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Orienting of attention in left unilateral neglect

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Abstract

After right posterior brain damage, patients may ignore events occurring on their left, a condition known as unilateral neglect. Although deficits at different levels of impairment may be at work in different patients, the frequency and severity of attentional problems in neglect patients have been repeatedly underlined. Recent advances in the knowledge of the mechanisms of spatial attention in normals may help characterizing these deficits. The present review focuses on studies exploring several aspect of attentional processing in unilateral neglect, with particular reference to the dichotomy between 'exogenous', or stimulus-related, and 'endogenous', or strategy-driven, orienting of attention. A large amount of neuropsychological evidence suggests that a basic mechanism leading to left neglect behavior is an impaired exogenous orienting toward left-sided targets. In contrast, endogenous processes seem to be relatively preserved, if slowed, in left unilateral neglect. Other component deficits, such as a general slowing of the operations of spatial attention, might contribute to neglect behavior. These results are presented and discussed, and their implications for hemispheric specialization in attentional orienting and for the mechanisms of visual consciousness are explored. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Spatial attention; Exogenous orienting; Endogenous orienting; Unilateral neglect; Brain damage

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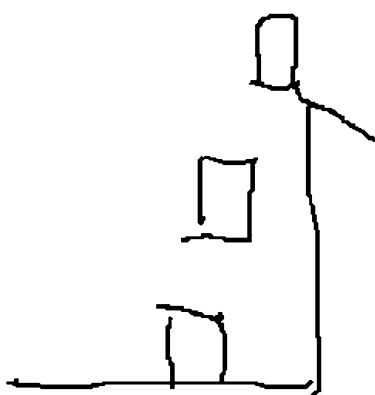
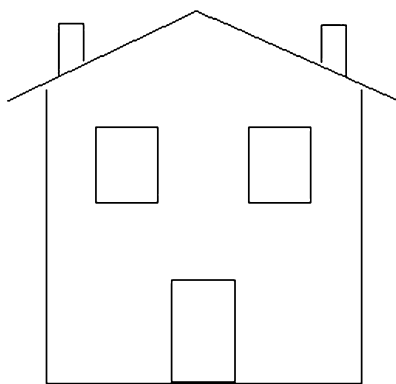


Fig. 1. Copy of an outline drawing by a left neglect patient.

1. Introduction

Left unilateral neglect is a severe disabling condition resulting from right-hemisphere damage, usually centered on the inferior parietal lobule [1] or on the superior temporal lobe [2]. Neglect patients ignore events occurring on their left (Fig. 1), sometimes to the dramatic extent of ‘forgetting’ to eat from the left part of their dish or of bumping into obstacles situated on their left.

Unilateral neglect negatively affects patients’ motor recovery [3] and social rehabilitation. Deficits at different levels of impairment may be at work in different patients; however, the frequency and severity of attentional problems in neglect patients have been repeatedly underlined [4]. A precise characterization of these deficits can shed light on how brain mechanisms process spatial information, and is necessary in order to devise rational strategies of rehabilitation. Recent advances in the knowledge of the mechanisms of spatial attention in normals may help to characterize these deficits. The present review focuses on studies which explore several aspects of attentional processing in unilateral neglect, with particular reference to the dichotomy between ‘exogenous’, or stimulus-related, and ‘endogenous’, or strategy-driven, orienting of attention. With

reference to this distinction, Gainotti suggested that a basic mechanism leading to left neglect behavior might be a relatively selective deficit of exogenous orienting towards left-sided targets [5,6]. A large amount of neuropsychological evidence is now available which is consistent with this proposal. Moreover, a number of studies have shown that endogenous processes are relatively preserved, if slowed, in left unilateral neglect. The present review aims at discussing these results and at exploring the implications of such a model of left neglect for hemispheric specialization for attentional orienting and for the mechanisms of visual consciousness.

2. Varieties of attention

The concept of attention refers to a heterogeneous set of processes that aim to maintain coherent behavior in the face of irrelevant distractions. James [7] observed that “my experience is what I agree to attend to... Without selective interest, experience is an utter chaos” (p. 402). In a recent review, Parasuraman [8] identified at least three independent but interacting components of attention: (1) *selection*, that is, mechanisms determining more extensive processing of some input rather than other; (2) *vigilance*, the capacity of sustaining attention over time; (3) *control*, the ability of planning and coordinating different activities.

Most attentional accounts of neglect postulate a problem in spatial orienting of selective attention. The concept of spatial selective attention refers operationally to the advantage in speed and accuracy of processing for objects lying in attended regions of space as compared to objects located in non-attended regions [9,10]. Even very simple artificial organisms display orienting behavior when their processing resources are insufficient to process the whole visual scene in parallel [11]. In addition to impairments of spatial selective attention mechanisms, also non-spatial attentional deficits have been described in unilateral neglect (Section 4.5).

2.1. Selective attention

Our visual system is overloaded constantly with information from the environment, hence the advantage of efficient selective mechanisms for directing resources towards relevant stimuli (see Refs. [12,13] for some logical and philosophical problems concerning selective attention and their possible solutions). When several events compete for limited processing capacity and control of behavior, attentional selection may resolve the competition. In their influential neurocognitive model of selective attention, Desimone and Duncan [14] proposed that competition is biased towards some stimuli over others. Two types of processes determine this bias: bottom-up processes are related to the sensory salience of stimuli; top-down processes result from the current behavioral goals. Thus, in the Desimone and Duncan [14] model of selective attention, a fundamental distinction is made between

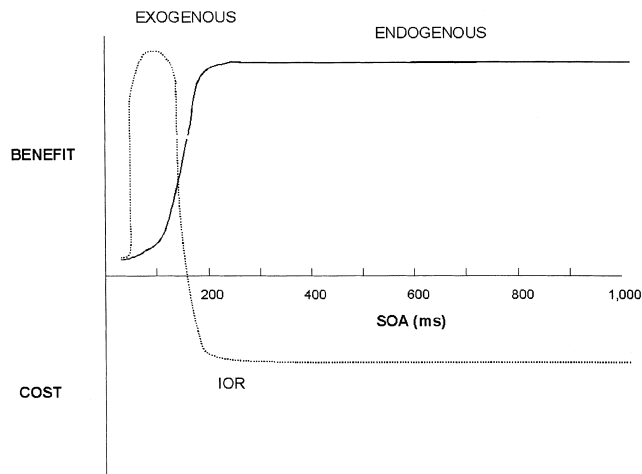


Fig. 2. Time course of the costs and benefits associated with exogenous and endogenous orienting of attention toward a cued location (modified from Ref. [30]). SOA, stimulus-onset asynchrony.

stimulus-related and goal-driven operations of attention. This distinction is detailed in Section 2.2.

2.2. The exogenous/endogenous dichotomy

To successfully cope with a continuously changing environment, an organism needs mechanisms that (a) allow for the processing of novel, unexpected events, that could be either advantageous or dangerous, in order to respond appropriately with either approaching or avoidance behavior; (b) allow for the maintenance of finalized behavior in spite of distracting events [15]. It is thereby plausible that different attentional processes serve these two partially conflicting goals. Attention can be directed to an object in space either in a relatively reflexive way (e.g. when a honking car attracts the attention of a pedestrian) or in a more controlled mode (e.g. when the pedestrian monitors the traffic light waiting for the 'go' signal to appear). This fundamental distinction was explicitly recognized by James [7], who distinguished between 'passive, reflex, non-voluntary, effortless' attention and 'active and voluntary' attention (p. 416). More recently, this distinction has been variously referred to as reflexive/voluntary, bottom-up/top-down, stimulus-driven/goal-directed or strategy-based, or exogenous/endogenous (see Ref. [16] for review). It is important to note that, logically speaking this dichotomy must be relative rather than absolute. As Pashler notes [17, p. 410], a strictly defined exogenous mechanism would not be influenced by psychological processes as attentional orienting. On the other hand, it is possible that, to endogenously direct one's attention towards an object, this must previously have been selected as such by exogenous processes (Sections 2.4 and 2.5). Endogenous orienting by itself can only facilitate location-based, and not object-based, processing [18]. Thus, exogenous and endogenous mechanisms normally interact during visual exploratory

behavior. With reference to the previously noted needs for responding to novelty while resisting to distraction, exogenous orienting processes are good candidates for being involved in drawing attention to novel events [19,20], both by enhancing the perceptual discrimination of the attended object [21] and by inhibiting repeated orientations towards the same object (inhibition of return (IOR): see Section 2.3). Endogenous orienting processes, on the other hand, would be responsible for directing the organism's attention towards its target despite the presence of distractors in the environment [22].

The phenomenological dichotomy between exogenous and endogenous orienting received strong experimental support from the Posner reaction time (RT) paradigm, as reviewed in Section 2.3.

2.3. The Posner paradigm

Attention can be oriented in space *overtly*, when eye and head movements align the fovea with the attended region, or *covertly*, in the absence of such movements. Posner and co-workers (see Ref. [9] for review) developed a manual RT paradigm to study the covert orienting of attention. Subjects are presented with three horizontally arranged boxes. They fixate the central box and respond by pressing a key to a target (an asterisk) appearing in one of two lateral boxes. The target is preceded by a cue indicating one of the two lateral boxes. Cues can be either *central* (an arrow presented in the central box), or *peripheral* (a brief brightening of one peripheral box). *Valid* cues correctly predict the box in which the target will appear, whereas *invalid* cues indicate the wrong box. Normal subjects usually show an advantage of valid cue–target trials as compared to invalid trials (cue validity effect). This suggests that the cue prompts an attentional orienting towards the cued location, which speeds up the processing of targets appearing in that region and slows down responses to targets appearing in other locations.

In this paradigm, it is often the case that a large majority (e.g. 80%) of cues are valid; in this case, cues are said to be *informative* of the future emplacement of the target. Alternatively, cues may be non-informative, when targets can appear with equal probabilities in the cued or in the uncued location. Peripheral non-informative cues attract attention automatically, or exogenously [23,24]. This exogenous attentional shift (revealed by a cue validity effect) is typically observed only for short stimulus-onset asynchronies (SOAs) between cue and target. For SOAs longer than ~300 ms, uncued targets evoke faster responses than cued targets [25–27], as if attention was inhibited from returning to previously explored objects. This phenomenon is known as IOR [28], and is often interpreted as reflecting a mechanism which promotes the exploration of the visual scene by inhibiting repeated orientations toward the same locations [26,29]. When peripheral informative cues are used, the cue validity effect persists even at longer SOAs,

thus suggesting that the initial exogenous shift is later replaced by a more controlled, endogenous shift towards the same location [30] (Fig. 2).

This endogenous shift would be motivated by strategic considerations, because subjects know that targets will appear with high probability at the cue location. Recent evidence suggests that this knowledge need not be explicitly acknowledged in the form of a verbal report [31,32], despite the traditional characterization of endogenous orienting as voluntary. The absence of an explicit verbal report, however, does not necessarily imply that the relevant processes are ‘unconscious’ [33,34].

Exogenous, or stimulus-dependent, and endogenous, or strategy-driven, mechanisms of attentional orienting are thus qualitatively different, though highly interactive, processes [24,30,35–37]. Any plausible computational model of attention has to include these two aspects of attentional orienting [38].

2.4. *Orienting of attention to visual objects*

Other studies highlighted the fact that attention cannot only be directed to a region of space, but also (and perhaps more importantly) to visual objects in space. For example, when normal subjects see a rectangle with a line struck through it, they can more easily report two attributes if they belong to the same object (e.g. if the line is dashed and tilted), than if they belong to two different objects (e.g. if the rectangle has a gap and the line is dotted), notwithstanding the fact that the two objects appear in the same spatial region [39]. In such a scenario, objects would be pre-attentively defined in the space array (but see Section 2.5 and Ref. [40] for the poor perceptual characteristics of ‘preattentive’ objects), and attention would then prompt selection of an entire object, and not of its spatial location. The demonstration that attention is directed to objects in space has since been confirmed by many studies (reviewed in Ref. [16]). As a matter of fact, normal observers find it extremely difficult, if not impossible, to covertly attend to a ‘blank’ region of space, where no object is present (see Experiment 2 in Ref. [21]). Object-based allocation of attention seems particularly sensitive to exogenous cues [18]. Thus, exogenous orienting might have a role in constituting an object as a distinct perceptual entity, which in turn can be the target of further attentional orienting, in order, for example, to be identified or discriminated from other objects.

