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# Pre-requisites for conscious awareness: Clues from electrophysiological and behavioral studies of unilateral neglect patients

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## Abstract

Encoding sensory events entails processing of several physical attributes. Is the processing of any of these attributes a pre-requisite of conscious awareness? This selective review examines a recent set of behavioral and event-related potentials, studies conducted in patients with visual and auditory unilateral neglect or extinction, with the aim of establishing what aspects of initial processing are impaired in these patients. These studies suggest that extinguished visual stimuli excite the sensory cortices, but perhaps to a lesser degree than acknowledged stimuli do. However, encoding spatial attributes of auditory and visual stimuli appear to be preferentially impaired. In light of results from patients with other neuro-behavioral deficits, it is argued that egocentric spatial information is an essential pre-requisite for knowing that an external event occurred. In contrast, information handled by mostly domain-specific circuits, such as in the ventral temporal lobe, supports awareness of the identity of a stimulus, but not of its mere presence. Without spatial information, the stimulus identity will remain implicit.

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## 1. Introduction

Understanding the neural correlates of conscious awareness (NCC) is a formidable task. Although we live in an era in which the skull is becoming more and more transparent, conceptual difficulties frequently block our progress as much as technical difficulties do. Nevertheless, in the last decade attempts to correlate the subjective percept with measures of neural activity increased. The majority of these studies looked at changes in neural activity (or its hemodynamic correlate) associated with changes in subjective perception, when the latter is dissociated from objective change in stimulation. Examples include the phenomena of binocular rivalry, bistable percepts, and change blindness (Beck, Rees, Frith, & Lavie, 2001; Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998; Lumer, Friston, & Rees, 1998; see also Logothetis (1998), for monkey studies). Changes in subjective perception, independent of the actual stimulation, correlated with changes of activity in ventral temporal visual areas (e.g., the “fusiform face area”), as well as parietal and dorso-lateral frontal regions (see summaries of the findings and further discussions in Crick & Koch, 1998; Rees, 2001; Rees, Krieman, & Koch, 2002; Rees & Lavie, 2001). Yet, most of these studies required the subjects to “detect” and report changes in subjective perception. Therefore, inasmuch as conscious awareness is not just an epiphenomenon of other cognitive processes, it is a methodological and conceptual challenge to dissociate the observed activations from effects of attention processes (see Rees & Lavie, 2001) and other processes related to target detection in general (Donchin & Coles, 1988; Halgren et al., 1995; Kiehl, Laurens, Duty, Forster, & Liddle, 2000; Verleger, 1988).

The studies I review here take a complementary approach to the study of conscious awareness (CA). Rather than starting “at the top,” trying to find correlates of CA as it is experienced, this approach starts “at the bottom,” asking what the pre-requisites of CA may be. That is, what stages of initial processing are necessary for the *occurrence of an external event* to become the subject of our CA? More specifically, are there some types of information, processes, or structures, operating at an early stage of stimulus analysis, which are *sine qua non* for the establishment of CA? These processes or structures are not candidates for instantiating CA itself, but would, rather, make CA possible under the right circumstances. I assume that by understanding what types of information are necessary for CA, we may gain some insight onto its origin, ecological role, and neural underpinnings. More precisely, within the tradition of neuropsychology, the present approach looks at the kinds of breakdown in information processing which are associated with lack of CA. In examining what data are missing in cases where CA is impaired, we may find good candidates for pre-requisites for normal CA.

Two points become immediately apparent within such an approach. First, cause and effect must be clearly defined. Some breakdown in information processing may result from, rather than contribute to, impairments in CA. In this review I will try to walk on somewhat safer ground by investigating early, automatic, pre-attentive processes, which most likely do not depend on conscious processing. Second, although behavior may disclose certain types of implicit information processing, the individual cannot usually provide reliable information about *missing* components. With lack of CA, the reliability of insight may become even more tenuous. It is

pertinent thus to use measures that tap into lower levels of information processing, irrespective of awareness. Hence, the focus here will be on electrophysiological methods, which provide information about stages of neural processing at the sub-second time scale. In particular, I will discuss electrophysiological studies of patients with the condition of unilateral neglect or extinction. Since past discussions of this topic concentrated almost exclusively on the visual modality, I will put special emphasis on recent evidence from auditory neglect, looking for converging information from both modalities.

