LD revealing fairly extensive damage to the right temporoparietal junction and the right posterior frontal region.
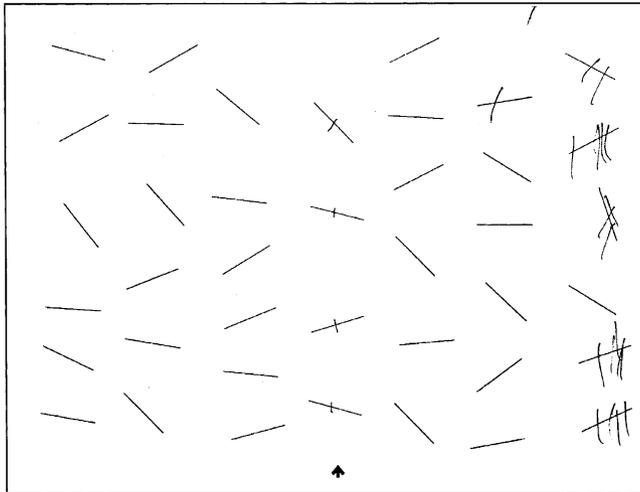
Fig. 2. Performance of LD on line-cancellation task showing severe left-sided neglect. Marks on the middle of the page were drawn as examples by the experimenter.

standard neglect tasks (Behavioral Inattention Test [33]), administered 2 weeks post-stroke, was severely impaired, showing an inability to respond to all but the most extremely ipsilesional stimuli (line crossing 18/36; letter cancellation 33/40; star cancellation 28/54; figure copying 1/4; line bisection 5/9; representational drawing 1/3; total conventional test score 86/146). Fig. 2 shows LD's performance on the line-cancellation task at the time this testing took place, between 5 and 7 months post-stroke.

2.2. Procedure

All experiments were carried out on a Macintosh Powerbook 540c computer using Psyscope experimental software [7]. LD sat at a distance of approximately 50 cm from the screen with the midpoint of the screen aligned with the midsagittal plane of his body. A fixation cross, a "+" sign in 36 point bold Geneva font, measuring $0.67°$ of visual angle, was present in the center of the screen throughout the experiment.

The stimuli were four upper case letters: A, S, T, and X, presented in 36 point bold Geneva font and measuring approximately $0.67°$ by $0.88°$. Stimuli could appear at two positions on the screen, either $3.78°$ (the relative left position) or $6.78°$ (the relative right position) to the right of the fixation cross. Note that both of these positions fell within LD's intact ipsilesional hemifield when he was fixating the cross.

LD was informed that on each trial either one or two letters would appear to the right of the fixation cross, and that, in every case, a letter could only be an A, S, T, or X. He was told that for trials when two letters appeared they would never be the same two letters, and that they would appear either simultaneously or separated by a brief time lag and he was to identify the letters. He was not required

to report them in any particular order and was instructed to guess when he was unsure of a letter's identity.

During the experiment, the experimenter was seated behind the computer screen, facing the subject. A trial was initiated when the experimenter depressed a mouse button, after checking to see that LD was fixating the center of the screen. After a randomly selected time lag of 200, 400, or 600 ms, the stimulus or stimuli appeared on the screen for 100 ms. LD was reminded to keep his gaze fixed on the cross several times during the experiment. The experimenter monitored eye movements during the trials. Trials in which LD moved his eyes were discarded and not replaced.

There were two types of trials, single stimulus trials or double stimuli trials. In a single stimulus trial, a single letter would appear randomly at one of the two possible stimulus positions. During double stimuli trials, two letters would appear, one at each of the two positions. The two stimuli were separated temporally by a randomly selected SOA. The SOAs used were −1100, −900, −700, −500, −400, −300, −100, 0, 100, 300, 500, 700, 900, 1100, and 1300 ms. A negative SOA indicates a trial in which the first letter appeared in the relative left position, and was followed by a letter on the right after a lag of the indicated length. An SOA of 0 ms refers to the case wherein both letters appeared simultaneously. A positive SOA indicates a trial in which the first letter appeared on the right, and was followed by a letter on the left. These two types of trials, single and double stimuli, were randomly interleaved during testing.

No feedback was given during the experiment. The experimenter, who was blind as to which letters appeared during the trials, recorded LD's responses. "No response" was recorded if LD provided no response after approximately 5 s. There was a pause of approximately 5 s between trials, and occasional longer breaks were taken as needed. Experiment 1 was carried out on 2 separate days of testing, with three blocks of trials per day: a block consisted of 112 trials on the first day of testing, and 144 trials on the second day. Forty-eight single stimulus trials were presented, 24 per stimulus position. Forty-eight double stimuli trials for each of the 15 SOA conditions (720 total) were also presented. Thus, there were 768 total trials presented over the 2 days. All trials were randomly interleaved within blocks. In addition, all letters were used an equal number of times, and appeared in a random order and with equal probability on the left or right.

Errors included both 'no response' reactions as well as incorrect identifications although the vast majority of LD's errors were omissions. Performance on the single stimulus trials provided a baseline against which to compare performance at the various SOAs in the double stimulus condition.

2.3. Results

LD was able to identify the single stimuli on 88% of trials for the left and on 83% for the right position, rates that were not found to be significantly different ($\chi^2(1) = 0.09$,
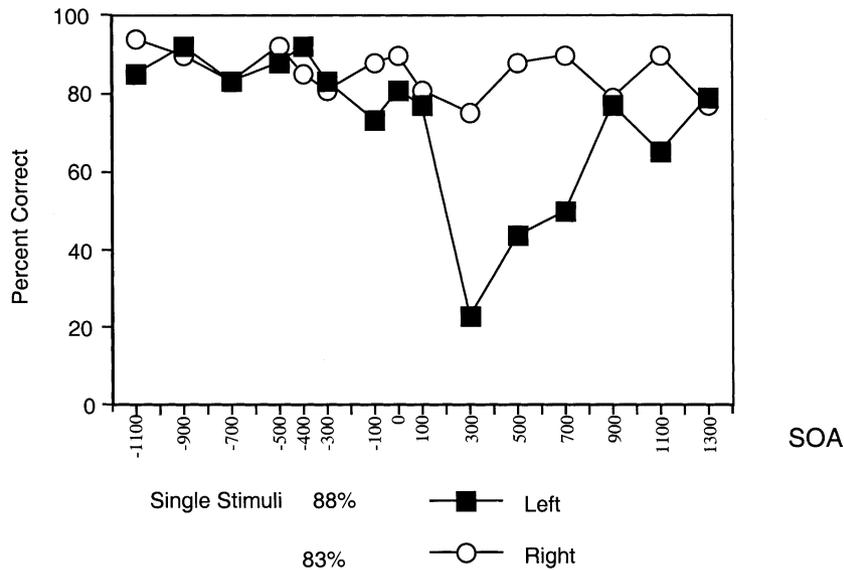
Fig. 3. Percent correct report of letters on left and right in double stimuli trials as a function of SOA in Experiment 1. Percentage correct for single stimuli trials is included for comparison.

$P = 0.77$). The single stimulus error rates, along with the error rates from double stimuli trials, are given in Fig. 3.

A loglinear analysis of accuracy in the double stimulus trials, including stimulus side and SOA as factors, confirmed the main effect for side with more errors for left than right stimuli ($\chi^2(1) = 19.51$, $P < 0.001$) and the main effect of SOA ($\chi^2(14) = 63.32$, $P < 0.001$), with more errors at SOAs between 300 and 700 ms.

Importantly, there was an interaction between stimulus side and SOA ($\chi^2(14) = 45.45$, $P < 0.001$) with an effect of SOA on error rates for the left stimuli only. When the left and right error rates were analyzed separately, there was a significant SOA effect for left ($\chi^2(14) = 102.53$, $P < 0.001$), but not for right stimuli ($\chi^2(14) = 16.02$, $P = 0.31$). Furthermore, the error rate for left stimuli was significantly different from its single stimulus error rate ($\chi^2(1) = 4.70$, $P = 0.030$), but the error rate for the right stimuli was not ($\chi^2(1) = 0.00$, $P = 0.96$).

2.4. Discussion

These findings show that extinction can be induced in the RVF of a neglect patient. LD's errors can be categorized as extinction errors, since he showed no disadvantage for left versus right stimuli presented individually. The pattern of extinction is interesting in that it shows that the relative decrement for left over right stimuli occurs within a specific time range, notably between 300 and 900 ms following the onset of a right stimulus. These results generally replicate those of di Pellegrino et al. [10], but for stimuli in the RVF. Because both stimuli are in the RVF, the extinction is not merely the result of an imbalance between an intact left hemisphere and a damaged right hemisphere, but rather

arise from a contralesional-to-ipsilesional gradient that exists entirely in the RVF.

Although the extinction is manifest within certain SOAs, as was true in di Pellegrino et al., the SOA-dependent pattern of errors in the two studies is very different. Whereas di Pellegrino et al. report extinction for both the left and right items, LD showed no decrement in performance for negative SOAs, nor even for short positive SOAs, but only when the right item had a temporal advantage of roughly 300–900 ms. These data are consistent with a competition account of extinction in which a more powerful or salient item wins out over a less salient item. In LD's case, the left item can be selected successfully, as the single stimulus results show, and a right item must build up activation for at least 300 ms in order to extinguish it. If, however, the left item has sufficient processing time, it can compete successfully with the right item and resist being extinguished. There are methodological differences between di Pellegrino et al.'s study and this one that may help to explain the differing SOA effects, which are considered more fully in the general discussion.