2.5. *Attention and visual object recognition*

Treisman and co-workers [41–43] employed a paradigm substantially different from Posner’s spatial cuing. They asked participants to search for a target among distractors presented in visual display. Results showed that the time for target detection increased substantially with the number of distractors if the target/distractor discrimination involved a conjunction of features (e.g. B/P). On the other hand, if the

task required the simple detection of a discriminating feature (e.g. P/R, in which a diagonal line is present only in R), this display size effect was much less marked. In Treisman’s theoretical framework, this pattern of results indicates that feature conjunction demands focal attention, whose involvement results in a serial search (one item at a time). When a single feature is sufficient to identify the target, the visual system can resort to a parallel search because focal attention is not needed. Global attention to the scene as a whole is enough for feature detection [44]. Efforts have been made to integrate Treisman’s concept of attention as a ‘glue’ binding different object features with Posner’s idea of attention as a ‘beam’ illuminating a region of space [35]. Interestingly, evidence suggests that what seems to integrate features is exogenously oriented attention; endogenous attentional shifts seem to have less effect on feature conjunction. In Briand and Klein’s study [35], participants searched for a target letter (R) with distractor letters that either could give rise to illusory conjunctions (PQ) or not (PB). Results showed that orienting attention in response to central cues (endogenous orienting) showed similar effects for both conjunction and feature search. However, when attention was oriented with peripheral visual cues (exogenous orienting), conjunction search showed larger effects of attention than did feature search (these results were later replicated by Briand [37] with colored forms). The authors concluded that only the attentional systems driven by exogenous orienting have a role in feature integration. These findings suggest that exogenous orienting might play a crucial role in the very constitution of a visual object or, in Kahneman and Treisman’s terminology, in the organization of the episodic representations called ‘object files’ or ‘tokens’ [18,45–47]. On the other hand, Klein [36] argued that endogenous orienting might play a role in earlier stages of perception, such as feature extraction, and in later stages, such as response selection (see also Ref. [48]). Theeuwes et al. [49] refined these notions by showing that a validity effect of exogenous cues may occur even for single, ‘pop-out’ features. The absence of a display size effects for these targets suggests that search is performed in parallel across the entire display, and is not capacity-limited [42]. Thus, Theeuwes et al.’s [49] results suggest a role for exogenous orienting of attention also in the earliest stages of perception, such as the detection of elementary features.

3. *Accounts of left unilateral neglect*

Even a superficial consideration of left neglect behavior immediately suggests that these patients have problems in orienting their attention toward the left side. However, a number of different hypotheses have been proposed to explain left neglect and there is no consensus about its causal mechanisms [50]. In a putative ‘sensation-to-action’ sequence [4], accounts of left neglect can be schematically

summarized as a visual sensory deficit [51], an amputation [52] or distortion [53] of a mental representation of space, a rightward shift of an egocentric frame of reference [54,55], an attentional asymmetry penalizing left events [56] or favoring right-sided ones [57] or a difficulty in programming left-directed movements [58]. Although different impairments may be at work in different neglect patients, some considerations seem to suggest that attentional impairments play a crucial role in most patients, thus justifying the naïve impression that one may get from observing neglect patients' behavior. Considering, for example, the sensory modalities of expression of neglect, evidence indicates that, although neglect is by no means exclusive to visually presented material (which by itself challenges explanations based on a unimodal sensory deficit [51]), when patients' performance in tactile or imagery tests is directly compared with their performance in visuospatial tests, neglect usually results more common and severe for visual than for non-visual stimuli, as tactile [59–61] or imagined [62] events. Also for auditory neglect, it has been shown that blind-folding improves the ability of neglect patients to correctly localize sound stimuli originating on the left [63]. Thus, one can conclude that visually presented stimuli exacerbate neglect [64].

This characteristic of neglect behavior closely parallels the properties of attentional processes. For example, costs and benefits provided by cues are maximal for visual targets and decrease for tactile and even more for acoustic targets [65]. This is perhaps related to the topographical organization of the visual system, which might emphasize the spatial aspects of cueing (see Ref.[66]). Moreover, the organization of the oculomotor system, with the possibility of rapidly bringing into foveal vision objects to be identified, calls for an efficient interface with the perceptual system. Seeing an object 'out of the corner of the eye' typically induces movements of the eyes and of the head to align the object with the retinal fovea, the region with the highest spatial definition for visual identification. The anisometry of the sensory surface, with a region (the fovea) which is much more sensitive than others, prompts the need for orienting movements to align the sensory input with this region. These characteristics are much less evident in other sensory systems. These considerations are strong arguments in favor of the role of attentional processes in the determinism of neglect. For example, a defective conceptualization of an hemispace [52,67–70], or a shift of the egocentric frame of reference [54,55], would have little reason to express themselves more in the visual than in the tactile or in the acoustic space.

But the mere statement that neglect patients suffer from attentional impairments adds little to the understanding of this dramatic condition. Attempts at further specifying the number and the nature of attentional impairments in neglect led to the proposal of a variety of different attentional mechanisms of left neglect. Thus, it has been suggested, for example, that left neglect essentially results from a right-

ward attentional bias [57] (perhaps in the context of a specialization of the right hemisphere for 'global' processing and of the left hemisphere for 'focal' processing [71]), from a deficit in disengaging attention from the right side to re-orient it to the left side [72,73], or from a deficit in orienting attention to the left contralesional hemispace [74]. These attentional impairments may express themselves in a scene- or an object-based frame of reference. Finally, also non-lateralized attentional impairments are thought to contribute to neglect behavior [75]. These different attentional accounts of left neglect are presented and discussed in Section 4.

4. Attentional disorders in left unilateral neglect

4.1. A rightward attentional bias in left neglect

A well-articulated account of neglect based on orienting of attention is the opponent processor model [57,76–78]. This model draws upon the very general biological evidence that reciprocally inhibiting opponent systems are an evolutionary advantageous way of solving the problem of deciding whether to turn right or left. The dominant system would achieve its goal of turning the organism by progressively inhibiting its contralateral counterpart. A first assumption of the opponent processor model is that each hemisphere shifts attention toward the contralateral hemispace by inhibiting the other hemisphere. A second assumption is that in the normal brain there is a tendency to rightward orienting supported by the left hemisphere, which has a stronger orienting tendency than the right hemisphere. Right-hemisphere lesions, by disinhibiting the left hemisphere, exaggerate this physiological rightward bias, thus giving rise to left neglect. Left neglect does not reflect an attentional deficit, but an attentional bias consisting of enhanced attention to the right. The verbal interaction between patient and examiner would further enhance left neglect by further activating the already disinhibited left hemisphere. Furthermore, left neglect patients would suffer from an abnormally tight focus of attention, which would deprive them of the possibility of a more general overview of the visual scene [78]. Right neglect would rarely be observed because much larger lesions of the left hemisphere are needed to overcome its stronger tendency to rightward orienting, and because the verbal exchanges with the examiner would now work in the opposite direction, thus minimizing right neglect.

This latter aspect of the model seems at variance with the common observation of neglect signs in everyday situations, when no verbal exchange takes place. Also, the basic assumptions of the opponent processing model about the functional organization of the brain hemispheres have been questioned. First, while the concept of mutually inhibitory lateral structures appears adequate to describe the mode of functioning of subcortical structures like the

superior colliculi, it looks as an excessive simplification of the relationship of structures much more complex as the cerebral hemispheres (among other considerations, callosal connections seem prevalently excitatory, and not inhibitory, in nature, see Ref. [79]). Moreover, the assumption of a left hemispheric dominance for attentional orienting seems challenged by PET data showing a preferential involvement of the right parietal lobe for both left- and right-sided attentional shifts, whereas the left parietal lobe is only activated by shifts in the right hemifield [80], and by ERP results suggesting that the right hemisphere is activated earlier than the left in visual perception [81].

Despite these problems, other aspects of the opponent processor model appeared to be confirmed by subsequent empirical evidence. For example, a patient who showed a severe left neglect following a first right-sided parietal infarct abruptly recovered from neglect 10 days later, when he suffered from a second, left side infarct in the dorsolateral frontal cortex [82]. However, inferences from this case report must be prudent. All the case history took place in the acute phase of the disease, when transient phenomena of neural depression in areas remote from the lesion [83] render difficult any firm conclusions about the effect of anatomical damage. As the authors reported, the second stroke induced a tonic leftward deviation of head and gaze; this occurrence might have contributed to minimizing left neglect signs, similarly to the effects of vestibular or optokinetic stimulations (see Refs. [84,85] for review and discussion of these stimulations).

The crucial mechanisms of left neglect according to the opponent processor model is a rightward attentional bias. It has been repeatedly demonstrated that patients do not simply neglect left objects, but are attracted by right ones. In an ingenious variant of the line cancellation task, Mark et al. [86] had 10 patients with left neglect erase lines or draw over them with a pencil mark, and found lesser neglect in the 'erase' than in the 'draw' condition. Mark et al. concluded that right-sided lines attracted patients' attention when they were crossed by a pencil mark, whereas rendering these lines invisible by erasing them obviously nullified this effect, thus decreasing neglect. Similarly, Marshall and Halligan [87] reported that targets could be omitted in a shape cancellation task independently of their position with respect of the midsagittal plane, and concluded that 'right attentional capture' might be a better description of patients' performance than 'left neglect'.

An important marker of the direction of attention is the position of gaze. While attention can be shifted while maintaining fixation [9], a gaze shift usually corresponds to an analogous shift in visual attention [88–90]. Brain lesions often induce a conjugated shift of gaze toward the side of the lesion. De Renzi et al. [91] importantly demonstrated that gaze deviation does not occur with equal frequency after left- and right-hemisphere lesions, but preferentially occurs after posterior lesions of the right hemisphere, and is often associated with left neglect, again suggesting that a

rightward attentional bias is an important component of left neglect. Neglect patients are indeed prone to orient their gaze toward the rightmost stimulus as soon as the visual scene unfolds [92]. This observation is reminiscent of the 'magnetic attraction' of gaze, originally described by Cohn [93] in hemianopic patients. This phenomenon can be observed during the clinical test of the visual fields by the confrontation method: as soon as the examiner outstretches her arms in the patient's visual fields, before the actual administration of stimuli, the patient compulsively looks at the hand on the right. Also this phenomenon, which can be considered as a lesser degree of tonic gaze paresis, is strictly associated with right-hemisphere lesions and left neglect (Experiment 1 in Ref. [5]). Moreover, RBD patients typically begin from the right side their exploration of a complex stimulus array (Experiment 2 in Ref. [5]), again suggesting an initial rightward attentional orienting, whereas normal controls and LBD patients start from the left. This set of phenomena may easily explain why neglect, even if it is not exclusive for visually presented material, is nevertheless exacerbated by the presence of visual stimuli. Under visual control, attention might be captured and maintained in the right hemispace by visual objects, thus increasing neglect for the left side. The absence of visual control would improve performance by eliminating this attentional capture exerted by right-sided visual stimuli. In this sense, right-sided external percepts might be more 'sticky' than, for example, internally generated mental images [94].