Unilateral neglect (UN) and extinction serve together as a prototypical model for impairment of CA following brain damage. Patients with UN are not aware of many events happening on the side opposite the side of their lesion (contralesional side). Therefore, a UN patient with right hemisphere damage (RHD) may not respond when addressed from the left side, may not eat food placed on the left side of his or her plate, and may even disregard the left side of his or her own body (Heilman, Watson, & Valenstein, 1993). On formal tests the patients typically fail to overtly detect simple stimuli on the left side of an array, and produce drawings missing details on the left side, either when copying a model or when freely drawing. Neglect phenomena may appear in the visual, auditory, and/or tactile modalities (e.g., Gainotti, De Bonis, Daniele, & Caltagirone, 1989; Soroker, Calamaro, Glickson, & Myslobodsky, 1997) and they are dissociable from primary sensory deficits (e.g., Halligan, Marshall, & Wade, 1990). Extinction denotes a situation where the failure to detect a stimulus on the contralesional side occurs during bilateral simultaneous stimulation, but not when the contralesional event appears in isolation (e.g., Rapcsak, Watson, & Heilman, 1987). Although some argue that UN and extinction are not identical entities, they most frequently co-occur (with extinction typically following UN in the course of recovery from stroke) and in many cases it is hard to tell whether a test considered a test for UN (e.g., detection of lines in a bilateral array) cannot be regarded a test for extinction as well (see Driver, Mattingley, Rorden, & Davis, 1997). More importantly for the present purposes, UN and extinction share the bias towards the ipsilesional side of space, with items on the other side dropping from CA. For the sake of brevity, I will use the term UN in the broader sense, as referring to both unilateral neglect proper and extinction, capturing this common bias. For the present discussion, it is important to note that UN provides a unique methodological advantage as every patient may serve as his or her own control, because the lack of CA is limited to one part of space but not others.

An intriguing aspect of UN is that tests employing measures of implicit processing reveal that neglected stimuli are in fact deeply processed, even up to a semantic level (e.g., Berti & Rizzolatti, 1992; Berti et al., 1992; Karnath & Hartje, 1987; Marshall & Halligan, 1989; McGlinchey-Beroth, Milberg, Verfaellie, Alexander, & Kilduff, 1993; Ro & Rafal, 1996; Volpe, Ledoux, & Gazzaniga, 1979). For example, an extinguished picture of an object (e.g., a baseball bat), of which the patient is not overtly aware, may facilitate (prime) the processing of a subsequent related word (e.g., “ball”) in a lexical decision task (McGlinchey-Beroth et al., 1993). In another example, the presentation of two different exemplars of the same category (e.g., two different fruits) can facilitate categorization relative to presentation of two exemplars of different categories (e.g., a fruit and an animal), even though the left of the two

exemplars is not consciously perceived in either case (Berti & Rizzolatti, 1992). This expanding body of evidence provides invaluable information about the kinds of processes that may take place without need for CA. At the same time, it fails to address the question of what is actually missing. Is the processing of neglected information fully intact, or are some aspects of the information consistently corrupted? To address this question, a few studies in the last decade have used event related potentials (ERPs), as an independent measure of information processing in UN. ERPs are extracted from the electroencephalogram (EEG) and reflect electrical brain activity time-locked to a stimulus or cognitive event with a resolution of milliseconds. These studies, addressing early stages of information processing in particular, will be described next (for a comprehensive review of older studies and those addressing later components see Deouell, Hämäläinen, & Bentin (2000)).