3. Experiment 2

Even when two stimuli appear within the ipsilesional hemifield, LD's ability to report the left item was critically dependent on the temporal interval such that extinction was maximal when the right item preceded the left item by 300 ms. The emphasis of Experiment 1 was on the time course of extinction, and the spatial position of the stimuli was held constant. Experiment 2 manipulates the spatial position of the stimuli as well as the SOA, in order to examine the interaction between spatial location and temporal

interval. In this experiment, extinction is measured when stimuli occupy various eccentricities within the ipsilesional field. According to a gradient account of attentional processing, one might expect that LD's performance would be better at more eccentric locations. Furthermore, this improvement might not only be expressed as a reduction in the number of errors committed, but also potentially by a shortening of the time course of the deficit, reflected in the range of SOAs affected, or by both.

3.1. Method

The stimuli and their presentation were identical to those used in Experiment 1, with the following exceptions. Four different stimulus positions were used, labeled 1, 2, 3, and 4 in Fig. 4. Each position consisted of a pair of locations, 3.0° apart, one for the leftward and one for the rightward stimulus of a double stimuli pair. The leftmost position (position 1) consisted of the same two locations used in Experiment 1, and essentially served as the baseline position against which the more rightward positions were compared. The other positions were chosen so that LD's SOA-dependent deficit could be measured when the stimuli appeared at successively greater eccentricities within his ipsilesional hemifield. Among the eight possible locations used, labeled A–F, two (C and D) could be occupied by either the left or right item of a pair, depending on the position. This allows for a comparison of identification of an item in the same retinal location but serving as the left or right item of a pair. Because of this overlap, even though there were four pairs of positions at which double stimuli trials could occur, there were only six possible locations at which single stimuli could occur.

Because several spatial positions are probed, only a subset of the SOAs used in Experiment 1 was used, in order to limit the total number of trials. The SOAs (300, 500, and 900 ms) that were shown to be sensitive to the extinction pattern previously were chosen, and in addition 0 and −300 ms were included to obtain other representative points. This distribution of SOAs created a bias such that right stimuli were more likely to appear first in a double stimuli trial, which probably encouraged LD to attend to these rightward positions. Neglect patients are sensitive to statistical regularities such as the spatial or temporal distribution of targets, which can modify the degree of their attentional deficits [13]. However, since the set of SOAs was constant across positions 1–4, any differences in performance across these positions cannot be attributed to a bias per se. As in Experiment 1, single and double stimulus trials were randomly interleaved during testing. Trials were also randomly interleaved with respect to SOA and stimulus position. LD was told that there would again be single and double stimulus trials, that there would be fewer single stimulus trials overall than in the previous experiment, and that he was to report the letters he detected.

Testing for Experiment 2 took place a week after Experiment 1 and was conducted over 3 days, with one block of trials, consisting of 224 trials, per day. Altogether, 12 single stimulus trials were presented at each of the six individual stimulus locations, for a total of 72 single stimulus trials. Additionally, 30 double stimuli trials were presented for each SOA condition for each of the four positions, for a total of 600 trials. As in Experiment 1, all letters were used an equal number of times, and appeared in a random order and position. All trials within a block were randomly interleaved with respect to position, SOA and number of stimuli.

In addition to loglinear analyses, logistic regressions were also performed. Loglinear analyses provide P-values for the main effects and interactions of independent variables (e.g.
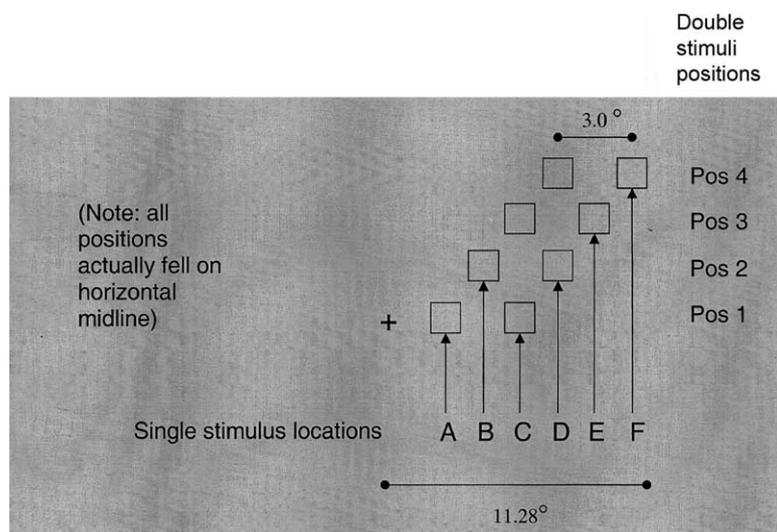
Fig. 4. Schematic depiction of spatial layout of Experiments 2 and 3. Double stimuli pairs could appear at four positions (1–4) and single stimuli could appear at six locations (A–F), all in the ipsilesional field. Boxes indicating stimulus locations are drawn for clarity; no boxes actually appeared in the display.

position and SOA), but do not indicate whether error rates associated with individual levels of these variables (e.g. 300 versus 500 ms SOA) differ from each other. Individual chi-square tests could be used to compare the error rates for different conditions, but these would collectively be prone to global type I error since so many comparisons would be performed. Instead, we rely on the odds ratios (coefficient for each level of each independent variable) produced by logistic regression analyses to provide a measure of the differences between levels of a variable.

The odds ratios indicate how much more likely it is that an error will be recorded in a given condition, relative to a pre-specified baseline condition. For example, an odds ratio of 5.0 means that an error is five times more likely to be recorded in a given condition. Similarly, an odds ratio of less than 1.0 indicates that correspondingly fewer errors are likely to be recorded.

In our analyses, odds ratios for specific SOAs were obtained by using the single stimulus baseline error rate for the position in question as the basis for comparison. Odds ratios for positions 2–4 were obtained by using the error rate for position 1 as the baseline rate. No odds ratios were calculated for position 1, since it served as the basis of comparison.

3.2. Results

Single stimulus baseline rates are reported in Fig. 5 along with the double stimuli error rates. Note that even though the figures list a total of eight baseline rates (the left and right stimulus baselines for four positions), these are based on six measurements, due to the overlap of positions described above. Performance for the single stimuli was approximately the same for the six single stimulus locations, although there was a slight drop in percentage correct report for positions 3 and 4 for the right stimuli. However, given that $N = 12$ for these conditions, this drop was not statistically significant ($\chi^2(5) = 2.77$, $P = 0.74$). Consistent with the data from Experiment 1, performance for single stimulus trials appears to be fairly uniform across the right hemifield with a slight reduction with increasing eccentricity for the right position.

A loglinear analysis was performed on the double stimuli error rates with stimulus side (left or right), positions (1–4)
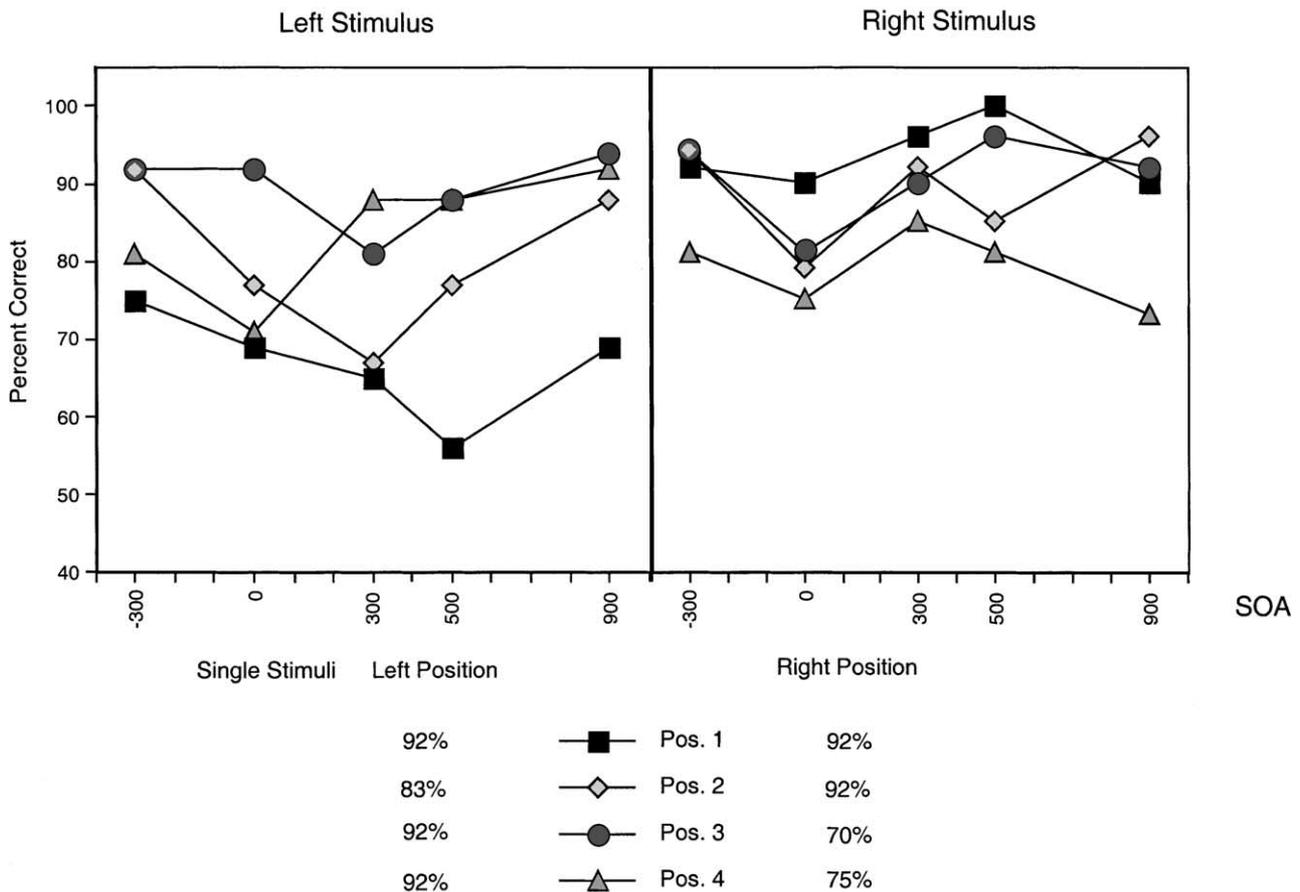
Fig. 5. Percentage correct report of the left and right letters from double stimuli trials as a function of SOA in Experiment 2. Stimulus location was unpredictable since location varied randomly across trials. Percent correct for single stimulus trials indicates how often LD reported a single letter when it appeared in the same position as either the left or the right stimulus of a double stimuli pair.