Therefore, an important question raised by these findings is the following: does the rightward bias reflect enhanced attention to the right (resulting from a left-hemisphere released from right-hemisphere inhibition), as postulated by the opponent processor model? Làdavas et al. [95] found that patients with left neglect responded faster to right-sided than to left-sided targets, even when all the stimuli were presented in the right visual field. RBD patients without neglect, on the contrary, were faster for left-sided than for right-sided stimuli, presumably because left targets appeared closer to the fovea. This finding is consistent with the opponent processor model, which holds that there is no special status for the patient's sagittal midline for dividing the attended from the neglected parts of space. In other words, independent of its absolute position, any object is likely to be neglected if it is 'left of' some other object that attract patients' attention [87]. Of particular interest is the finding by Làdavas et al. [95] that neglect patients' response times for right targets were faster than those of RBD patients without neglect. Neglect patients' attention for right targets seemed thus enhanced with respect to RBD control patients, consistent with the opponent processor model. As Làdavas et al. [95] pointed out, according to this model neglect patients should be faster for right-sided stimuli even with respect to normal individuals without brain damage; this, however, would be an unlikely result, given that right brain lesions cause a deficit in arousal [96]. Indeed, subsequent RT studies [97–101] invariably found that left neglect

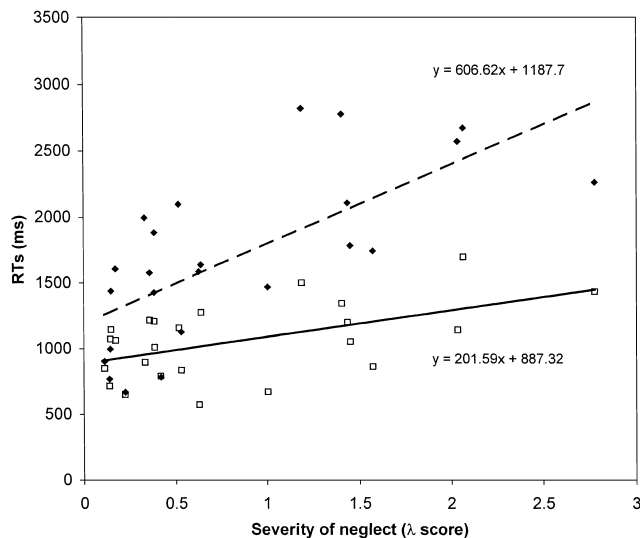


Fig. 3. Regression plot of RTs to left (filled symbols) and right (open symbols) targets as a function of the severity of left neglect (assessed by a laterality score) in 24 right brain-damaged patients (data from Ref. [102]).

patients were slower than normal controls when responding to right (ipsilesional) stimuli (Fig. 6). Recent evidence [102] indicates that this slowing for ipsilesional targets does not simply reflect a non-specific arousal deficit, but is strictly related to the severity of left neglect. The manual response times to lateralized visual stimuli of 24 left-neglect patients were plotted against a laterality score measuring their neglect independent of the overall level of performance. That is, for example, right-sided omissions in cancellation tests with equal number of left omissions would decrease the amount of the score; thus, a non-lateralized pattern of omissions in paper-and-pencil tests, such as the one expected with a non-specific arousal deficit, would not inflate the score.

Results (Fig. 3) showed that not only RTs to left targets, but also RTs to right targets increased with increasing neglect, contrary to the opponent processor model, which would have rather predicted a progressive decrease of RTs to right targets, reflecting increasing disinhibition of the left hemisphere. The two regression lines were not, however, parallel. With increasing neglect, responses to left targets increased more steeply than those to right targets did, suggesting that a rightward attentional bias participates in left neglect. However, this rightward bias seems one of defective, and not enhanced, attention.

That left neglect does not result from a hyperactive left hemisphere is also suggested by functional brain imaging studies of diaschisis in left neglect [103–105], which demonstrate a widespread hypometabolism in both the lesioned and the intact hemisphere. Recovery from neglect seems to correlate with restoration of normal metabolism not only in the unaffected regions of the right hemisphere, but also in the left hemisphere [104,105]. An increase of neural activity, metabolism and perfusion in the unaffected hemisphere seems indeed a general mechanism of

prolonged recovery from neurological and neuropsychological impairments after unilateral strokes [83].

4.2. A directional deficit of disengaging attention

Posner et al. [72] had six RBD and seven LBD patients with predominantly parietal lesions perform the cued detection task described in Section 2.1. Patients were disproportionately slow when a contralesional target was preceded by an ipsilesional (invalid) cue. This RT pattern was present in both RBD and LBD patients, but considerably larger in RBD patients, and evident with both central cues (arrow) and peripheral cues (brightening of the box). Posner et al. [72] argued that this effect, reminiscent of extinction of contralesional stimuli in double visual stimulation, resulted from an impaired disengagement of attention from the ipsilesional side. The amount of the observed RT effect correlated significantly with the extension of lesion in the superior parietal lobe. Note, however, that in a subsequent study, Friedrich et al. [106] compared patients with chronic lesions of the superior parietal lobe with patients with lesions of the temporal–parietal junction, all without clinical signs of neglect or extinction, and found an extinction-like RT pattern only for the temporal–parietal group. Because control patients with frontal or temporal lesions did not present this ‘extinction-like’ RT pattern, Posner et al. [72] concluded that an important role of each parietal lobe was one of disengaging attention from previously attended locations in the ipsilateral hemispace. A problem of disengagement from ipsilesional stimuli could in principle explain some aspects of neglect, such as the failure to explore the contralesional parts of a cancellation test. However, the parietal patients in the Posner et al.’s study [72] showed little or no contralesional neglect (no neglect in five patients, minimal neglect in two, mild in five and moderate in one). Thus, in this study there was no direct evidence for a relationship between the observed extinction-like RT pattern and neglect. This issue was addressed more directly by Morrow and Ratcliff [73], who tested 12 RBD and 10 LBD patients using a RT paradigm with peripheral cues. All patients had lesions including the parietal lobe, contralesional neglect, or both. Only RBD patients showed a significant extinction-like RT pattern (though LBD patients’ results did go in the same direction (see Fig. 1 in Ref. [73])). For RBD patients, the cost for invalid contralesional targets correlated with a measure of left neglect, thus suggesting a causal relationship between the two phenomena.

Nevertheless, for such a right-disengagement deficit to produce clinical left neglect, attention must logically have been engaged to the right *before* the occurrence of the disengagement problem [5,107]. D’Erme et al. [97] produced evidence for such an early rightward engagement by manipulating the Posner RT paradigm. As described in Section 2.1, in this paradigm targets appear in boxes displayed to facilitate position expectancy. D’Erme et al.

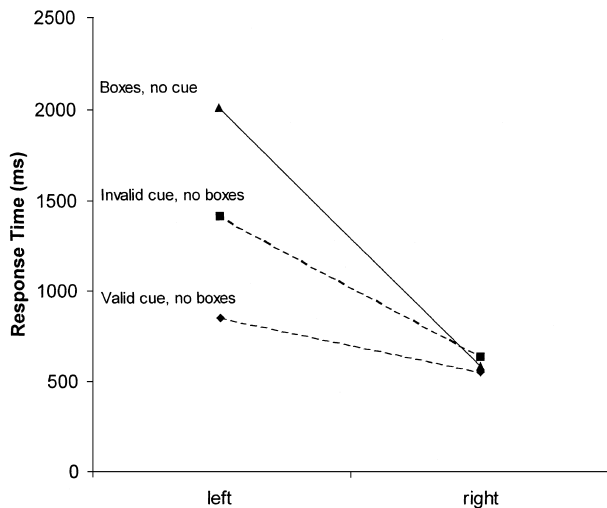


Fig. 4. Left neglect patients' cued response times to left and right targets, framed or not by placeholder boxes (based on data in Ref. [97]). Targets were black asterisks ($1.29^\circ \times 0.96^\circ$). Cues were empty ellipses ($0.65^\circ \times 0.80^\circ$), appearing at one of the two possible target locations.

[97] reasoned that, by analogy with the magnetic attraction phenomenon, the mere appearance on the computer screen of the positional expectancy boxes should elicit a shift of patients' attention toward the rightmost box. This study contrasted the traditional RT paradigm in which targets appeared in boxes with a condition in which targets appeared in a blank screen, not surrounded by boxes. The presence of the boxes considerably increased the left/right RT difference for neglect patients, as if the right-sided box acted as an invalid cue for left targets (indeed the boxes seemed to induce a stronger extinction-like RT pattern than actual right-sided cues, Fig. 4).

Because the boxes were not informative about the future location of the targets, the type of orienting elicited by the boxes could best be characterized as reflexive, or exogenous, as opposed to the voluntary, or endogenous orienting elicited by central cues or by peripheral informative cues

[24]. Thus, D'Erme et al. [97] proposed that the attentional imbalance in neglect was primarily one of exogenous attention, in keeping with previous similar suggestions based on the apparent 'automaticity' of rightward attentional attraction in left neglect [5]. In this last study, two different investigations in unselected groups of patients with right and left brain damage were carried out. The first investigation, conducted to evaluate forms of lateral orienting bias severe enough to provoke an overt gaze deviation, consisted of the systematic assessment of the phenomenon of magnetic gaze attraction (the compulsive tendency to direct one's gaze to the ipsilesional stimulus upon presentation of bilateral stimuli, see Section 4.1). The second investigation, aimed at detecting milder forms of orienting bias, explored the temporal sequence followed in identifying the pictures displayed in a task requiring identification of overlapping figures, to see if patients tended to identify first figures presented in the half space ipsilateral to the lesion. In both investigations, results consistently showed: (a) that RBD patients tended to initially orient their attention toward the ipsilateral half space more than did LBD patients; (b) that this tendency was generally associated with behavioral manifestations of unilateral neglect. Gainotti and co-workers [5] concluded that left neglect was a multi-component phenomenon, reflecting an initial exogenous orienting of attention toward right events, followed by a difficulty in disengaging attention from these events in order to reorient attention leftward.

The early rightward orientation of attention may be observed as a residual sign of spatial bias in patients who had recovered from left neglect [98,107,108]. Thus, to produce clinical neglect, either the initial rightward orienting bias must be present in a certain critical amount, or it must be accompanied by other component deficits. Concerning this last possibility, the disengagement problem [72,73], subsequent to the early ipsilesional engagement, would seem a good candidate. Patients would be initially attracted by a right-sided object, and would subsequently be

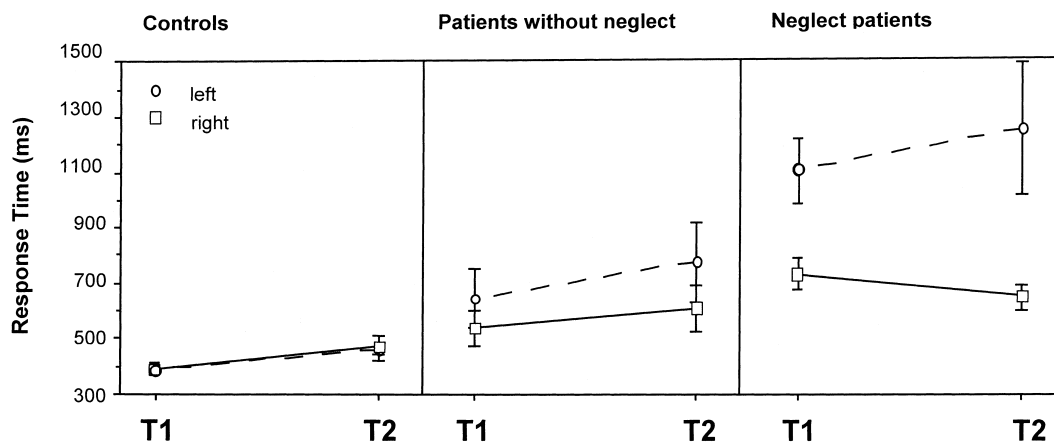


Fig. 5. Response times to pairs of consecutive targets occurring in the same spatial location (left: open symbols, dashed line; right: filled symbols, solid line), for normal controls and patients with lesions in the right hemisphere without or with left neglect. Error bars indicate the s.e.m. (from Ref. [109]).