## **2. Strength of cortical response**

ERPs have been used to investigate UN in vision, audition, and tactile sensation. Visual, auditory, and somatosensory evoked potentials (VEPs, AEPs, and SEPs, respectively) refer to an obligatory series of positive and negative potentials evoked by supra-threshold stimuli in their respective modalities. The latency of these potentials ranges from around 20 to 200 ms from stimulus onset, depending on the transmission time from the periphery to the particular primary and secondary sensory cortices where these potentials are assumed to originate. Early attempts to test SEPs and VEPs in UN revealed no major differences between stimuli presented to the neglected side and those presented to the intact side. For example, Vallar, Sandroni, Rusconi, and Barbieri (1991) applied unilateral electrical stimuli to the wrists of three UN patients with lesions in the right fronto-temporo-parietal regions and one patient with damage in the right occipital periventricular region. The SEPs recorded over the right hemisphere in response to left wrist stimulation were normal and comparable to the SEPs recorded over the left hemisphere in response to right wrist stimulation. Despite the similarity in electrical brain response, the patients were aware of the electrical shocks applied to their right wrist but not to those applied to their left wrist. Similarly, VEPs were within normal range in two of the patients who neglected visual stimuli on their left side, and whose primary visual cortex was largely spared (Vallar et al., 1991). Vallar et al. concluded that the impairment in CA in their UN patients was in “defective access of the output of preserved primary sensory analyses to successive processes involved in conscious perception and in overt verbal response” (p. 1921). Likewise, Viggiano, Spinelli, and Mecacci (1995) concluded, based on a steady-state VEP study (see details of this method below) of a larger group of patients, that “the hypothesis of an important deficit in early sensory processing of information presented to the (neglected) left visual field is weakened.” Other studies suggest however that the pattern of electrical responses to stimuli on the neglected side is in fact abnormal.

First, the inter-hemispheric balance seems to be altered in UN patients. Normally, both auditory and visual lateralized stimuli elicit a stronger early cortical response over the hemisphere contralateral to the side of the stimulus. In contrast, in one

study of UN patients, although the amplitude of the auditory N1 (a negative ERP around 100 ms after stimulus onset, with a major source in the primary auditory cortex) was within normal range over both hemispheres, the response over the intact hemisphere was larger than over the lesioned hemisphere, regardless of the sound-source location (Deouell, Bentin, & Soroker, 2000a). An abnormal contralateral dominance effect for left sided stimuli was observed also for the visual N1 (Verleger, Heide, Butt, Wascher, & Kömpf, 1996). Very recently, Marzi, Girelli, Natale, and Miniussi (2001) reported a different pattern in a group of four patients with UN. In this particular group, not only were the VEPs to contralateral peripheral stimuli smaller when the stimulus was on the left than on the right, but the ipsilateral responses, mediated by callosal transfer, were virtually abolished, for both left *and* right stimuli. Consequently, Marzi et al. suggested that a deficit in transfer of information to a “decision making” center in the left hemisphere might contribute to the neglect of the left side stimuli following right hemisphere damage. Notably, this lack of ipsilateral response was not observed in other studies involving larger groups of patients (Deouell et al., 2000a; Verleger et al., 1996; and R. Verleger, personal communication, January, 2002; compare for example Fig. 1 in Deouell et al., 2000a with Fig. 3 in Marzi et al., 2001). It would be interesting to find out whether the distribution of the lesions can explain the difference between the results of these studies.