and SOA as factors. As in Experiment 1, LD performed consistently worse for left (80% correct) than for right stimuli (89% correct) ($\chi^2(1) = 15.86$, $P < 0.001$). There were also main effects of position ($\chi^2(3) = 14.29$, $P = 0.0025$) and SOA ($\chi^2(4) = 15.13$, $P = 0.0044$) although the interaction between them was not significant ($\chi^2(12) = 16.57$, $P = 0.17$). However, because our a priori interest was on the separate effects for left and right stimuli, we examined the data separately for left and right error rates.

When left items are considered alone, there was a main effect for position ($\chi^2(3) = 46.98$, $P < 0.001$), confirming the visible trend for fewer errors at the more eccentric positions. A logistic regression analysis of the left stimuli confirmed that the error rates for positions 2–4 were all significantly lower than for position 1. Highly significant odds ratios were observed for position 2 (0.43: $\chi^2(1) = 9.93$, $P = 0.0016$), position 3 (0.19: $\chi^2(1) = 32.05$, $P < 0.0001$), and position 4 (0.32: $\chi^2(1) = 17.05$, $P < 0.0001$).

The SOA effect on the left stimuli was also significant ($\chi^2(4) = 13.04$, $P = 0.011$) and it interacted with position, albeit with marginal significance ($\chi^2(12) = 19.70$, $P = 0.073$). This marginal effect arises because for each position there was an SOA at which errors were maximal but these "troughs" were different for the different positions which eliminates the position by SOA interaction in the loglinear analysis. However, there is a trend for the trough to occur at shorter SOAs for more eccentric positions. Fig. 5 indicates that the trough SOA is at 500 ms for position 1, at 300 ms for position 2 at 300 ms for position 3, and at 0 ms for position 4. These troughs were determined from the graphical analysis, but individual loglinear analyses for each of the four positions reveal significant SOA effects for position 2 ($\chi^2(4) = 12.50$, $P = 0.014$), and position 4 ($\chi^2(4) = 9.80$, $P = 0.044$), indicating that at least two of the troughs are not spurious.

The left stimuli error rates suggest that as stimuli appeared more eccentrically, fewer errors were committed. Additionally, the length of the time lag that produced maximal extinction became shorter. When stimuli were more eccentric, their baseline activations were presumably higher and rose faster so that the competition between left and right stimuli could take place earlier and the extinction could be manifest at shorter time intervals.

The loglinear analysis on the right stimuli showed a significant effect for position ($\chi^2(3) = 22.66$, $P < 0.0001$). A logistic regression for these data indicated that for right stimuli *more* errors were committed at eccentric locations, the opposite of the trend seen in the left stimuli. The odds ratios indicated increased error rates (relative to position 1) for positions 2, 3, and 4 (1.80, 1.67, and 4.28, respectively). The *P*-values for these odds ratios are marginally significant for position 2 ($\chi^2(1) = 3.12$, $P = 0.077$), not significant for position 3 ($\chi^2(1) = 2.31$, $P = 0.13$), but highly significant for position 4 ($\chi^2(1) = 22.05$, $P < 0.0001$).

There was also a significant effect of SOA ($\chi^2(4) = 12.81$, $P = 0.012$) on the report of the right letter but

no interaction between SOA and position ($\chi^2(12) = 11.63$, $P = 0.48$), indicating that unlike the left stimuli, the errors followed the same pattern of SOAs for all positions.

In general, right stimuli error rates were much less affected by the position and SOA manipulations than the left stimuli error rates. The effects that are present are in the opposite direction of the effects for the left stimuli.

3.3. Discussion

As expected, performance for the left stimulus of a pair is worse than performance for the right counterpart. This left–right difference, however, is jointly affected by the spatial positions occupied by the two stimuli as well as by the temporal interval between them. At more ipsilesional positions, LD's impairment in detecting left stimuli of a double trial becomes less severe. This supports gradient theories of neglect in which accuracy for stimuli at ipsilesional positions is high and reaction times fast (and in some cases, even faster than those obtained for normal subject) [20,29]. One interpretation of this finding is that, at more ipsilesional positions, the competition between left and right stimuli is more balanced and the left stimulus less disadvantaged.

Additionally, as stimuli occupied more ipsilateral positions, the SOA at which maximum extinction was observed was reduced, suggesting that processing time for the left stimulus is faster at more ipsilesional locations. This interpretation agrees with the results of di Pellegrino et al.'s study [11].

In summary, the fact that manipulating position had a real effect only on double but not on single stimuli also supports the competition interpretation over an interpretation of a leftward orienting problem. The factors that determine poor performance on the double stimuli are (1) relative position within a pair of competing stimuli; (2) SOA; and (3) position within the RVF.

4. Experiment 3

In Experiment 2, joint effects of stimulus position and SOA were obtained in mixed blocks of trials when position was randomized. This experiment examines the influence of top–down attention on these joint effects by blocking the trials on stimulus position. It is possible, for example, that LD might be able to deploy attention to a more narrowly defined, fixed region of space when stimulus position is predictable, altering the nature of the competition between left and right items.

4.1. Method

The method used was the same as that used in Experiment 2, with the following changes. Double stimuli pairs

always appeared at the same position within a block of trials. Double and single stimulus trials were still randomly interleaved, and the single stimulus always appeared (randomly) at one of the two locations specified by the double stimulus position used in that block. Six SOAs: −300, 0, 300, 500, 900, and 1300 ms, were used and were randomly interleaved within blocks. Forty-eight double stimuli trials per SOA per position were collected, and 48 single stimulus trials per possible stimulus location were collected.

New data were only actually collected for positions 2–4, and these are the only positions for which results are reported. We initially incorporated the position 1 data gathered in Experiment 1 into the analysis, but since Experiments 1 and 3 used different sets of SOAs, it was decided that it would not be valid to compare these data. The greater number of negative (left-first) SOAs in Experiment 1 probably created a greater incentive to attend to the left, which could have produced a lower rate of extinction errors than in Experiment 3.

4.2. Results

Performance for single stimuli is uniform across the right hemifield (see Fig. 6), although the single stimulus baseline for the left side of position 3 was significantly lower than all the other baselines ($\chi^2(7) = 14.48$, $P = 0.04$). This unusual result from position 3 does not lend itself to an obvious explanation and, aside from this, performance is approximately even across all positions.

A loglinear analysis indicated that LD's performance continued to be worse for left (68% correct) than for right stimuli (83% correct) in the double stimulus trials ($\chi^2(1) = 45.05$, $P < 0.0001$). There was no main effect of position ($\chi^2(2) = 1.78$, $P = 0.41$), but the main effect of SOA ($\chi^2(5) = 19.97$, $P = 0.001$) and the position by SOA interaction ($\chi^2(10) = 18.07$, $P = 0.05$) were significant. The three-way side by position by SOA interaction was not found to be significant ($\chi^2(10) = 8.01$, $P = 0.63$).