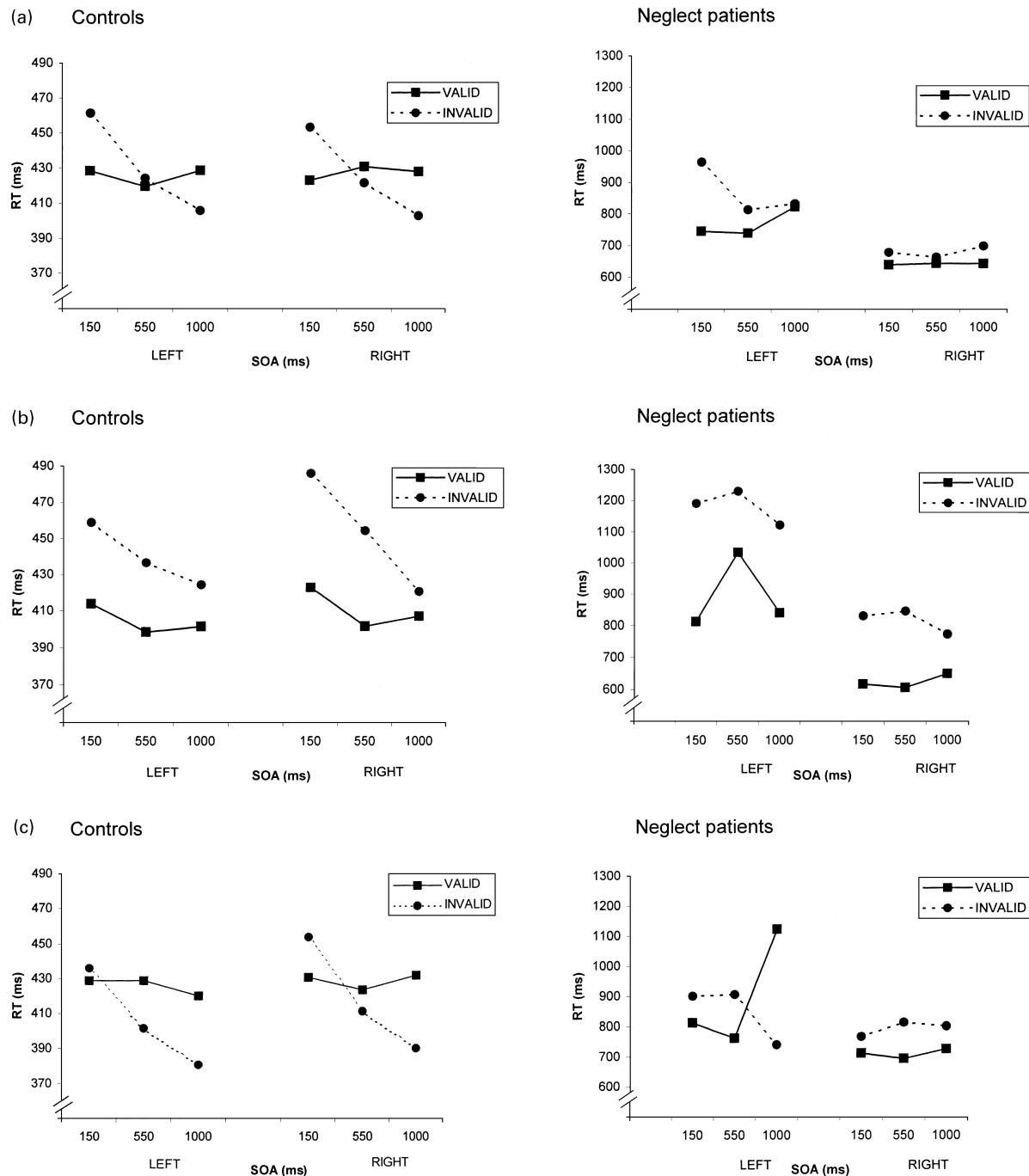


Fig. 6. Response latencies of normal controls and neglect patients (note the different time scales) for valid and invalid trials on a cued RT task with non-informative peripheral cues (a), 80% valid cues (b), or 80% invalid cues (c). SOA, stimulus-onset asynchrony (based on data in Ref. [100]).

unable to rapidly remobilize their attention from that location. However, the disengagement problem has been demonstrated in patients without clinical signs of neglect [106]. It remains to understand, therefore, the conditions under which these impairments do or do not produce clinical neglect. Perhaps, these depend in a quantitative manner on the severity of deficit. This is suggested by the correlation between the amount of extinction-like RT pattern and the severity of neglect [73]. Alternatively or in addition, other

deficits could add to those described in order to produce a clinically evident spatial bias. For example, preliminary results seem to suggest that IOR (Section 2.3) does not work properly in neglect. Left neglect patients seem to show facilitation, instead of normal inhibition, for repeated events occurring on the right, allegedly 'normal' side [109] (Fig. 5).

A persisting, unopposed attentional facilitation for right-sided items could explain why neglect patients cannot

explore the remaining portions of space once their attention has been captured by a right-sided object. In addition, the fact that IOR seems to be a phenomenon exclusive of exogenous orienting [25] further suggests that this form of orienting is particularly impaired in left unilateral neglect.

In a recent meta-analysis of results obtained in brain-damaged patients with the Posner paradigm, Losier and Klein [110] took advantage of the greater statistical power of the cumulated evidence from several studies, and concluded that (1) the disengage deficit is robust following peripheral cues, but not following central cues; (2) the disengage deficit is large at shorter SOAs, and decreases as SOA increases; (3) the disengage deficit is larger in patients showing signs of unilateral neglect. The first two characteristics are typical of the operations of exogenous orienting; the third clearly links the disengage deficit to unilateral neglect. Thus, the results of this meta-analysis give strong support to the hypothesis of a bias of exogenous orienting in left neglect. Additional evidence relevant to this issue is summarized in Section 4.3.

4.3. Impaired orienting of attention in neglect: exogenous vs. endogenous

In a study employing simple RTs to lateralized visual stimuli, Smania et al. [101] produced evidence for preserved endogenous orienting in neglect. In this study, neglect patients had faster RTs for both hemifields when the side of stimulus presentation was predictable as compared to the case when stimuli were presented randomly. Làdavas et al. [111] also addressed the issue as to which mode of attentional orienting (exogenous or endogenous) is preferentially biased in left neglect. They noticed that the use of informative cues in the study of Posner et al. [72] made it difficult to discriminate between these two modes of orienting, and contrasted the effects on target detection of central informative cues (an arrow presented near fixation) with that of peripheral non-informative cues (an arrow presented earlier one of the placeholder boxes). Làdavas et al. [111] found that central cues pointing toward the left were able to decrease the number of omissions of left targets in neglect patients (RTs for left targets were not analyzed because of the high rate of omissions, probably resulting from the very short time, 75 ms, of target presentation), whereas peripheral cues presented on the left side had no significant effect on patients' accuracy. The authors concluded that neglect patients were not able to orient their attention leftward exogenously, but they could do so voluntarily. However, besides their different effects on exogenous and endogenous orienting, central and peripheral cues might act on distinct stages of information processing (an early perceptual stage for peripheral cues, and a late perceptual or a decision stage for central cues [48]), thus rendering difficult any direct comparison between their respective effects on performance. Moreover, in the case of patients suffering from a spatial bias, the different spatial localiza-

tion of central and peripheral cues may complicate the interpretation of the results.

To investigate exogenous and endogenous orienting in neglect, Bartolomeo et al. [100] employed a Posner-type RT task with exclusively peripheral cues. They studied six patients with right-hemisphere damage and left unilateral neglect and 18 age-matched participants without brain damage. Participants performed three experiments employing a cued RT task to targets, which could appear in one of two lateral boxes. Cues consisted in a brief brightening of the contour of one of the boxes. The target followed the cue at 150, 550, or 1000-ms SOA. In Experiment 1, the cues were not informative about the future location of the target, and thus evoked an exogenous shift of attention towards the cued box [24], particularly at short SOAs [30], in relative independence of endogenous processes. Controls (Fig. 6(a)) showed slowed RTs to the cued locations at longer SOAs, consistent with the notion of IOR (Section 2.3). In agreement with the previous results [109] reviewed in Section 4.2, neglect patients had no evidence of IOR for right targets; they showed a disproportionate cost for left targets preceded by right (invalid) cues; this cost was maximal at the shortest SOA, consistent with the idea of a biased exogenous orienting in neglect (Fig. 6(a)).

In Experiment 2, cues predicted the future location of the target with 80% accuracy, thus evoking an exogenous orienting of attention at short SOAs and an endogenous orienting at long SOAs [30]. Neglect patients (Fig. 6(b)) showed again a cost for left invalidly cued targets, which this time persisted at SOAs > 150 ms, as if patients' attention had been cued to the right side not only exogenously, but also endogenously, thus rendering more difficult an endogenous reorienting toward the left. In Experiment 3, most cues (80%) were invalid, and predicted that the target would appear in the box opposite to that cued. In this situation, cues should normally prompt an initial exogenous orienting toward the cued box, later followed by an inhibition of this exogenous shift, to be replaced by an endogenous shift towards the uncued box [112]. Thus, for long enough SOAs this condition explores endogenous orienting in relative isolation. Controls (Fig. 6(c)) were able to take advantage of invalid cues to rapidly respond to targets. Neglect patients (Fig. 6(c)) were remarkably able to nullify their spatial asymmetry; they achieved their fastest RTs to left targets, which were in the range of their RTs to right targets. However for neglect patients, fast responses to left targets occurred only at 1000-ms SOA, while controls were able to redirect their attention to the uncued box already at 550-ms SOA. Altogether, these results indicate that endogenous orienting is relatively spared, if slowed, in unilateral neglect, whereas exogenous orienting appears heavily biased toward the right side. The slowing of endogenous processes in neglect might result from the general slowing of attentional operation in this condition (Section 4.5). As a corollary, the results of this study suggested an

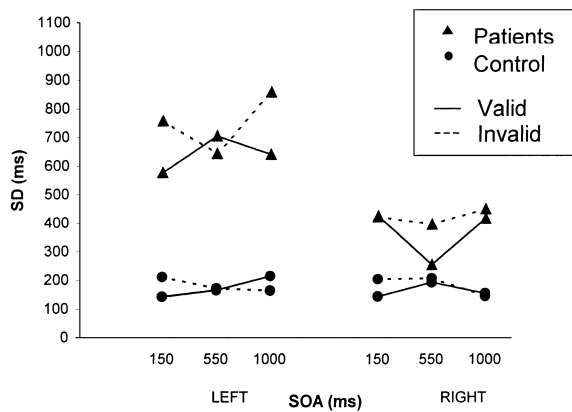


Fig. 7. Within-subjects variability (SDs) for response latencies of normal controls (circles) and neglect patients (triangles) on a cued RT task with non-informative peripheral cues (see Fig. 6(a) for the corresponding response latencies). Solid lines, valid condition; dashed lines, invalid condition. SOA, stimulus-onset asynchrony (from Ref. [114]).

explanation for the variability of performance often shown by neglect patients in their neglected hemispace.

Anderson et al. [113] have recently brought attention to this issue by reporting a progressive increase of variability of RTs from the right to the left side in left neglect patients. They proposed that this lack of consistency might contribute to patients' defective performance independently of other mechanisms causing neglect. It is, however, possible that an increase of variability, and not only of RTs, simply results from attention being exogenously biased away from the probed location. If so, space-based variability could be interpreted in the framework of existing models of unilateral neglect. According to the model of neglect at issue here, a basic impairment in left neglect is a bias toward rightward exogenous orienting of attention. As a result of this bias, left targets often fail to rapidly capture patients' attention, thus yielding slow RTs. However, since the probability for a left target attracting attention is low but not null [78], relatively fast RTs can occur on those rare occasions in which a left target does capture patients' attention. The coexistence of these relatively fast RTs with slow RTs could be at the basis of space-based variability in neglect. A re-analysis for variability of RTs in Experiment 1 of Bartolomeo et al. [100] gave empirical support to this proposal. Recall that in this experiment cues were peripheral and non-informative, thus eliciting an exogenous attentional shift. The re-analysis [114], whose results are displayed in Fig. 7, showed that, for normal individuals, invalid trials yielded less consistent response times than valid trials at short (150 ms) SOA, that is, the time interval most likely concerned with exogenous attentional shifts.

For neglect patients, a similar phenomenon occurred for left invalidly cued targets, thus paralleling the disproportionate cost in RTs typically evoked by this condition in unilateral neglect [72,73,100]. Thus, in both normals and neglect patients, variability of RTs closely paralleled their medians, with both variables increasing when participants'

attention was exogenously diverted away from the target. The phenomenon of space-based variability has implications for current models of left unilateral neglect. It does not agree with models based on a rightward shift of a reference frame for space exploration [55], which would predict, rather, impaired but stable performance for left targets. Also models based on an amputation [69] or on a distortion [53,115] of a mental representation of space seem unlikely to readily explain such variability. A distorted spatial representation, for example, would be expected to impair performance on the left side, but it should not increase variability, because stimuli arising in a given location would always fall in the same place on the (distorted) representational medium, thus presumably always evoking the same response. Thus, the phenomenon of space-based variability also supports models of left neglect based on a primarily exogenous attentional asymmetry.