Second, there is indication from recent single-case studies that extinguished stimuli do in fact elicit smaller amplitude ERPs compared to detected stimuli. Unlike the studies described above, which compared the processing of left and right stimuli including all trials (i.e., whether or not the subject detected the stimulus), these newer studies compared the electrical response to extinguished contralesional stimuli with the response to detected contralesional stimuli, in the context of a bilateral stimulation. This design takes advantage of the fact that most patients extinguish left sided stimuli on some but not all bilateral presentation trials. In one RHD stroke patient, studied by Marzi, Girelli, Miniussi, Smania, and Maravita (2000), detected brief light flashes on the left elicited the normal VEP pattern of P1 and N1 potentials, whereas extinguished stimuli did not produce observable responses. Both P1 and N1 are non-specific obligatory responses normally elicited by visual stimuli regardless of their identity, with latencies of circa 100 and 170 ms after stimulus onset, respectively. They are attributed to different locations in extrastriate cortex (see Martinez et al., 2001, for a recent review of cortical sources of these potentials). The RHD patient studied by Eimer and colleagues elicited VEPs in response to extinguished stimuli, albeit with reduced amplitudes compared to detected stimuli (unpublished data cited in Driver, Vuilleumier, Eimer, & Rees, 2001). A third patient, tested by Vuilleumier et al. (2001), showed mixed results. As with Marzi et al.’s (2000) patient described above, the P1 component was not detectable when stimuli were extinguished, but was evident when the same stimuli were perceived. In contrast, the N1 component was similarly present in response to both extinguished and detected stimuli. Since Vuilleumier et al. used drawings of faces and objects as their stimuli, they also examined later ERPs, which are normally preferentially evoked by faces rather than other types of objects. Here again, the results were equivocal. The N170 component (Bentin, McCarthy, Perez, Puce, & Allison, 1996), observed over posterior temporal

electrodes 170 ms after stimulus onset, was apparently elicited by detected and extinguished faces alike. In contrast, the P190, another face sensitive component observed over the right central scalp (Jeffreys, 1993), was reduced when the faces were extinguished.

Additional single-case fMRI studies, conducted with some of the same patients and with similar stimuli, showed reduced, but existing, activation of primary and secondary visual cortex, in response to extinguished stimuli (see Driver et al., 2001, for review). The question of whether category-specific areas are activated when stimuli (faces) are extinguished again resulted in mixed fMRI results, as in one study activation of the fusiform “face-area” (FFA) by extinguished faces could not be detected (Vuilleumier et al., 2001), whereas in the other study the FFA was activated even by extinguished stimuli (Rees et al., 2000; see also Driver et al., 2001).

A prudent interpretation of these preliminary and mixed results (obtained from very few patients altogether) is that extinguished visual stimuli result in neural responses at extrastriate sites, including perhaps category-specific regions, but at least some of these responses may be diminished, starting as early as 80 ms after stimulus onset. Lack of awareness may be correlated with diminished activity. A few hypotheses, not necessarily mutually exclusive, have been proposed to explain the lack of awareness despite activation of extrastriate cortex (Crick & Koch, 1998; Driver et al., 2001; Rees, 2001). First, a threshold mechanism may be invoked, whereby only stimuli that drive the amplitude or duration of the neural response beyond some threshold may become conscious (cf. Grill-Spector, Kushnir, Hendler, & Malach, 2000; Zeki & fytche, 1998). Second, whereas the first volley of information may reach the visual cortex, impairment of reentrant activity from higher order areas may preclude awareness (Tononi, Sporns, & Edelman, 1992). FMRI signal, which reflects an integration of activity over seconds, is likely to be sensitive to changes in reentrant processes that serve to prolong firing (cf. Martinez et al., 2001). Third, conscious awareness may require interaction with frontal and parietal circuits (e.g., related to working memory, attention, response selection, etc.) and this may be compromised in the case of the patients (cf. Crick & Koch, 1998; Driver et al., 2001; Vuilleumier et al., 2001). Congruent with this idea, Vuilleumier et al. (2001) found reduced interaction between V1 and left frontal areas and between the left fusiform and left frontal, parietal and temporal regions when stimuli were extinguished (see also Lumer & Rees, 1999).