An analysis of the left-sided error rates revealed highly significant effects for position ($\chi^2(2) = 22.61$,
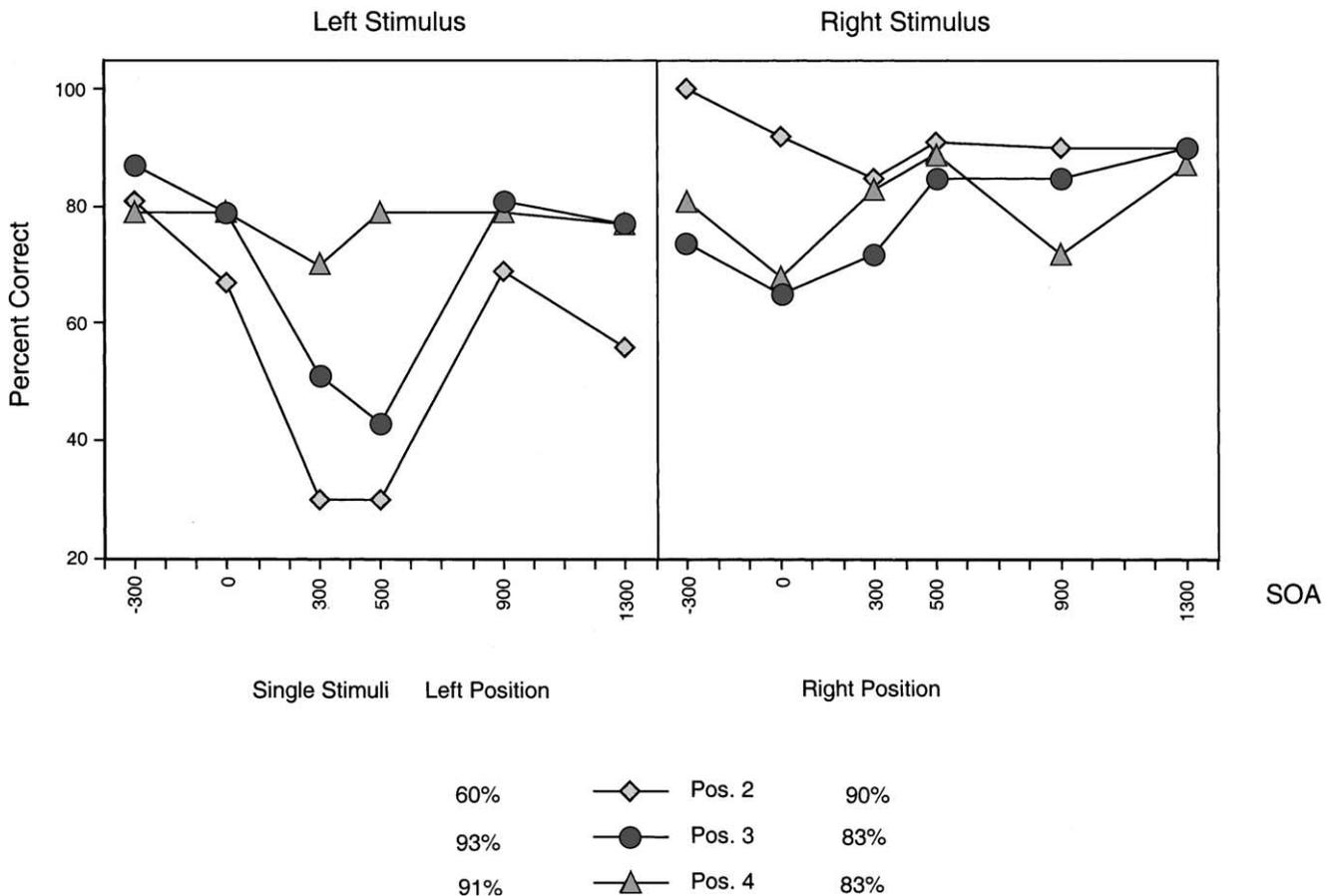
Fig. 6. Percentage correct report of the left and right letters from double stimuli trials as a function of SOA in Experiment 3. Percent correct for single stimulus trials is included for comparison. Stimulus location was predictable since location was blocked. Note that left stimulus performance is much worse than in Experiment 2 (see Fig. 5), and that the disparity between left and right stimulus performance is greater.

$P < 0.0001$), SOA ($\chi^2(5) = 50.50$, $P < 0.0001$), and their interaction ($\chi^2(10) = 18.71$, $P = 0.04$). A logistic regression confirmed that as stimuli were presented further eccentrically, fewer errors were made, with odds ratios of 0.63 for position 3 ($\chi^2(1) = 7.10$, $P = 0.008$) and 0.36 for position 4 ($\chi^2(1) = 29.79$, $P < 0.0001$).

The logistic regression also showed that error rates for the 300 and 500 ms SOAs were higher than the single stimulus baseline (same odds ratio for both: 4.21 ($\chi^2(1) = 17.70$, $P < 0.0001$)). No other SOAs were significantly different.

When the positions of stimuli were predictable, the time course of the deficit remained constant across positions. This is in contrast to Experiment 2, where stimulus position was unpredictable. In that case, error rates were high, but confined to a limited range of SOAs.

An analysis of the right-sided stimuli revealed a significant effect for position ($\chi^2(2) = 9.82$, $P = 0.007$), but not for SOA ($\chi^2(5) = 9.58$, $P = 0.08$) nor for the interaction ($\chi^2(10) = 9.25$, $P = 0.50$). In contrast to the left stimuli, error rates were higher at eccentric positions. A logistic regression yielded significant odds ratios for position 3 (1.99: $\chi^2(1) = 9.22$, $P = 0.002$) and position 4 (1.88: $\chi^2(1) = 7.35$, $P = 0.007$). It seems that the reduction in error rates for left stimuli at eccentric positions was accompanied by a concomitant increase in right stimulus error rates.

4.3. Comparison of Experiments 2 and 3

We compare Experiments 2 and 3 based on the data for positions 2–4. Collapsed across all factors, LD's performance was much better in Experiment 2 (85%), when stimulus location was not predictable, than in Experiment 3 (75%), when it was ($\chi^2(1) = 47.27$, $P < 0.0001$). Performance decreased for left stimuli only when position was made predictable. Left stimulus performance (collapsed across all positions and SOAs) dropped from 84 to 68% correct ($\chi^2(1) = 55.39$, $P < 0.0001$), while right stimulus performance only changed from 86 to 83% correct, a difference that only approached significance ($\chi^2(1) = 3.40$, $P = 0.07$). Indeed, the disparity or extent of left–right competition was much greater when location was predictable than when it was not. There was a left–right difference of 14 errors (out of 1440 trials) in Experiment 2, compared to a difference of 130 errors (out of 1598 trials) in Experiment 3 ($\chi^2(1) = 55.60$, $P < 0.0001$).

Notably, single stimulus performance was unaffected. The total single stimulus error rate for Experiment 2 was 83%, compared to 81% for Experiment 3, a non-significant difference ($\chi^2(1) = 0.06$, $P = 0.80$). This supports the idea that top–down attention modulates performance for pairs of stimuli by altering the degree of competition between them, more so than by affecting the processing of each item independently.

4.4. Discussion

The finding from this study was that predictability does influence LD's performance, but only on double stimuli trials. The absence of an effect of predictability on the single stimuli trials is inconsistent with the findings of Smania et al. [29], but this difference may be due to the different dependent measures used (correct identification versus reaction time).

Overall performance was poorer here than in Experiment 2 and unlike in that experiment, there was no interaction between the time course of processing and location; errors were committed almost exclusively between 300 and 900 ms SOAs in all positions. Predictability appears to create a greater disparity between left and right stimulus performance, as discussed below.

5. Experiment 4

Experiments 1–3 examined the performance of a patient with hemispatial neglect on a task involving stimuli that appeared exclusively within the ipsilesional hemifield. However, gradient theories of neglect propose that gradients occur across the entire visual field. To extend our findings and confirm that this is indeed the case, we repeated Experiment 2 with a second neglect patient who was not hemianopic and in whom we could present stimuli that spanned the left and RVFs.

5.1. Subject

RB is a 66-year-old right-handed native English-speaking male. In January 1993 he suffered a right cerebral haemorrhage and hematoma. A CT scan (see Fig. 7) revealed right inferior parietal, right superior and middle temporal, and right middle occipital damage. He exhibited moderate neglect on the Behavioral Inattention Test administered 20 months post-stroke (line crossing 34/36; letter cancellation 26/40; star cancellation 36/54; figure copying 2/4; line bisection 7/9; representational drawing 2/3; total conventional test score 108/146). RB had an intact LVF to confrontation testing and only failed to detect the left stimulus when it was accompanied by a concurrent right stimulus, indicative of extinction.

5.2. Procedure

The overall methods were similar to those used previously. The same stimulus set and task were adopted. There were three positions in which pairs of stimuli could appear (see Fig. 8) and these were randomly interleaved in a block of trials, making position unpredictable.

In pair 1, both stimuli appeared in the left (contralesional) hemifield. In pair 2, the stimuli straddled the fixation point, so that the leftward stimulus appeared in the left hemifield,
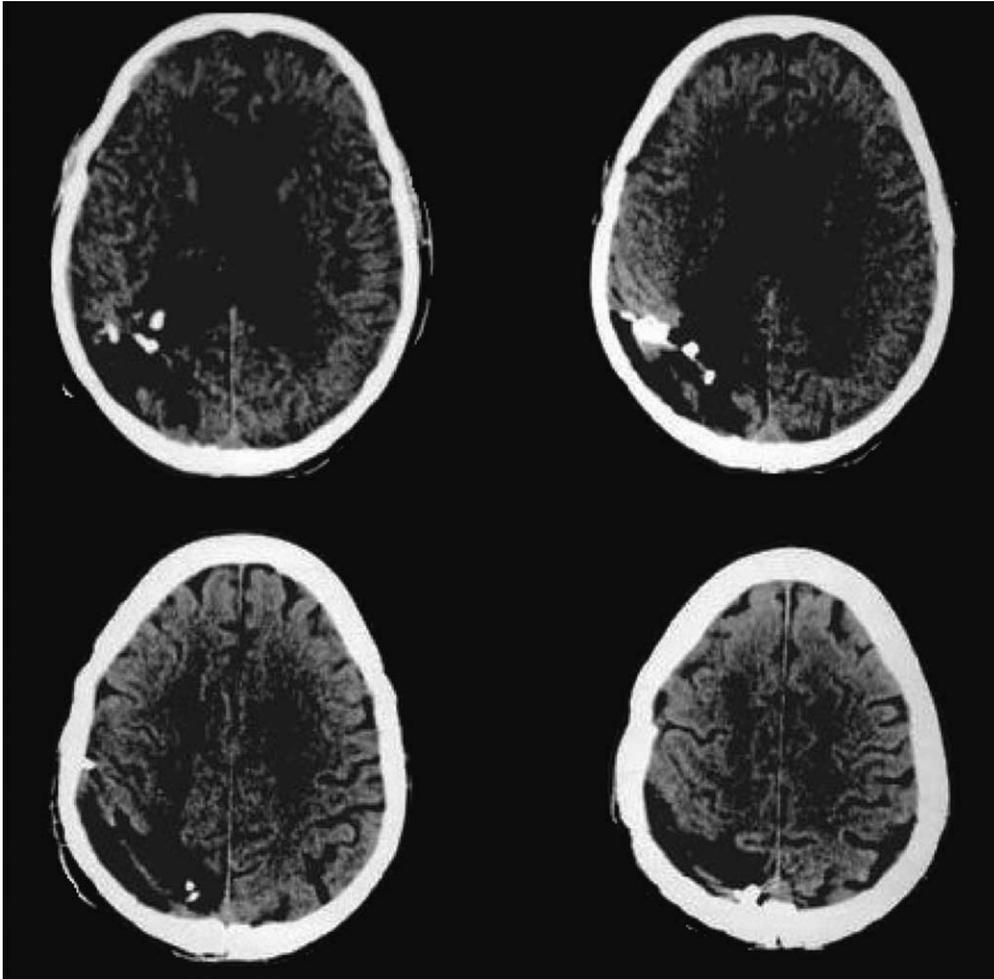
Fig. 7. CT scan for patient RB revealing damage to the right parietal and occipital region.