Results from experimental tasks other than the Posner paradigm seems to converge in indicating an essentially stimulus-based bias, with relatively preserved top-down control, in unilateral neglect. Duncan et al. [116] explored neglect patients' behavior in terms of Bundesen's Theory of Visual Attention [117]. Duncan et al. [116] tested nine patients with lesions affecting the right parietal lobe and variable left unilateral neglect (which was absent in two patients and resolving in one). Patients were shown letters briefly presented in bilaterally arranged arrays and had to report either all of the letters or only those letters in a pre-specified color. Patients not only often failed to report left-sided letters (as was expected), but also, they failed to report right-sided ones, albeit to a lesser extent. This result is consistent with the notion of a non-lateralized attentional impairment (Section 4.5). However, when target letters were defined by color, patients' capacity of discriminating targets from non-targets was similar to controls', independent of the side of presentation. In other words, target letters received attentional priority over non-targets even on the neglected side, thus indicating an unexpected, bilateral preservation of top-down attentional control in neglect patients. Duncan et al. [116] recalled that top-down control is often associated with frontal lobe function. This might explain its preservation in patients with predominantly posterior lesions. Alternatively, a left-hemisphere superiority for selective attention, recently suggested by results obtained by Chokron et al. [118] using a visual detection paradigm [119], might account for its preservation in RBD patients.

Accounts of neglect based on an orienting of attention, though undoubtedly in need of further specification, seem consistent with several neglect phenomena, provided that these accounts are articulated as an association of a number of concurrent deficits. An asymmetry of exogenous orienting, with rightward attentional shifts being easier than leftward shifts, compounded with non-lateralized deficits such as arousal problems, seems to accommodate the experimental evidence coming from most cases of left unilateral neglect.

Danziger et al. [120] obtained results challenging this conclusion, and suggesting that leftward exogenous orienting may be spared in left neglect. They asked two left neglect patients to perform a Posner-type task in which cues and targets could appear in one of four (or six) boxes aligned vertically to the left and right of a central fixation point. Cues consisted of a brightening of either a single box or two boxes bilaterally. There were two conditions. In a first condition, only cues were presented. Patients had to say whether they saw a single cue or two bilateral cues. In a second condition, cues and targets were displayed. Patients had to respond to targets by a keypress. Cues were uninformative about the future location of the target. In the cue-detection condition patients extinguished more than 90% of the left cues on bilateral cueing. Despite this, in the target-detection condition, their responses to validly cued left targets was speeded up by these same bilateral cues. The authors concluded that an unconscious leftward orienting might occur in left neglect. However, it should be noted that the two experimental conditions were not exactly matched for stimulus saliency. Cues were less salient in the cue-detection condition than were cues plus targets for valid trials in the target-detection condition, where temporal and spatial summation of the cue and target energy was likely to occur. As a consequence, validly cued targets were more likely to attract patients' attention than cues only. This could explain (1) the extinction of most left cues in the cue-detection condition, where there was no asymmetry in stimulus salience between the two bilateral cues, and (2) the validity effect observed for contralesional targets after bilateral cueing in the target-detection condition, where the presentation of left cue plus target in valid trials was more salient than the presentation of the sole target in the invalid condition.

Also problematic for accounts of neglect based on an orienting bias is the fact that, on some occasions, neglect patients do seem to orient toward neglected stimuli, yet fail nonetheless to produce the correct response. For example, Bisiach et al. [121] observed neglect patients who occasionally followed with their index finger, the complete contour of a drawing, but failed to notice the details on its left side. When bisecting lines, some patients with left neglect and hemianopia can look at the left part of the line, but this leftward search does not influence the final bisection decision, which remains rightward-biased [122,123]. Similarly, neglect patients may fail to produce the appropriate manual response to left-sided stimuli despite having looked at them [124]. These puzzling patterns of behavior are reminiscent of the possibility that some patients may show an implicit (or 'covert') knowledge of otherwise neglected details [125–127], which influence patients' behavior despite their being unavailable for direct verbal report. Future research should compare more closely the characteristics of ineffective exploratory behavior with those of orienting behavior associated with normal responses.

4.4. Object-based neglect

As mentioned in Section 2.4, spatial attention can perhaps be better described as orienting towards objects in space rather than towards blank regions of space. If neglect results from an attentional impairment, then, it should be possible to observe instances of neglect of the left part of objects, independent of the absolute location of these objects in space. Indeed, when copying drawings consisting of a number of elements arranged horizontally on the sheet (e.g. a landscape with a house and trees), patients sometimes do not neglect the left part of the scene as a whole, but copy only the right part of each element, in a 'piecemeal' fashion [128,129], as if an object-based attentional bias were at work. Consistent with this possibility, a patient was found to be impaired in reporting the left-sided details of a vertically elongated shape both when the shape was upright and also when it was tilted by 45° toward the right, so that these details were now on the right with respect to the patient's sagittal midline [130]. Three other patients showed similar effects when reporting gaps on one side of triangles whose perceived principal axis was manipulated by context [131]. Also, a left-handed patient with left-hemisphere damage and right neglect produced errors on the final part of words, irrespective of whether the words were presented in a horizontal, vertical, or mirror-reversed format [132]. However, Farah et al. [133] found no evidence of object-based neglect in a group of 10 left neglect patients. When identifying single letters scattered over drawings of familiar objects, patients failed to report left-sided letters when the objects were upright, but they correctly reported these same letters when the objects were tilted (but a subsequent reanalysis [134] of Farah et al.'s data indicated that three patients did omit more letters printed on the left side of the object, even when the object was rotated, thus showing evidence of object-based neglect). Behrmann and Moscovitch [135] reasoned that object-based neglect might emerge only for those objects which have an intrinsic handedness, where a vertical reference axis allows the definition of left and right with respect to the object itself [130]. Consistent with this prediction, they demonstrated object-based neglect with upper-case letters presenting a left-right asymmetry (e.g. B, E), but not with symmetrical letters (A, X).

Using another paradigm to demonstrate object-based effects, Behrmann and Tipper [136] had left neglect patients respond to targets appearing inside one of two horizontally aligned circles of different colors. As expected, patients responded faster to right than to left targets (space-based neglect). However, for some patients this effect was reversed when the two circles were connected by a line, like a barbell (thus forming a single perceptual object), and when the barbell rotated by 180° just before the target appeared. In this case, RTs for the targets now on the left side, but appearing in a previously right-sided circle, were faster than RTs for the targets appearing on the right, thus suggesting object-based neglect. In other words, the *same*

neglect patients could show either space- or object-based neglect depending on the experimental conditions. An implication of these findings is that dissociation in performance of neglect patients does not necessarily indicate different impairments, but perhaps different strategies evoked by the experimental conditions.

How to reconcile object-based neglect with our claim of a deficient exogenous orienting? Here we can offer only a conjectural account. It might be that the spatial grain of the exogenous orienting deficit varies between or even within patients. For example, during recovery from neglect, patients might re-acquire some ability to direct attention leftward. However, when an object is thus selected, its right-sided features might still exogenously attract patients' attention, sometimes to the point of making patients ignore the left part of the object.

4.5. Non-lateralized attentional impairments

Other component deficits of neglect might not necessarily be lateralized or directional problems. For example, it has been suggested that neglect results not only from an asymmetry in selective spatial attention, but also from impairments in other, non-lateralized attentional components (see the taxonomy in Section 2), such as arousal or vigilance [75]. Such non-lateralized deficits may be invoked to explain the fact that neglect patients are slower than normal individuals when responding to visual targets even in the ipsilesional, non-neglected space. Indeed, this ipsilesional slowing might disappear with recovery of neglect [98]. The normal timing of attentional events also seems to be disrupted in neglect for centrally presented visual stimuli. When normal individuals have to identify two visual events appearing one shortly after another in the same spatial location, the second event goes undetected if presented in a time window of 100–450 ms after the first event ('attentional blink' [137]). Husain et al. [138] had eight left neglect patients perform this dual identification task, and found that neglect patients needed about 1.5 s of inter-stimulus interval to detect the second target, thus showing an important slowing of the time to select visual information. Non-lateralized impairments interact with lateralized spatial asymmetry in neglect, as demonstrated by the fact that a warning 'beep', which arouses vigilance, is able to decrease visuospatial asymmetry of performance in neglect patients [139]. Phenomena of transcallosal diaschisis [83,140] might constitute the anatomo-functional basis for such non-lateralized impairments.

Non-lateralized attentional impairments could account for the hemispheric asymmetry of unilateral neglect. Right brain damage slows down RTs more than left-hemispheric lesions [96], which can be interpreted as an arousal deficit [141]. The preferential occurrence of a deficit of arousal after right, rather than left, brain damage might be one of the bases of the predominance in frequency and severity of contralesional neglect after right, as opposed to left, hemi-

spheric lesions [56,142]. One could speculate that a unilateral brain lesion generally delays the processing of information coming from the contralesional field. An additional, non-lateralized slowing of attentional operation, resulting from right brain damage, might further hold back the processing of left stimuli, to the point of exceeding a deadline after which this information cannot affect behavior anymore. For example, these added delays might render the time needed to decide whether a left target is in fact present [143] too long to react to it (e.g. by programming a saccade).

5. Impaired exogenous orienting in unilateral neglect: implications for the neural implementation of attentional mechanisms

The proposal that left unilateral neglect primarily results from an asymmetrical exogenous orienting has implications for both the interhemispheric and the intrahemispheric implementation of attentional mechanisms. The importance for attentional orienting of brain regions in the parietal [144,145] and frontal [80,146] lobes has long been known. Gottlieb et al. [147] have recently identified neurons in the macaque lateral intraparietal area which selectively respond to visual stimuli with abrupt onset, a typical feature of attention-capturing stimuli in exogenous orienting [20]. Interestingly, the posterior bank of the intraparietal fissure is one of the main sources of cortical projection to the intermediate and deeper layers of the superior colliculus [148,149], a subcortical structure involved in programming saccades to visual targets. Another phenomenon related to exogenous orienting [25] is IOR. The role of extrageniculate visual pathways, and particularly of the superior colliculus, in mediating this phenomenon is well known [27,150]. A parieto-collicular dysfunction, originating from large lesions encompassing the inferior parietal lobule, could thus be at the basis of the exogenous attentional bias in unilateral neglect (a collicular imbalance in neglect has been suggested by Kinsbourne [77]). Note, however, that mechanisms related to exogenous attentional shifts need not be confined to the parietal lobe. More specifically, the right temporoparietal junction might be concerned with the process of target detection, particularly when targets appear at an unattended location [151], and consequently require an attentional shift in order to be detected. This evidence is consistent with the findings of a disengage deficit in patients with lesions of the temporoparietal junction [106], and of damage to the right superior temporal lobe in a group of patients with left unilateral neglect [2].

The common occurrence of unilateral neglect after right, as opposed to left, hemisphere lesions might suggest a right-hemisphere specialization for exogenous attentional shifts [6]. Another component of attention, arousal, might be disrupted more by right than by left-hemisphere lesions [96,141]. Since, as we have seen, an arousal deficit seems to contribute to neglect behavior [75,102,139], this could be

another basis for the asymmetry of occurrence of neglect after unilateral brain lesions [56,142].