Whereas all or some of these factors may be necessary for conscious awareness, it should be noted that the diminished activity in the ventral temporal areas elicited on extinction trials might also be the result (rather than the cause) of lack of awareness. This is because the studies that compared extinguished and non-extinguished stimuli necessarily required patients to attend and overtly respond to stimuli, and activity in visual cortical areas is heavily modulated by attention (for reviews of ERP evidence see Hillyard & Anllo-Vento, 1998; Mangun, 1995; Näätänen, 1992; for functional neuroimaging studies see discussions in Brefczynski & DeYoe, 1999; Rees & Lavie, 2001; Schroeder, Mehta, & Foxe, 2001). In other words, on non-extinction trials the detection of the left side stimulus would naturally draw attention to it, augmenting or prolonging the neural response. Rees and Lavie (2001) recently described the close relationship between circuits related to attention deployment and visual awareness,

highlighting the difficulty of distinguishing neurally between these two theoretical concepts. Another set of ERP studies of UN patients concentrated on conditions that do not require a response or discrimination from the patient. These are described in the next section.

### **3. Processing of spatial and non-spatial features**

Deouell et al. (2000a) examined the response to deviations in the auditory environment using the Mismatch Negativity (MMN; Näätänen, 1990; Näätänen, Gailard, & Mäntysalo, 1978). The MMN is an ERP elicited 100–250 ms following the occurrence of a small deviation from regularity in the acoustic environment (e.g., a pitch change in a series of repetitive tones). In contrast to target detection paradigms, elicitation of the MMN does not require the subject to perform a task nor does it impose any attentional requirements. It is typically elicited when the deviation occurs outside the focus of attention and is assumed to reflect an automatically elicited, pre-attentive process (Alho, Sams, Paavilainen, Reinikainen, & Näätänen, 1989; Alho, Woods, Algazi, & Näätänen, 1992; Näätänen, 1991; but see Woldorff, Hackley, & Hillyard, 1991; Woldorff, Hillyard, Gallen, Hampson, & Bloom, 1998). Therefore, the MMN allows assessment of information processing independent from the subjects' report.

Importantly for the present discussion, the MMN paradigm also allows one to examine separately feature-specific processing of auditory stimuli (see Deacon, Nousak, Pilotti, Ritter, & Yang, 1998; Deouell & Bentin, 1998; Schröger, 1995; see Ritter, Deacon, Gomes, Ja. & Vaughan, 1995, for a discussion of the feature-specificity of MMN). Thus, Deouell et al. (2000a) examined the automatic response to deviations in source location (in free field), pitch and duration of auditory stimuli in 10 RHD patients with visual and auditory neglect and their age-matched healthy controls, all instructed to ignore the sounds and concentrate on a silent movie presented straight ahead. The features were chosen to represent extrinsic (location, duration) and intrinsic (pitch) features. Deviations on the right and on the left were compared in a within-subject design. Overall there was a decrease of the MMN elicited by left side deviations relative to the right side deviations. However, of the individual features examined, the only significant and robust difference between left and right side deviations was found for spatial location. No MMN was found for location deviants on the left. This dissociation was absent in a group of six RHD patients without signs of UN (Deouell, Bentin, & Soroker, 2000b), suggesting a specific impairment in pre-attentive, early encoding of auditory spatial information in UN.

This deficit does not appear to be limited to the auditory modality however. Spinelli and her colleagues used a similar approach of examining the processing of distinct features, using steady state-state VEPs (SS-VEPs; Spinelli, Angelelli, De Luca, & Burr, 1996). In this technique the subject is presented with a visual pattern (e.g., a black and white circular checkerboard, or a sinusoidal horizontal grating) reversing its spatial phase (e.g., black checks turn white and vice versa) with a frequency of more than four times a second. This drives the VEPs over visual areas into