while the rightward one appeared in the right hemifield. In pair 3, both stimuli appeared in the right (ipsilesional) hemifield. In all cases the two stimuli were approximately 4° apart. Thus, the right stimulus in pair 1 occupied the same retinal location ($-2°$) as the left stimulus in pair 2 (called position B), and the left stimulus in pair 3 occupied the same location ($2°$) as the right stimulus in pair 2 (called
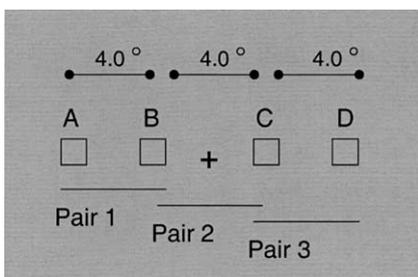
Fig. 8. Schematic depiction of spatial layout of Experiments 4 and 5. Double stimuli pairs could appear at three positions (pairs 1–3) and single stimuli could appear at four locations (A–D). Again, no boxes actually appeared in the display.

position C), allowing for the additional analysis of these 'overlapping' positions.

There were six possible SOAs for the double stimulus trials (20 trials per SOA condition): -300, -100, 0, 100, 300, and 500 ms. SOAs were randomly interleaved within blocks. Again, although this distribution of SOAs may have biased RB to attend to the right, the SOAs were consistent across positions. There were five blocks of 88 trials, administered over 2 days. The 440 total trials consisted of 80 single stimulus trials (20 per possible stimulus location) and 360 double stimuli trials (20 per position per SOA). Single and double stimulus trials were randomly interleaved within blocks.

Instructions and procedure were the same as in previous experiments. Error rates (omissions and incorrect identifications) were recorded for each condition, and trials where RB moved his eyes were discarded and not replaced.

5.3. Results

Single stimulus performance was significantly different at the four possible stimulus locations ($\chi^2(3) = 11.85$,
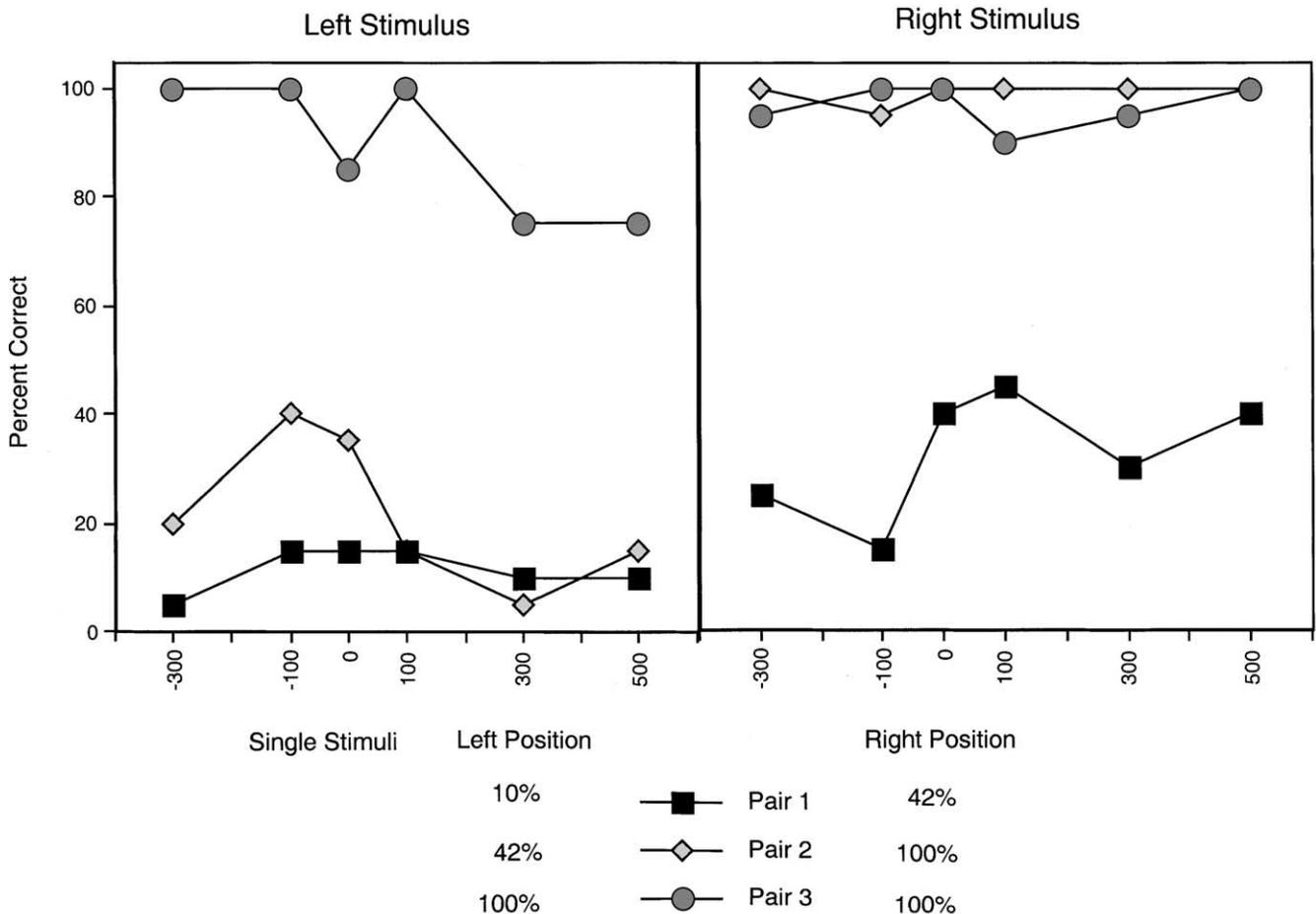
Fig. 9. Percentage correct report of the left and right letters from double stimuli trials as a function of SOA in Experiment 4. Percent correct for single stimulus trials is included for comparison. Stimulus location was unpredictable since location varied randomly across trials.

$P = 0.0079$), as shown in Fig. 9. There were no errors for any single stimuli in the right (ipsilesional) hemifield, whereas in the left field there were more errors for position B (42%) than for the more eccentric position A (10% correct) ($\chi^2(1) = 5.26$, $P = 0.022$).

A loglinear analysis of the double stimuli error rates revealed significantly more errors for left than for right stimuli ($\chi^2(1) = 20.58$, $P < 0.0001$) and for stimuli in the left versus right hemifield ($\chi^2(1) = 73.38$, $P < 0.0001$). There was neither a main effect of SOA ($\chi^2(5) = 1.85$, $P = 0.87$) nor an interaction with position ($\chi^2(10) = 4.01$, $P = 0.95$). The three-way side by position by SOA interaction was not significant ($\chi^2(10) = 5.65$, $P = 0.84$).

A loglinear analysis of the left stimuli yielded a significant effect for position ($\chi^2(2) = 30.48$, $P < 0.0001$). A logistic regression of these data confirms that pairs 2 and 3 yielded much lower error rates than pair 1. The odds ratio for position 2 was 0.37 ($\chi^2(1) = 8.73$, $P = 0.003$), and for position 3 it was 0.01 ($\chi^2(1) = 115.30$, $P < 0.0001$). The error rates also suggest that in those cases when performance was not at ceiling or floor, performance was worse at some SOAs than at others. However, the

loglinear analysis showed no significant effect for SOA ($\chi^2(5) = 9.13$, $P = 0.10$), nor a significant position by SOA interaction ($\chi^2(10) = 7.67$, $P = 0.66$). Although there is no main effect for SOA, given the importance of the window around 300–900 ms in Experiments 1–3, we explored the effects of the logistic regression analysis in this range and found that the 300 and 500 ms SOAs were the only ones that produced more errors than the single stimulus baseline rate. The odds ratios for 300 and 500 ms were high (7.21 and 5.02, respectively), and interestingly, these were the only two odds ratios with significant P-values ($\chi^2(1) = 11.54$, $P = 0.0007$ and $\chi^2(1) = 8.17$, $P = 0.0043$).