As for endogenous, strategy-driven forms of orienting, Gainotti [6] notes that they are often related to propositional-verbal behavior, and could thus be preferentially mediated by the left hemisphere. Rehabilitation of neglect based on a conscious, verbally induced exploration of the neglected hemispace [152] could indeed draw upon left-hemisphere resources. More specific research on attentional orienting in normal individuals and brain-damaged patients is needed to evaluate this proposal. More generally, the frontal lobes, and particularly their dorsolateral aspects, might be crucial for intentionally direct one's attention. Patients with frontal damage are impaired in orienting attention in response to central informative cues [153], as well as in executing antisaccades (i.e. saccades toward the direction opposite to an abrupt-onset target [154]). Furthermore, a functional MRI study [155], employing the Posner RT paradigm to identify the brain areas involved in exogenous and endogenous orienting, demonstrated largely overlapping activations in the parietal and dorsal premotor regions for both modes of orienting, except for an activation in the right dorsolateral prefrontal cortex (BA 46), that was exclusive to the endogenous condition. One important aspect of endogenous orienting, that is, likely to be subsumed by frontal cortical areas is the inhibitory suppression of distractor activity [22]. An efficient distractor suppression might be a necessary condition for the production of antisaccades [156], or its *covert* analogous, i.e. the reorienting of attention away from a peripheral cue (as when most cues are invalid; see, e.g. Experiment 3 in Ref. [100]). These considerations are compatible with a hierarchical model of attentional orienting [142], in which a frontal system controls more posterior areas. This could be the basis for the fact that voluntary control can have a relative influence on exogenous orienting; for example, abrupt onsets of visual stimuli capture attention only when attention is unfocused [19]. Also consistent with these ideas is the proposal [98,157] that frontal cognitive abilities are important for recovery from neglect; this recovery is indeed more rapid in patients without injury to the right frontal cortex [158], and is related to the restoration of metabolism in the ipsi- and contralesional frontal cortices [104,105,159].

6. Impaired exogenous orienting in unilateral neglect: implications for phenomenal consciousness

As mentioned in Section 2.5, attention is thought to be crucial for binding together the different features (color, location, etc.) of an object [44]; in particular, exogenous orienting influences feature detection [49] and binding [35]. Failure to exogenously orient one's attention toward an object may thus result in incomplete feature processing, which in turn may cause either a complete lack of awareness of the object (whose perception is too inconsistent to be

attributed to a specific external source), or fleeting awareness doomed to rapid forgetting [160]. In other words, exogenous orienting might be essential for the constitution of a perceptual object. Indeed, the traditional view that the cognitive operations involved in the constitution of objects as perceptual units requires only pre-attentive processing (see, e.g. Ref. [161]) is increasingly challenged [49,162,163].

It may seem implausible that an asymmetry in exogenous attentional shifts can produce such a profound impairment of visual consciousness as that suffered by neglect patients. Normal individuals, however, also suffer from (less dramatic) forms of neglect, missing salient visual details when their attention is exogenously diverted away from the occurrence of the target event. For example, normal observers may not notice salient changes in a visual scene (e.g. large object shifting or disappearing) when the attention-grabbing capacity of these events is disrupted by the concurrent presentation of distracting material, like 'mudsplashes' [164], or when observers do not expect to see the change because they are making a difficult perceptual judgment about other elements in the scene [165]. In these 'change blindness' experiments, normal observers are totally unaware of an important part of what is going on in their visual field, and often incredulous of having missed such major modifications of the visual scene. One possible mechanism underlying the lack of awareness for events from which attention has been exogenously diverted could be a defective integration of elementary features for these events. If normal individuals can miss salient visual details in experimental situations perturbing exogenous orienting processes, it is perhaps no wonder that brain-damaged patients with disorders of exogenous orienting lack visual awareness for a substantial part of their visual world, sometimes to the point of getting hurt by bumping into left-sided obstacles or of getting lost as a consequence of neglecting left-sided topographical details. The presence of additional attentional disorders, such as those reviewed in Sections 4.4 and 4.5, concerning object-based and non-lateralized attentional deficits, can only add to the impairment of visual awareness in these patients.

It is important to note that, although in view of the earlier consideration exogenous orienting of attention appears to be a *necessary* condition for visual awareness, it seems by no means *sufficient* for awareness. McCormick [166] demonstrated that exogenous cues presented below a subjective threshold of awareness can capture attention automatically and without awareness. The hemianopic patient GY, who shows blindsight phenomena in his blind visual field [167], presents RT validity effects for cues and targets of which he is not aware [168]. These findings are reminiscent of the 'covert knowledge' phenomena described in neglect (Section 4.5), in which some form of orienting toward left-sided objects seems to occur in neglect patients, yet it is insufficient to result in full awareness of these objects.

Drawing on change blindness and other similar phenomena, O'Regan and Noë [169] have recently proposed that visual consciousness is not the result of having built a detailed mental representation of the visual environment, but is nothing over and above the mastery of the laws which govern the sensorimotor contingencies associated with visual exploration. For example, our consciousness of the presence of an object on our left would principally result from our capacity to direct a saccade toward that object. There is no need to build a detailed mental representation of the visual environment, because the visual world is already outside there, each detail being immediately available for visual exploration [170]. We believe that consideration of neglect behavior, through the studies discussed in the present review, lends substantial support to these notions [171]. Much of the empirical evidence reviewed here suggests that a crucial mechanism of this disorder is a directional asymmetry in exogenous orienting of attention. Parietal lesions in the right hemisphere might disrupt to variable extent leftward attentional shifts in the exogenous mode, that is, the capacity of left-sided events to attract patients' attention when they have to compete with (relatively) right-side events. This disorder might impair the patients' knowledge of the sensorimotor contingencies associated with leftward orienting. In the terms of the proposal advanced by O'Regan and Noë [169], it is thus not surprising that such an asymmetry in exogenous orienting may entail a dramatic lack of awareness for left-sided events when a concurrent right-sided event grabs patients' attention. Importantly, neglect patients may benefit from maneuvers, such as active movements of their left limbs [172], or active adaptation to optical prisms that displace the visual scene rightward [173], which might be understood as temporarily restoring patients' mastery of sensorimotor contingencies associated with leftward orienting. We believe that these notions are promising and convincingly show that converging evidence from experimental psychology and neuropsychology may ultimately allow us to map in detail the ways in which attentional processes constitute 'the mechanisms of consciousness' [174].

References

- [1] Vallar G. The anatomical basis of spatial hemineglect in humans. In: Robertson IH, Marshall JC, editors. *Unilateral neglect: clinical and experimental studies*, Hove, UK: Lawrence Erlbaum, 1993. p. 27–59.
- [2] Karnath HO, Ferber S, Himmelbach M. Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature* 2001; 411(6840):950–63.
- [3] Denes G, Semenza C, Stoppa E, Lis A. Unilateral spatial neglect and recovery from hemiplegia: a follow-up study. *Brain* 1982;105(3): 543–52.
- [4] Bartolomeo P, Chokron S. Levels of impairment in unilateral neglect. In: Boller F, Grafman J, editors. *Handbook of neuropsychology*, vol. 4. Amsterdam: Elsevier, 2001. p. 67–98.
- [5] Gainotti G, D'Erme P, Bartolomeo P. Early orientation of attention toward the half space ipsilateral to the lesion in patients with unilateral brain damage. *J Neurol Neurosurg Psychiatry* 1991;54:1082–9.
- [6] Gainotti G. Lateralization of brain mechanisms underlying automatic and controlled forms of spatial orienting of attention. *Neurosci Biobehav Rev* 1996;20(4):617–22.
- [7] James W. *The principles of psychology*. New York: Henry Holt, 1890.
- [8] Parasuraman R. The attentive brain: issues and prospects. In: Parasuraman R, editor. *The attentive brain*, Cambridge, MA: MIT Press, 1998. p. 3–15.
- [9] Posner MI. Orienting of attention. *Q J Exp Psychol* 1980;32:3–25.
- [10] Umiltà C. Visuospatial attention. In: Boller F, Grafman J, editors. *Handbook of neuropsychology*, vol. 1. Amsterdam: Elsevier, 2001. p. 393–425.
- [11] Bartolomeo P, Pagliarini L, Parisi D. Emergence of orienting behavior in ecological neural networks. *Neural Process Lett* 2002;15(1).
- [12] Arvidson PS. Transformations in consciousness: continuity, the self and marginal consciousness. *J Consciousness Stud* 2000;7(3):3–26.
- [13] Johnston WA, Dark VJ. Selective attention. *Annu Rev Psychol* 1986;37:43–75.
- [14] Desimone R, Duncan J. Neural mechanisms of selective visual attention. *Annu Rev Neurosci* 1995;18:193–222.
- [15] Allport DA. Visual attention. In: Posner MI, editor. *Foundations of cognitive science*, Cambridge, MA: MIT Press, 1989. p. 631–87.
- [16] Egeth H, Yantis S. Visual attention: control, representation, and time course. *Annu Rev Psychol* 1997;48:269–97.
- [17] Pashler HE. *The psychology of attention*. Cambridge, MA: MIT Press, 1998.
- [18] Macquistan AD. Object-based allocation of visual attention in response to exogenous, but not endogenous, spatial precues. *Psychon Bull Rev* 1997;4(4):512–5.
- [19] Yantis S, Jonides J. Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *J Exp Psychol Hum Percept Perform* 1990;16(1):121–34.
- [20] Yantis S. Attentional capture in vision. In: Kramer AF, Coles GH, Logan GD, editors. *Converging operations in the study of visual selective attention*, Washington, DC: American Psychological Association, 1995. p. 45–76.
- [21] Nakayama K, Mackeben M. Sustained and transient components of focal visual attention. *Vision Res* 1989;29(11):1631–47.
- [22] LaBerge D, Auclair L, Siéroff E. Preparatory attention: experiment and theory. *Conscious Cogn* 2000;9:396–434.
- [23] Jonides J. Voluntary versus automatic control over the mind's eye's movement. In: Long J, Baddeley A, editors. *Attention and performance XI*, Hillsdale, NJ: Lawrence Erlbaum, 1981. p. 187–283.
- [24] Müller HJ, Rabbitt PM. Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *J Exp Psychol Hum Percept Perform* 1989;15(2):315–30.
- [25] Maylor EA, Hockey R. Inhibitory component of externally controlled covert orienting in visual space. *J Exp Psychol Hum Percept Perform* 1985;11:777–87.
- [26] Posner MI, Cohen Y. Components of visual orienting. In: Bouma H, Bouwhuis D, editors. *Attention and performance X*, London: Lawrence Erlbaum, 1984. p. 531–56.
- [27] Rafal R, Henik A. The neurology of inhibition: integrating controlled and automatic processes. In: Dagenbach D, Carr TH, editors. *Inhibitory processes in attention, memory and language*, San Diego, CA: Academic Press, 1994. p. 1–51.
- [28] Posner MI, Rafal RD, Choate LS, Vaughan J. Inhibition of return: neural basis and function. *Cogn Neuropsychol* 1985;2:211–28.
- [29] Klein RM. Inhibition of return. *Trends Cogn Sci* 2000;4(4):138–47.
- [30] Müller HJ, Findlay JM. The effect of visual attention on peripheral discrimination thresholds in single and multiple element displays. *Acta Psychol* 1988;69(2):129–55.
- [31] Lambert A, Naikar N, McLahan K, Aitken V. A new component of visual orienting: implicit effects of peripheral information and subthreshold cues on covert attention. *J Exp Psychol Hum Percept Perform* 1999;25(2):321–40.
- [32] Decaix C, Bartolomeo P, Siéroff E. How voluntary is 'voluntary'

- orienting of attention? Poster presented at the 20th European Workshop on Cognitive Neuropsychology, Bressanone (Italy), January 2002.
- [33] Holender D. Semantic activation without conscious identification in dichotic listening, parafoveal vision, and visual masking. *Behav Brain Sci* 1986;9:1–23.
 - [34] Goldman AI. Can science know when you're conscious? Epistemological foundations of consciousness research. *J Consciousness Stud* 2000;7(5):3–22.
 - [35] Briand KA, Klein RM. Is Posner's "beam" the same as Treisman's "glue"? on the relation between visual orienting and feature integration theory. *J Exp Psychol Hum Percept Perform* 1987;13:228–41.
 - [36] Klein RM. Perceptual-motor expectancies interact with covert visual orienting under conditions of endogenous but not exogenous control. *Can J Exp Psychol* 1994;48(2):167–81.
 - [37] Briand KA. Feature integration and spatial attention: more evidence of a dissociation between endogenous and exogenous orienting. *J Exp Psychol Hum Percept Perform* 1998;24(4):1243–56.
 - [38] Itti L, Koch C. Computational modelling of visual attention. *Nat Rev Neurosci* 2001;2(3):194–203.
 - [39] Duncan J. Selective attention and the organization of visual information. *J Exp Psychol Gen* 1984;113(4):501–17.
 - [40] Wolfe JM, Bennett SC. Preattentive object files: shapeless bundles of basic features. *Vision Res* 1997;37(1):25–43.
 - [41] Treisman AM, Gelade G. A feature-integration theory of attention. *Cogn Psychol* 1980;12(1):97–136.
 - [42] Treisman A. Features and objects: the fourteenth Bartlett memorial lecture. *Q J Exp Psychol* 1988;40(2):201–37.
 - [43] Treisman A, Gormican S. Feature analysis in early vision: evidence from search asymmetries. *Psychol Rev* 1988;95(1):15–48.
 - [44] Treisman A. The binding problem. *Curr Opin Neurobiol* 1996;6:171–8.
 - [45] Kahneman D, Treisman A. Changing views of attention and automaticity. In: Parasuraman R, Davies DR, editors. *Varieties of attention*. Orlando, FL: Academic Press, 1984.
 - [46] Kahneman D, Treisman A, Gibbs BJ. The reviewing of object files: object-specific integration of information. *Cogn Psychol* 1992;24(2):175–219.
 - [47] Treisman AM, Kanwisher NG. Perceiving visually presented objects: recognition, awareness, and modularity. *Curr Opin Neurobiol* 1998;8(2):218–26.
 - [48] Riggio L, Kirsner K. The relationship between central cues and peripheral cues in covert visual orientation. *Percept Psychophys* 1997;59(6):885–99.
 - [49] Theeuwes J, Kramer AF, Atchley P. Attentional effects on preattentive vision: spatial precues affect the detection of simple features. *J Exp Psychol Hum Percept Perform* 1999;25(2):341–7.
 - [50] Halligan PW, Marshall JC. Spatial neglect: position papers on theory and practice. *Neuropsychol Rehab* 1994;4:99–240.
 - [51] Battersby WS, Bender MB, Pollack M, Kahn RL. Unilateral spatial agnosia (inattention) in patients with cerebral lesions. *Brain* 1956;79:68–93.
 - [52] Bisiach E. Mental representation in unilateral neglect and related disorders. *Q J Exp Psychol* 1993;46A(3):435–61.
 - [53] Bisiach E, Pizzamiglio L, Nico D, Antonucci G. Beyond unilateral neglect. *Brain* 1996;119:851–7.
 - [54] Jeannerod M, Biguer B. The directional coding of reaching movements. A visuomotor conception of visuospatial neglect. In: Jeannerod M, editor. *Neurophysiological and neuropsychological aspects of spatial neglect*, vol. 45. Amsterdam: Elsevier, 1987. p. 87–113.
 - [55] Karnath H-O. Subjective body orientation in neglect and the interactive contribution of neck muscle proprioception and vestibular stimulation. *Brain* 1994;117:1001–12.
 - [56] Heilman KM, Watson RT, Valenstein E. Neglect and related disorders. In: Heilman KM, Valenstein E, editors. *Clinical neuropsychology*. New York: Oxford University Press, 1993. p. 279–336.
 - [57] Kinsbourne M. A model for the mechanism of unilateral neglect of space. *Trans Am Neurol Assoc* 1970;95:143–6.
 - [58] Heilman KM, Bowers D, Coslett HB, Whelan H, Watson RT. Directional hypokinesia: prolonged reaction times for leftward movements in patients with right hemisphere lesions and neglect. *Neurology* 1985;35:855–9.
 - [59] Gentilini M, Barbieri C, De Renzi E, Faglioni P. Space exploration with and without the aid of vision in hemisphere-damaged patients. *Cortex* 1989;25:643–51.
 - [60] Fujii T, Fukatsu R, Kimura I, Saso S, Kogure K. Unilateral spatial neglect in visual and tactile modalities. *Cortex* 1991;27:339–43.
 - [61] Hjalton H, Caneman G, Tegnér R. Visual and tactile rod bisection in unilateral neglect. *Cortex* 1993;583–8.
 - [62] Bartolomeo P, D'Erme P, Gainotti G. The relationship between visuospatial and representational neglect. *Neurology* 1994;44:1710–4.
 - [63] Soroker N, Calamaro N, Glicksohn J, Myslobodsky MS. Auditory inattention in right-hemisphere-damaged patients with and without visual neglect. *Neuropsychologia* 1997;35:249–56.
 - [64] Hjalton H, Tegnér R. Darkness improves line bisection in unilateral spatial neglect. *Cortex* 1992;28:353–8.
 - [65] Posner MI. *Chronometric explorations of mind*. Hillsdale, NJ: Lawrence Erlbaum, 1978.
 - [66] Reuter-Lorenz PA, Jha AP, Rosenquist JN. What is inhibited in inhibition of return? *J Exp Psychol Hum Percept Perform* 1996;22:367–78.
 - [67] Bisiach E, Luzzatti C. Unilateral neglect of representational space. *Cortex* 1978;14:129–33.
 - [68] Bisiach E, Luzzatti C, Perani D. Unilateral neglect, representational schema and consciousness. *Brain* 1979;102:609–18.
 - [69] Bisiach E, Capitani E, Luzzatti C, Perani D. Brain and conscious representation of outside reality. *Neuropsychologia* 1981;19:543–51.
 - [70] Bisiach E, Berti A. Dyschiria. An attempt at its systemic explanation. In: Jeannerod M, editor. *Neurophysiological and neuropsychological aspects of spatial neglect*. Amsterdam: Elsevier, 1987. p. 183–201.
 - [71] Halligan PW, Marshall JC. Toward a principled explanation of unilateral neglect. *Cogn Neuropsychol* 1994;11(2):167–206.
 - [72] Posner MI, Walker JA, Friedrich FJ, Rafal RD. Effects of parietal injury on covert orienting of attention. *J Neurosci* 1984;4:1863–74.
 - [73] Morrow LA, Ratcliff G. The disengagement of covert attention and the neglect syndrome. *Psychobiology* 1988;16(3):261–9.
 - [74] Heilman KM, Valenstein E. Mechanisms underlying hemispatial neglect. *Ann Neurol* 1979;5:166–70.
 - [75] Robertson IH. The relationship between lateralised and non-lateralised attentional deficits in unilateral neglect. In: Robertson IH, Marshall JC, editors. *Unilateral neglect: clinical and experimental studies*. Hove, UK: Lawrence Erlbaum, 1993. p. 257–75.
 - [76] Kinsbourne M. Hemi-neglect and hemisphere rivalry. In: Weinstein EA, Friedland RP, editors. *Hemi-inattention and hemisphere specialization*, vol. 18. New York: Raven Press, 1977. p. 41–9.
 - [77] Kinsbourne M. Mechanisms of unilateral neglect. In: Jeannerod M, editor. *Neurophysiological and neuropsychological aspects of spatial neglect*. Amsterdam: Elsevier, 1987. p. 69–86.
 - [78] Kinsbourne M. Orientational bias model of unilateral neglect: evidence from attentional gradients within hemispace. In: Robertson IH, Marshall JC, editors. *Unilateral neglect: clinical and experimental studies*. Hove, UK: Lawrence Erlbaum, 1993. p. 63–86.
 - [79] Berlucchi G. Two hemispheres but one brain. *Behav Brain Sci* 1983;6:171–2.
 - [80] Corbetta M, Miezin FM, Shulman GL, Petersen SE. A PET study of visuospatial attention. *J Neurosci* 1993;13(3):1202–26.
 - [81] Compton PE, Grossenbacher P, Posner MI, Tucker DM. A cognitive-anatomical approach to attention in lexical access. *J Cogn Neurosci* 1991;3(4):304–12.