A loglinear analysis of the right stimuli similarly showed a significant effect of position ($\chi^2(2) = 44.37$, $P < 0.0001$), but not of SOA ($\chi^2(5) = 0.78$, $P = 0.97$) nor of an interaction ($\chi^2(10) = 4.58$, $P = 0.92$). A logistic regression confirmed that performance for positions 2 and 3 (in which the right stimuli fell in the right hemifield) was much better than for position 1 (in which the right stimulus fell in the left hemifield). The odds ratios for positions 2 and 3 were 0.003 ($\chi^2(1) = 31.20$, $P < 0.0001$) and 0.01 ($\chi^2(1) = 61.10$,

$P < 0.0001$), respectively. Although there was no main effect for SOA in the loglinear analysis, it is notable that the logistic regression only yielded one significant odds ratio, 4.19 ($\chi^2(1) = 4.68$, $P = 0.031$), which was for the right-first SOA of -100 ms.

5.4. Discussion

The results of Experiment 4 are straightforward: LVF stimuli were often neglected, even if they appeared alone, with performance worse at more contralesional positions. These data are consistent with those of Smania et al. using single stimuli trials. In the case of double stimuli, both the left and right stimuli suffered in the left hemifield relative to the other positions. However, the disparity between the left and right stimuli was greatest in the bilateral condition, when the two stimuli were in different hemifields (22% left, 99% right: 93 error difference), compared to that of pair 1 (12% left, 33% right: 25 errors), and pair 3 (89% left, 97% right: 9 errors). This suggests that competition for selection between stimulus pairs separated by the vertical meridian is more unbalanced than similar pairs that lie in the same hemifield, even when both are weakly activated as in the left field.

In addition to the effect of field and side of the pair, SOA also influenced performance as seen in the distinct trend toward a main effect of SOA for left stimuli in double stimulus trials. When a right stimulus preceded the left stimulus by about 300–500 ms, the left stimulus was more likely to be omitted than under any other SOA condition.

Although there are some differences between the results from RB and LD, what is striking is the clear presence of extinction of the left stimulus in the 300–500 ms range. Notwithstanding the fact that RB performs better on RVF stimuli than does LD and that LD could only be tested for positions in the RVF, the fact that they both extinguish more contralesional stimuli and that the time course of the extinction is in the same, positive range, lends strength to the claim that both spatial and temporal influences are important in determining the nature of the stimulus competition and the outcome thereof.

6. Experiment 5

This final experiment examines RB's performance when location is predictable and allows us to evaluate whether predictability manifests in an increased left–right disparity, as observed with LD, and whether this disparity is influenced by stimulus position.

6.1. Method

The same method was used as in Experiment 4 except that position was held constant in three separate blocks of trials. Each block contained 160 trials, administered over 2 days. The 480 total trials consisted of 360 double stimulus trials and 120 single stimulus trials. There were 40 more single stimulus trials than in Experiment 4, because separate single stimulus baseline rates were recorded for each of the three blocks. Since the three positions corresponding to the three blocks included two "overlapping" locations (locations B and C, in Fig. 8), single stimulus baselines were recorded for these locations twice. Double and single stimulus trials were again randomly interleaved within blocks.

6.2. Results

Three sets of single stimulus error rates were obtained, one set for each double stimuli position, as shown in Fig. 10. Note that due to the overlap between positions, two different baseline rates were recorded for positions B and C.

Although there is a numeric trend for performance to be better for position A than for position B, 60 versus 35%, this difference does not hold statistically ($\chi^2(1) = 2.45$, $P = 0.12$). This is rather different from the single stimulus performance in the previous experiment in which performance for the left stimulus improved monotonically from left to right. For position B, the baseline rate was significantly different depending on whether the single stimuli were presented in a pair 1 block (all stimuli left of fixation) or a pair 2 block (stimuli bilateral): 75 versus 35% correct ($\chi^2(1) = 6.07$, $P = 0.014$). RB's performance did not improve steadily from left to right as it did in Experiment 4. It appears then that top–down attention or expectancy affects even single stimulus performance such that a stimulus in the same retinal position is interpreted as occupying a relative left or right position depending on the position of the other stimuli in the same block of trials. The two rates measured for position C were not found to be significantly different: 95 versus 100% ($\chi^2(1) = 0.50$, $P = 0.48$), and there was no disparity in performance between the two pair 3 stimuli, C and D (both 100% correct).

A loglinear analysis of the double stimuli error rates showed a significant effect of stimulus side ($\chi^2(1) = 18.44$, $P < 0.0001$), as seen in Fig. 10. As before, the disparity between left and right stimulus performance was much greater for pair 2 (40% correct left, 96% right: a difference of 68 errors) than for pair 1 (47% left, 81% right: 41 errors) ($\chi^2(1) = 125.94$, $P < 0.001$) or pair 3 (93% left, 99% right: a difference of 7 errors) ($\chi^2(1) = 146.45$, $P < 0.001$).

A loglinear analysis of the left stimuli only showed significant effects for position ($\chi^2(2) = 21.25$, $P < 0.0001$) and SOA ($\chi^2(5) = 12.88$, $P = 0.023$), but not for their interaction ($\chi^2(10) = 8.78$, $P = 0.55$). Unlike in Experiment 4, the error rate for pair 1 (47% correct) did not differ from that of pair 2 (40% correct: $\chi^2(1) = 1.08$, $P = 0.298$) although it did differ from pair 3 (odds ratio 0.05: $\chi^2(1) = 53.00$, $P < 0.0001$).

The logistic regression also showed that the only two SOAs that produced error rates significantly different from baseline were the 300 and 500 ms SOAs with more errors

Left Stimulus   Right Stimulus
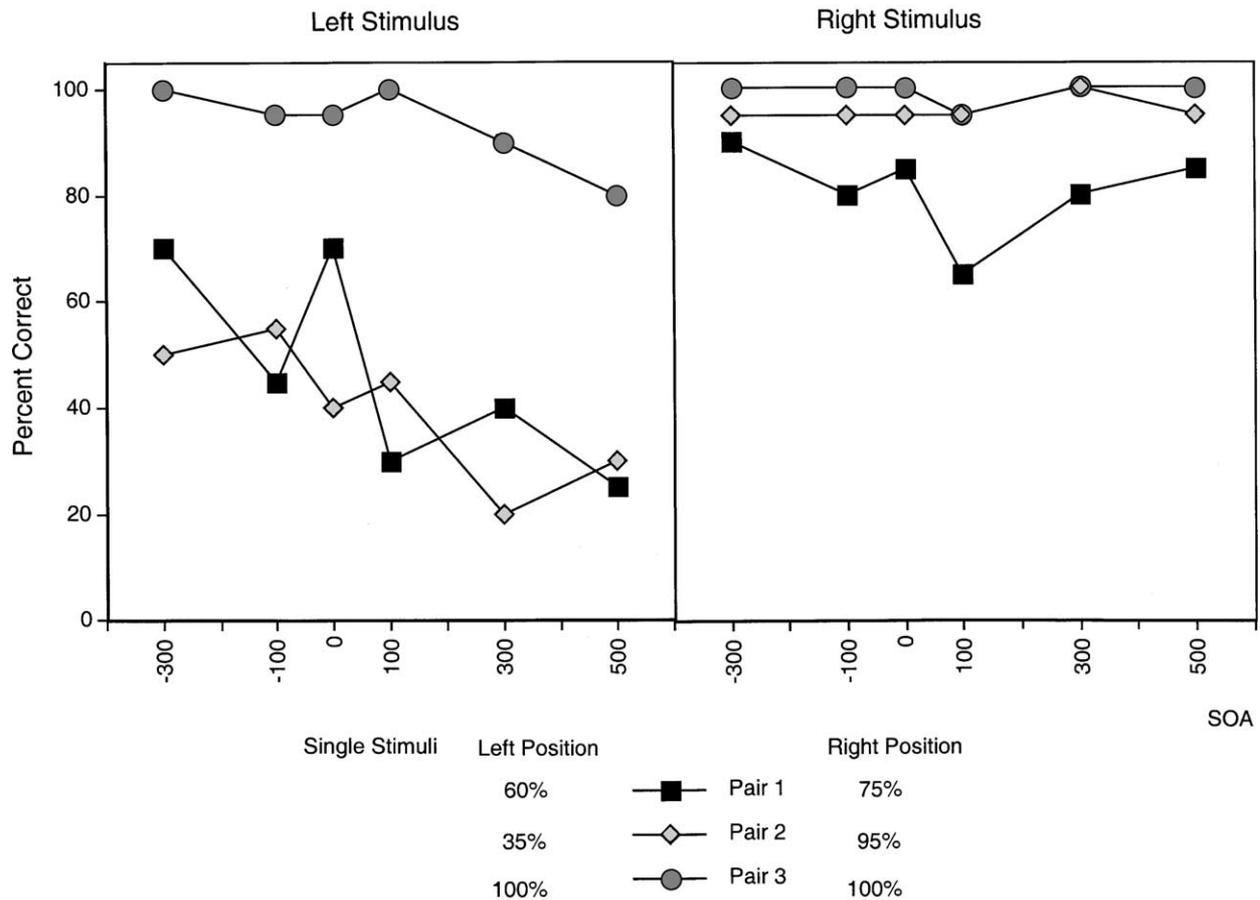
Fig. 10. Percentage correct report of the left and right letters from double stimuli trials as a function of SOA in Experiment 5. Percent correct for single stimulus trials is included for comparison. Stimulus location was predictable since location was blocked. Note that in contrast to Experiment 4 (see Fig. 9), performance was lowest for the left position of pair 2, which was immediately to the left of fixation.

with the latter SOA. The odds ratio for 300 ms was 2.37 ($\chi^2(1) = 3.77$, P=0.052) and the odds ratio for 500 ms was 3.24 ($\chi^2(1) = 6.70$, $P = 0.0096$). At these SOAs extinction appears to have been induced even for the left stimulus within the right hemifield (pair 1), and seems to have been exacerbated for the left hemifield (pair 1) and bilateral (pair 2) stimuli.