- [82] Vuilleumier P, Hester D, Assal G, Regli F. Unilateral spatial neglect recovery after sequential strokes. *Neurology* 1996;46:184–9.
- [83] Meyer JS, Obara K, Muramatsu K. Diaschisis. *Neurol Res* 1993;15(6):362–6.
- [84] Vallar G, Guariglia C, Rusconi ML. Modulation of the neglect syndrome by sensory stimulation. In: Thier P, Karnath HO, editors. *Parietal lobe contributions to orientation in 3D-space*. Heidelberg: Springer, 1997. p. 555–78.
- [85] Chokron S, Bartolomeo P. Réduire expérimentalement la négligence spatiale unilatérale: revue de la littérature et implications théoriques. *Rev Neuropsychol* 1999;9(2–3):129–65.
- [86] Mark VW, Kooistra CA, Heilman KM. Hemispatial neglect affected by non-neglected stimuli. *Neurology* 1988;38(8):640–3.
- [87] Marshall JC, Halligan PW. Does the midsagittal plane play any privileged role in left neglect? *Cogn Neuropsychol* 1989;6(4):403–22.
- [88] Shepherd M, Findlay JM, Hockey RJ. The relationship between eye movements and spatial attention. *Q J Exp Psychol* 1986;38A:475–791.
- [89] Kowler E, Anderson E, Doshier B, Blaser E. The role of attention in the programming of saccades. *Vision Res* 1995;35(13):1897–916.
- [90] Hoffman JE, Subramaniam B. The role of visual attention in saccadic eye movements. *Percept Psychophys* 1995;57(6):787–95.
- [91] De Renzi E, Colombo A, Faglioni P, Gibertoni M. Conjugate gaze paresis in stroke patients with unilateral damage: an unexpected instance of hemispheric asymmetry. *Arch Neurol* 1982;39:482–6.
- [92] De Renzi E, Gentilini M, Faglioni P, Barbieri C. Attentional shifts toward the rightmost stimuli in patients with left visual neglect. *Cortex* 1989;25:231–7.
- [93] Cohn R. Eyeball movements in homonymous hemianopia following simultaneous bitemporal object presentation. *Neurology* 1972;22:12–4.
- [94] Anderson B. Spared awareness for the left side of internal visual images in patients with left-sided extrapersonal neglect. *Neurology* 1993;43:213–6.
- [95] Ládavas E, Petronio A, Umiltà C. The deployment of visual attention in the intact field of hemineglect patients. *Cortex* 1990;26(3):307–17.
- [96] Howes D, Boller F. Simple reaction time: evidence for focal impairment from lesions of the right hemisphere. *Brain* 1975;98:317–32.
- [97] D'Erme P, Robertson I, Bartolomeo P, Daniele A, Gainotti G. Early rightwards orienting of attention on simple reaction time performance in patients with left-sided neglect. *Neuropsychologia* 1992;30(11):989–1000.
- [98] Bartolomeo P. The novelty effect in recovered hemineglect. *Cortex* 1997;33(2):323–32.
- [99] Bartolomeo P, D'Erme P, Perri R, Gainotti G. Perception and action in hemispatial neglect. *Neuropsychologia* 1998;36(3):227–37.
- [100] Bartolomeo P, Siéoff E, Decaix C, Chokron S. Modulating the attentional bias in unilateral neglect: the effects of the strategic set. *Exp Brain Res* 2001;137(3/4):424–31.
- [101] Smania N, Martini MC, Gambina G, Tomelleri G, Palamara A, Natale E, Marzi CA. The spatial distribution of visual attention in hemineglect and extinction patients. *Brain* 1998;121(Pt 9):1759–70.
- [102] Bartolomeo P, Chokron S. Left unilateral neglect or right hyperattention? *Neurology* 1999;53:2023–7.
- [103] Fiorelli M, Blin J, Bakchine S, Laplane D, Baron JC. PET studies of cortical diaschisis in patients with motor hemineglect. *J Neurol Sci* 1991;104:135–42.
- [104] Pantano P, Di Piero V, Fieschi C, Judica A, Guariglia C, Pizzamiglio L. Pattern of CBF in the rehabilitation of visual spatial neglect. *Int J Neurosci* 1992;66:153–61.
- [105] Perani D, Vallar G, Paulesu E, Alberoni M, Fazio F. Left and right hemisphere contribution to recovery from neglect after right hemisphere damage—an [¹⁸F]FDG PET study of two cases. *Neuropsychologia* 1993;31(2):115–25.
- [106] Friedrich FJ, Egly R, Rafal RD, Beck D. Spatial attention deficits in humans: a comparison of superior parietal and temporal–parietal junction lesions. *Neuropsychologia* 1998;12:193–207.
- [107] Karnath H-O. Deficits of attention in acute and recovered hemineglect. *Neuropsychologia* 1988;20:27–45.
- [108] Mattingley JB, Bradshaw JL, Bradshaw JA, Nettleton NC. Residual rightward attentional bias after apparent recovery from right hemisphere damage: implications for a multicomponent model of neglect. *J Neurol Neurosurg Psychiatry* 1994;57:597–604.
- [109] Bartolomeo P, Chokron S, Siéoff E. Facilitation instead of inhibition for repeated right-sided events in left neglect. *NeuroReport* 1999;10(16):3353–7.
- [110] Losier BJ, Klein RM. A review of the evidence for a disengage deficit following parietal lobe damage. *Neurosci Biobehav Rev* 2001;25(1):1–13.
- [111] Ládavas E, Carletti M, Gori G. Automatic and voluntary orienting of attention in patients with visual neglect: horizontal and vertical dimensions. *Neuropsychologia* 1994;32:1195–208.
- [112] Posner MI, Cohen Y, Rafal RD. Neural systems control of spatial orienting. *Philos Trans R Soc Lond B* 1982;298(1089):187–98.
- [113] Anderson B, Mennemeier M, Chatterjee A. Variability not ability: another basis for performance decrements in neglect. *Neuropsychologia* 2000;38(6):785–96.
- [114] Bartolomeo P, Siéoff E, Chokron S, Decaix C. Variability of response times as a marker of diverted attention. *Neuropsychologia* 2001;39(4):358–63.
- [115] Milner AD, Harvey M. Distortion of size perception in visuospatial neglect. *Curr Biol* 1995;5(1):85–9.
- [116] Duncan J, Bundesen C, Olson A, Humphreys G, Chavda S, Shibuya H. Systematic analysis of deficits in visual attention. *J Exp Psychol Gen* 1999;128(4):450–78.
- [117] Bundesen C. A theory of visual attention. *Psychol Rev* 1990;97(4):523–47.
- [118] Chokron S, Brickman AM, Wei T, Buchsbaum MS. Hemispheric asymmetry for selective attention. *Cogn Brain Res* 2000;9(1):85–90.
- [119] Tabert MH, Chokron S, Tang CY, Wei T, Brickman AM, Buchsbaum MS. Visual target detection paradigm for the study of selective attention. *Brain Res Protocols* 2000;6(1–2):80–5.
- [120] Danziger S, Kingstone A, Rafal RD. Orienting to extinguished signals in hemispatial neglect. *Psychol Sci* 1998;9(2):119–23.
- [121] Bisiach E, Rusconi ML, Peretti VA, Vallar G. Challenging current accounts of unilateral neglect. *Neuropsychologia* 1994;32:1431–4.
- [122] Ishiai S, Seki K, Koyama Y, Gono S. Ineffective leftward search in line bisection and mechanisms of left unilateral spatial neglect. *J Neurol* 1996;243(5):381–7.
- [123] Barton JJ, Behrmann M, Black S. Ocular search during line bisection. The effects of hemi-neglect and hemianopia. *Brain* 1998;121(Pt 6):1117–31.
- [124] Ládavas E, Zeloni G, Zaccara G, Gangemi P. Eye movements and orienting of attention in patients with visual neglect. *J Cogn Neurosci* 1997;9(1):67–74.
- [125] Volpe BT, Ledoux JE, Gazzaniga MS. Information processing of visual stimuli in an extinguished field. *Nature* 1979;282(5740):722–4.
- [126] Marshall JC, Halligan PW. Blindsight and insight into visuo-spatial neglect. *Nature* 1988;336:766–7.
- [127] D'Erme P, Robertson I, Bartolomeo P, Daniele A. Unilateral neglect: the fate of the extinguished visual stimuli. *Behav Neurol* 1993;6:143–50.
- [128] Gainotti G, Messerli P, Tissot R. Qualitative analysis of unilateral spatial neglect in relation to the laterality of cerebral lesions. *J Neurol Neurosurg Psychiatry* 1972;35:545–50.
- [129] Gainotti G, D'Erme P, Monteleone D, Silveri MC. Mechanisms of unilateral spatial neglect in relation to laterality of cerebral lesions. *Brain* 1986;109:599–612.
- [130] Driver J, Halligan PW. Can visual neglect operate in object-centered co-ordinates? An affirmative single-case study. *Cogn Neuropsychol* 1991;8(6):475–96.

- [131] Driver J, Baylis GC, Goodrich SJ, Rafal RD. Axis-based neglect of visual shapes. *Neuropsychologia* 1994;32(11):1353–65.
- [132] Caramazza A, Hillis AE. Spatial representation of words in the brain implied by studies of a unilateral neglect patient. *Nature* 1990;346(6281):267–9.
- [133] Farah MJ, Brunn JL, Wong AB, Wallace MA, Carpenter PA. Frames of reference for allocating attention to space: evidence from the neglect syndrome. *Neuropsychologia* 1990;28(4):335–47.
- [134] Hillis AE, Rapp B. Unilateral spatial neglect in dissociable frames of reference: a comment on Farah, Brunn, Wong, Wallace, and Carpenter (1990). *Neuropsychologia* 1998;36(11):1257–62.
- [135] Behrmann M, Moscovitch M. Object-centered neglect in patients with unilateral neglect: effects of left-right coordinates of objects. *J Cogn Neurosci* 1994;6(1):1–16.
- [136] Behrmann M, Tipper SP. Attention accesses multiple reference frames: evidence from visual neglect. *J Exp Psychol Hum Percept Perform* 1999;25(1):83–101.
- [137] Raymond JE, Shapiro KL, Arnell KM. Temporary suppression of visual processing in an RSVP task: an attentional blink? *J Exp Psychol Hum Percept Perform* 1992;18(3):849–60.
- [138] Husain M, Shapiro K, Martin J, Kennard C. Abnormal temporal dynamics of visual attention in spatial neglect patients. *Nature* 1997;385:154–6.
- [139] Robertson IH, Mattingley JB, Rorden C, Driver J. Phasic alerting of neglect patients overcomes their spatial deficit in visual awareness. *Nature* 1998;395(6698):169–72.
- [140] Feeney DM, Baron JC. Diaschisis. *Stroke* 1986;17(5):817–30.
- [141] Posner MI, Inhoff AW, Friedrich FJ, Cohen A. Isolating attentional mechanisms: a cognitive-anatomical analysis. *Psychobiology* 1987;15:107–12.
- [142] Posner MI, Petersen SE. The attention system of human brain. *Annu Rev Neurosci* 1990;13:25–42.
- [143] Carpenter RH, Williams ML. Neural computation of log likelihood in control of saccadic eye movements. *Nature* 1995;377(6544):59–62.
- [144] Lynch JC, Mountcastle VB, Talbot WH, Yin TC. Parietal lobe mechanisms for directed visual attention. *J Neurophysiol* 1977;40(2):362–89.
- [145] Colby CL, Goldberg ME. Space and attention in parietal cortex. *Annu Rev Neurosci* 1999;22:319–49.
- [146] Knight RT, Grabowecky MF, Scabini D. Role of human prefrontal cortex in attention control. *Adv Neurol* 1995;66:21–34.
- [147] Gottlieb JP, Kusunoki M, Goldberg ME. The representation of visual salience in monkey parietal cortex. *Nature* 1998;391(6666):481–4.
- [148] Fries W. Cortical projections to the superior colliculus in the macaque monkey: a retrograde study using horseradish peroxidase. *J Comp Neurol* 1984;230(1):55–76.
- [149] Paré M, Wurtz RH. Monkey posterior parietal cortex neurons antidromically activated from superior colliculus. *J Neurophysiol* 1997;78(6):3493–7.
- [150] Sapir A, Soroker N, Berger A, Henik A. Inhibition of return in spatial attention: direct evidence for collicular generation. *Nat Neurosci* 1999;2(12):1053–4.
- [151] Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman GL. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci* 2000;3(3):292–7.
- [152] Pizzamiglio L, Antonucci G, Judica A, Montenero P, Razzano C, Zoccolotti P. Cognitive rehabilitation of the hemineglect disorder in chronic patients with unilateral right brain damage. *J Clin Exp Neuropsychol* 1992;14(6):901–23.
- [153] Alivisatos B, Milner B. Effects of frontal or temporal lobectomy on the use of advance information in a choice reaction time task. *Neuropsychologia* 1989;27(4):495–503.
- [154] Guitton D, Bachtel HA, Douglas RM. Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal-directed saccades. *Exp Brain Res* 1985;58:455–72.
- [155] Rosen AC, Rao SM, Caffarra P, Scaglioni A, Bobholz JA, Woodley SJ, Hammeke TA, Cunningham JM, Prieto TE, Binder JR. Neural basis of endogenous and exogenous spatial orienting. A functional MRI study. *J Cogn Neurosci* 1999;11(2):135–52.
- [156] Funahashi S, Chafee MV, Goldman-Rakic PS. Prefrontal neuronal activity in rhesus monkeys performing a delayed anti-saccade task. *Nature* 1993;365(6448):753–6.
- [157] Bartolomeo P. Inhibitory processes and compensation for spatial bias after right hemisphere damage. *Neuropsychol Rehab* 2000;10(5):511–26.
- [158] Hier DB, Mondlock J, Caplan LR. Recovery of behavioral abnormalities after right hemisphere stroke. *Neurology* 1983;33:345–50.
- [159] Pizzamiglio L, Perani D, Cappa SF, Vallar G, Paolucci S, Grassi F, Paulesu E, Fazio F. Recovery of neglect after right hemispheric damage: H2(15)O positron emission tomographic activation study. *Arch Neurol* 1998;55:561–8.
- [160] Kanwisher N. Neural events and perceptual awareness. *Cognition* 2001;79(1–2):89–113.
- [161] Neisser U. *Cognitive psychology*. New York: Appleton (Century/Crofts), 1967.
- [162] Joseph JS, Chun MM, Nakayama K. Attentional requirements in a preattentive feature search task. *Nature* 1997;387(6635):805–7.
- [163] Di Lollo V., Kawahara J, Zuvic SM, Visser TA. The preattentive emperor has no clothes: a dynamic redressing. *J Exp Psychol Gen* 2001;130(3):479–92.
- [164] O'Regan JK, Rensink RA, Clark JJ. Change-blindness as a result of 'mudsplashes'. *Nature* 1999;398(6722):34.
- [165] Mack A, Rock I. *Inattention blindness*. Cambridge, MA: MIT Press, 1998.
- [166] McCormick PA. Orienting attention without awareness. *J Exp Psychol Hum Percept Perform* 1997;23(1):168–80.
- [167] Weiskrantz L. *Consciousness lost and found: a neuropsychological exploration*. Oxford: Oxford University Press, 1997.
- [168] Kentridge RW, Heywood CA, Weiskrantz L. Attention without awareness in blindsight. *Proc R Soc Lond B Biol Sci* 1999;266(1430):1805–11.
- [169] O'Regan JK, Noë A. A sensorimotor account of vision and visual consciousness. *Behav Brain Sci* 2001;24(5) in press.
- [170] O'Regan JK. Solving the real mysteries of visual perception: the world as an outside memory. *Can J Psychol* 1992;46(3):461–88.
- [171] Bartolomeo P, Chokron S. Visual awareness relies on exogenous orienting of attention: evidence from unilateral neglect (commentary on O'Regan and Noë: a sensorimotor account of vision and visual consciousness). *Behav Brain Sci* 2001;24(5) in press.
- [172] Robertson IH, Hawkins K. Limb activation and unilateral neglect. *Neurocase* 1999;5:153–60.
- [173] Rossetti Y, Rode G, Pisella L, Farnè A, Li L, Boisson D, Perenin MT. Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature* 1998;395:166–9.
- [174] Posner MI. Attention: the mechanisms of consciousness. *Proc Natl Acad Sci USA* 1994;91(16):7398–403.