A loglinear analysis of the right stimuli only showed a significant effect of position ($\chi^2(2) = 13.63$, $P = 0.0011$), but not SOA ($\chi^2(5) = 3.07$, $P = 0.69$) nor their interaction ($\chi^2(10) = 2.25$, $P = 0.99$). A logistic regression confirmed that fewer errors were made for pairs 2 and 3, compared to pair 1. The odds ratio for pair 2 was 0.173 ($\chi^2(1) = 13.79$, $P = 0.0002$), and the odds ratio for pair 3 was 0.03 ($\chi^2(1) = 12.20$, $P = 0.0005$).

6.3. Comparison of Experiments 4 and 5

RB's overall correct identification rate, collapsed across all positions, SOAs and stimulus types (left and right) was significantly better in Experiment 5 (76%), when target location was predictable, compared to 59% in Experiment 4,

when it was not ($\chi^2(1) = 44.89$, $P < 0.0001$). This was true both for left (60 versus 41% correct, $\chi^2(1) = 26.12$, $P < 0.0001$), and right stimulus performance (92 versus 76% correct, $\chi^2(1) = 30.85$, $P < 0.0001$).

However, these differences were entirely due to improved performance for stimuli in the LVF. An examination of all LVF stimuli (all stimuli appearing at positions A and B, regardless of whether they were left or right stimuli) reveals that performance improved from 22 to 56% correct when location was made predictable ($\chi^2(1) = 82.24$, $P < 0.0001$). In contrast, performance for all RVF stimuli (those appearing at positions C and D) barely improved from 95 to 96% correct ($\chi^2(1) = 0.52$, $P = 0.47$).

The disparity between left and right stimulus performance was also affected by predictability. For pair 1, in which both stimuli were in the LVF, this disparity became greater when stimulus location was predictable, much as it did for LD in Experiments 2 and 3. The pair 1 disparity in Experiment 4 (12% left, 33% right: a difference of 25 errors) was significantly smaller than the pair 1 disparity in Experiment 5 (47% left, 81% right: 41 errors) ($\chi^2(1) = 4.19$, $P = 0.041$). Making location predictable improved performance overall,

but it also had the effect of widening the disparity between left and right stimuli in the same visual field.

For pair 2, where stimuli were in opposite hemifields, the disparity became smaller when stimulus location was predictable, although this was probably due to a ceiling effect. The pair 2 disparity in Experiment 4 (22% left, 99% right: 93 errors) was significantly different from the pair 2 disparity in Experiment 5 (40% left, 96% right: 67 errors) ($\chi^2(1) = 5.39$, $P = 0.020$). However, since the right stimulus was in the RVF in this case, the lessening of the disparity is simply due to the improved left stimulus performance. The left–right disparity is negligible for pair 3, in which both stimuli appeared in the RVF and performance was at ceiling.

6.4. Discussion

The results of Experiment 5 allow us to compare RB's performance for LVF, bilateral, and RVF stimulus pairs when performance was not at floor in any condition. There was a trend for single stimulus performance to be worst *not* at the more contralesional position (position A), but instead at the position closer to fixation (position B). Similarly, single stimulus performance improved from Experiments 4 to 5 for position A, but not for position B.

Related to this is the fact that the greatest disparity in left–right stimulus performance occurred for pair 2 (bilateral), and not for pair 3 (LVF). Indeed, left stimulus performance appeared to be slightly worse (or at least equal) at position B than at position A. This contradicts the established phenomenon that performance steadily decreases at more contralesional positions. This suggests that competition for selection is more uneven when two stimuli are in opposite hemifields, compared to two stimuli separated by the same distance in the same hemifield. Again, positive SOAs produced more severe deficits. Presenting the stimuli at SOAs of 300–500 ms can even bring RB's performance below ceiling for RVF stimuli. Finally, making location predictable increases the left–right disparity especially for stimuli in the LVF.

7. General discussion

The goal of the five studies we have conducted is to examine the influence of spatial position and temporal interval on the ability of two patients with hemispatial neglect to report the identity of letters. Both single- and double-stimulus trials were run, with the former serving as a baseline to determine the effect of space and time on report in a double-stimulus trial. The results indicate that both spatial and temporal factors significantly affect the behavior of the patients. First, the horizontal position of the stimuli within a hemifield determines the severity of the left-neglect deficit. Behavioral report also differs depending on whether stimuli appear within one hemifield, or span the midline and occupy both hemifields. Second, the temporal separation of the two stimuli

profoundly affects patients' ability to report the left stimulus, and this holds true even when the stimuli appear in the RVF where these patients typically do not make extinction errors. Moreover, the spatial and temporal factors appear to interact: the further ipsilesional the stimuli, the shorter the temporal interval that produces poorest report of the left stimulus. A final factor that modulates behavior is the engagement of top–down, directed attention. By blocking trials so that subjects could predict the location of the stimulus, the report of single stimuli improves. Interestingly, however, the disparity in report of left versus right stimuli is exaggerated under this manipulation, reflecting the increased competition when a smaller region of space is attended.

All of these phenomena can be accounted for by a gradient of attention (or representation) that incorporates biased competition. In essence, we propose that neurons in a group representing the same location mutually excite each other, whereas groups of neurons representing separate locations mutually inhibit each other, as in the Cohen et al. [8] model. This pattern of interaction has two main consequences. First, stimuli appearing at rightward regions, represented by many neurons, will tend to suppress the activity of leftward stimuli represented by fewer neurons. Second, the collective activity of a group of neurons representing a right stimulus will tend to rise more quickly than a group representing a left stimulus, since its larger number of neurons will provide more mutual excitation than a smaller group. In this way, both spatial and temporal influences on extinction can be accounted for within the same theoretical framework and, indeed, emerge from the same underlying impairment. Below we address how this general framework explains the more detailed aspects of our findings.

7.1. Spatial influences

7.1.1. Within-field gradient

Consistent with previous findings, Experiments 1–3 showed that performance was poorer for a left than right stimulus in the RVF. Interpreted in terms of biased competition, the horizontal separation of the left and the right stimuli set up a disparity in competitive weights between them, such that the left stimulus has a lower weight than the right stimulus. Importantly, report of the left stimulus improves at more ipsilesional positions, consistent with the gradient theory.

However, it is important to note that the horizontal separation of stimulus pairs in Experiments 2 and 3 was the same for all positions. If the gradient has a uniform slope across the RVF, then one might expect no difference in the weight disparity for different locations, and thus no difference in performance. One could simply assume that the gradient does not have a uniform slope, but whether this is the case or not, we think that our results can be feasibly accounted for by a uniform gradient.

Fig. 11 is a schematic diagram of the hypothesized RVF gradient of attentional ability. The abscissa plots horizontal
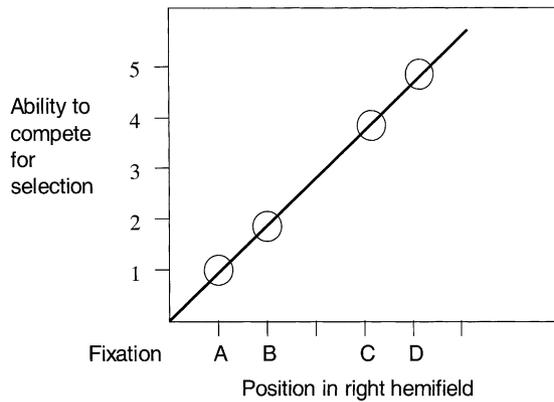
Fig. 11. Schematic diagram of a hypothesized RVF gradient of attentional ability. The abscissa plots horizontal eccentricity. The ordinate plots competitive weight in arbitrary units. The ratio of weights for a pair of stimuli appearing at points A and B is 1/2, which is a smaller value than the ratio for a pair appearing at C and D (4/5). Although for both pairs the weight difference is the same (1 U), the weight ratio increases with increased distance from fixation. It is proposed that a higher ratio represents greater competitive equality between two stimuli, and thus a lower probability that the left stimulus will be extinguished.

Fig. 12. Schematic diagram of the hypothesized gradient of attentional ability showing its distribution across the visual field. It is proposed that a contralesional-to-ipsilesional gradient is present within both hemifields, and that there is a discontinuity at the vertical meridian.

eccentricity, and the ordinate represents competitive weight values in arbitrary units. The diagonal line shows that positions towards the right are associated with higher weights. Points A and B, and C and D represent two pairs of stimulus locations. Since A and B, and C and D are the same distance apart, the difference in competitive weight is the same for both pairs: one unit. However, the ratio of weights is different for the two pairs: 1/2 versus 4/5. In terms of proportionality of weights, A and B are more disparate than C and D. We propose that this proportional relationship is important in determining the outcome of mutually inhibitory competition for selection.

7.1.2. Hemifield effect

The hemifield in which stimuli appear may also influence the severity of the deficit; performance for stimuli appearing in the RVF is much better than performance for LVF stimuli. The disparity between RVF and LVF performance may be greater than can be accounted for by a uniform contralesional-to-ipsilesional gradient of attentional ability that spans the entire visual field; consider single stimulus performance in Experiment 4, in which the performance difference for letters $4°$ apart within the same hemifield was much smaller than the difference for letters the same distance apart but in opposite hemifields.

Psychophysical evidence shows that both the vertical and horizontal meridians form boundaries of the regions in which attentional precueing will aid or detract from stimulus detection [15]. Although this difference in performance is not ordinarily noticeable in normal subjects, PP damage may bring the vertical meridian boundary to the fore. However, this study did not probe interhemisphere differences comprehensively, and the hemifield effects we report
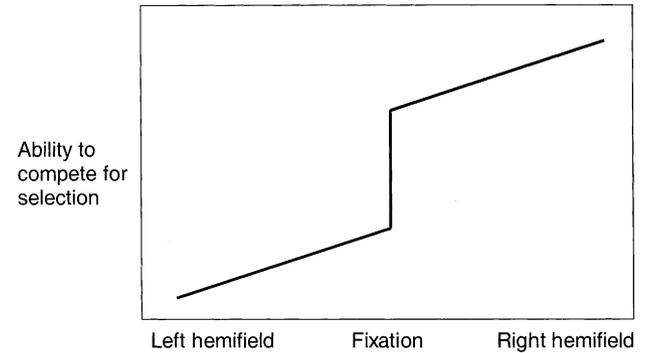
should be investigated further as a consideration for future work.

It is fairly clear that if extinction is caused by a gradient of attentional ability, then this gradient extends into both hemifields. Patient RB missed stimuli on the relative left both in the RVF and LVF. Therefore, we propose that the attentional abilities of PP patients follow the general scheme illustrated in Fig. 12. In this scheme, attentional ability follows a contralesional-to-ipsilesional gradient within both hemifields, and the overall ability level increases sharply at the vertical meridian. We cannot speculate on the exact slope of the gradient in either hemifield, since we measured only two points in each hemifield in patient RB. The gradient may or may not be linear, and the slopes describing the gradients in the two hemifields may or may not be equal, although Fig. 12 depicts them this way for the sake of simplicity. More precise and thorough measurements, involving the sampling of many points within each hemifield, would be required to draw conclusions about this.

Our conception of the gradient underlying the patients' performance is consistent with aspects of at least two theories of neglect. Our results support the Rizzolatti et al. hypothesis that the left hemisphere's representation of space follows a contralesional-to-ipsilesional gradient, and they also support the idea put forth by Heilman and Van Den Abell [14] that the left hemisphere primarily represents the contralateral hemifield [9].

7.2. Temporal influences

A robust and replicable finding across both patients is that maximal extinction occurs at positive SOAs, and almost always at SOAs of 300 ms or longer. Even when pairs of stimuli were presented in the RVF, and the patients' performance was otherwise at ceiling levels, presenting the left stimulus 300 ms or more after the right stimulus produced severe deficits.

These results can easily be explained in terms of biased competition for attentional selection. This argument has been

well made by a number of authors recently to explain PP patient performance, notably di Pellegrino et al. [10], and Ward et al. [31]. Essentially, they argue that stimuli at positions represented by larger cell populations will win out over stimuli represented by fewer cells. The above studies presented all stimuli bilaterally, and explained the disparity in competitive ability in terms of the difference between cell populations in the two parietal hemispheres. To explain our within-hemifield results, the only additional assumption necessary is the existence of a horizontal gradient of attentional ability across the entire visual field.

Our results are different from those of di Pellegrino et al. [10], since no extinction occurred at negative SOAs, even in conditions where stimuli were presented bilaterally. However, this could be due to the fact that patient FB performed blocks of exclusively double stimuli trials. This may have led him to attend more toward the right even on negative (left-first) SOAs, since a stimulus appeared at the rightward position on every trial (di Pellegrino, personal communication). Since FB's instructions were to report both of the letters presented, he could potentially boost his performance by attending preferentially to the rightward stimulus. In effect, this kind of a bias would allow a left neglect patient to cut his losses by attending to an easy-to-identify stimulus at the cost of ignoring a difficult-to-identify one.

However, it needs to be noted that at least one other study has shown maximal extinction at 0 ms SOA, like di Pellegrino et al.'s study. Baylis et al. [1] presented both single (unilateral) and double (bilateral) stimulus trials to neglect patients, and found maximal extinction when the stimuli appeared simultaneously on double trials. Different details of the system of stimulus presentation clearly influence the results of experiments in this vein, so the results of such studies, including the present one, must be interpreted with this fact in mind.

In this study, LD's and RB's result suggest that stimuli presented simultaneously and even at short SOAs are still able to compete rather equally for selection. It seems that the right stimulus needs to be the sole stimulus present for about 300 ms before neurons representing it build up enough activity to inhibit the processing of the left stimulus. The SOA-dependent pattern of performance obtained presumably reflects the time course of the processing necessary for the patients to detect the stimulus. Before this processing is complete, activity of neurons processing other stimuli can inhibit the processing.

Note that the temporal effect interacts with spatial position: Experiment 2 shows that SOAs at which LD extinguished left stimuli became increasingly shorter as stimuli were presented more ipsilesionally (at least when stimulus location was unpredictable). Since the PP representation towards the ipsilesional end of the RVF is especially high, we think that the shortening of this extinction period reflects the quicker activity rise time inherent in regions represented by large numbers of PP neurons. The larger numbers of neurons allow for greater mutual excitation, which results in faster activation. Since processing is completed quickly at these regions, the temporal window during which the left stimuli can be extinguished is short.

When both stimuli are in the RVF, the 300 ms "head start" is crucial for the right stimulus to extinguish the left. Thus the necessity of a several hundred millisecond period of activity build-up seen in Rorden et al. and di Pellegrino et al. studies also applies to stimuli that appear within the same hemifield. Similar "head start" effects are also present in the literature on attentional capacity in normal subjects. In many attentional blink studies, the maximum deficit occurs not when the second target immediately follows the first, but when the second target appears 200–500 ms after the first [6]. This phenomenon, called "lag-1 sparing" [30], is modulated by the precise demands of the RSVP task.

Interestingly, frontal lesions in animals can also produce a deficit for which a substantial head start is required for a contralesional stimulus to be selected. Schiller and Chou [28] found that monkeys with unilateral anterior arcuate lesions seldom made saccades to the contralesional target of a pair of visual targets. The contralesional target required a head start of 100 ms before the monkeys would favor it by making a saccade to it on more than 50% of trials. While the cortical region and task involved in Schiller and Chou's study obviously differ from those of the present study, we cite it as an example of how unilateral damage can result in visual deficits expressed in the temporal dimension.

7.3. Top–down influences

Finally and interestingly, the report of letters is affected by task demands or expectancies. We have shown that directing attention to a location improves processing for that location and this is consistent with findings reporting a reduction in RT to detect single flashes of light in PP patients [29]. Despite this improvement in performance, in double stimuli trials, top–down attention can result in even greater left–right disparity and poorer left single stimulus performance than is the case when position is uncertain. While directing attention to a location may be able to boost the processing activity of neurons associated with that location [12], activity for the entire attended region of the gradient will rise. This is reflected by the fact that single stimulus performance is higher in Experiment 5 (stimulus locations predictable) than in Experiment 4 (locations unpredictable). However, activity will probably not be boosted uniformly across the attended region, especially if this region is large enough to fit a pair of stimuli. A version of the competition that takes place when stimuli are actually visible may occur in this region, even when the stimuli are absent. Activity in the right portion of the region will be greatly enhanced, while the left portion will be relatively suppressed, in a rich-get-richer, poor-get-poorer fashion [21]. The activity of the left portion will still be raised above baseline levels, but the disparity in activity between the left and right portions will also increase.

This idea is supported by our experimental data. The left–right disparity for double stimuli was much greater in Experiment 5 (locations predictable) than in Experiment 4 (unpredictable). While single stimulus performance was higher in Experiment 5 than in Experiment 4, single stimulus performance did not increase when RB needed to attend to a region spanning the midline, a region where there is likely to be an especially high left–right gradient.

The left–right disparity also became greater for patient LD in Experiment 3 (predictable) compared to Experiment 2 (unpredictable). We think it is better to characterize LD's Experiment 3 drop in left stimulus performance as a case of *increased left–right disparity*, rather than merely worse performance. Since LD's performance was generally at ceiling levels, because all stimuli appeared in the RVF, such an increase in disparity could only be expressed as a drop in left stimulus performance. In summary, applying top–down attention to a gradient may raise overall processing ability, but will enhance the disparity in competitive weights between the left and right ends of the attended region.

Our interpretation explains why LD's left stimulus performance drops when stimulus locations are predictable. However, it remains puzzling why predictability would also eliminate the SOA-position interaction seen in Experiment 2. In Experiment 3 nearly all of LD's errors were committed in the same 300–900 ms window, across all positions. It is also unclear why right stimulus performance would drop in Experiment 3, in addition to the widening of the left–right performance disparity.

In summary, we argue that a gradient of neural representation, characterized by a left-to-right slope with a discontinuity at the vertical meridian, can explain the spatial, temporal, and top–down attentional effects observed in these experiments. Together with evidence from other recent experiments, this study illustrates how an underlying neural phenomenon, an uneven distribution of spatial receptive fields, can be expressed in multiple facets of behavior. The deficits of patients with hemispatial neglect must be considered in all of their dimensions in order to provide a clear understanding of these disorders.

Acknowledgements

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