displaying a periodic series of peaks, reflecting the frequency of reversal of the evoking pattern. In a series of studies involving relatively large groups of patients with and without UN, Spinelli and her colleagues found that although the amplitude of SS-VEP was not affected significantly in UN patients (Viggiano et al., 1995), the apparent latency (derived from the phase information) of the SS-VEPs elicited by left-side stimuli was prolonged by about 30 ms (Angelelli, De Luca, & Spinelli, 1996; Pitzalis, Spinelli, & Zoccolotti, 1997; Spinelli, Burr, & Morrone, 1994). Next, the latency effect was tested in a group of 10 patients, comparing between luminance-modulated stimuli reversed at a high temporal frequency, and equiluminant gratings where hues were modulated at low temporal frequencies (Spinelli et al., 1996; see also Doricchi, Angelelli, De Luca, & Spinelli, 1996). These two types of stimuli fall within the sensitivity of two rather distinct branches of the visual system, the magnocellular and the parvocellular, starting at the retina and continuing through the lateral geniculate body in the thalamus and the striate and extrastriate visual areas (Hubel & Livingstone, 1987, 1990). The magnocellular system is sensitive to luminance but not to hue differences. Cells in the magnocellular pathway are frequently orientation selective, sensitive to binocular disparity, and capable of following relatively rapid changes in luminance. In contrast, cells in the parvocellular system have smaller receptive fields, are sensitive to hue differences, but are less tuned to spatial configuration and are more sluggish in their response. Congruent with these functional properties, the magnocellular system is a major contributor to spatial processing, whereas the parvocellular system is crucial for fine details and color vision (Hubel & Livingstone, 1987; Livingstone & Hubel, 1987). For example, equiluminant pictures, which can be analyzed in detail by the parvocellular system, but for which the magnocellular system is blind, fail to elicit depth or motion perception (Livingstone, 1988; Livingstone & Hubel, 1987).<sup>1</sup>

Coming back to Spinelli et al.'s (1996) study of UN patients, latency prolongation of SS-VEPs was found for the stimuli presumably tapping the "magnocellular" pathway, but not for the more "parvocellular" stimuli. Considering the characteristics of these pathways, this finding is congruent with a deficit in processing spatial information on the neglected side, sparing non-spatial information. If this is the case, a basic deficit in automatic handling of spatial information within the neglected field is found in both the visual and the auditory modalities. From among the major theoretical accounts of UN, the current findings seem mostly compatible with the notion of a spatial representation deficit underlying UN and extinction (Bisiach & Berti, 1987). The ERP results contribute to our understanding of the functional locus of the spatial deficit by objectively teasing apart processing of different features and by pointing to a deficit in early automatic encoding of spatial information.

Behaviorally, several studies of auditory UN support a specific deficit in spatial information processing. In one of the earlier studies of UN in the auditory modality,

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<sup>1</sup> The magnocellular and the parvocellular pathways should not be confused here with the dorsal and ventral visual pathways. As discussed by Milner and Goodale (1995), although the dorsal system receives a major contribution from the magnocellular system, the input to the ventral visual pathway is more equally mixed.

Bisiach, Cornacchia, Sterzi, and Vallar (1984) found that biased localization of the stimuli is one of the hallmarks of auditory UN. Patients with UN tend to localize stimuli more towards the ipsilesional side than their true location (at least in the case of cortical lesions, see Bellmann, Meuli, & Clarke, 2001; Tanaka, Hachisuka, & Ogata, 1999). Deouell and Soroker (2000) provided behavioral evidence for a specific deficit of auditory localization with relatively preserved non-spatial processing. UN patients were presented with unilateral left, unilateral right, or bilateral pairs of consonant–vowel syllables (e.g., ‘ba’, ‘ga’, etc.), which they were required first to localize as left, right or both, and then to identify. Some patients produced errors of localization and identification even with unilateral left stimuli. However, the most robust deficit was found in the bilateral condition. In this condition, two different, non-fusing syllables were presented simultaneously, one on each side of the patient. On average, the patients extinguished the left stimulus on 77% of the bilateral trials, responding “right” instead of “both.” However, when left extinction trials were examined separately for *identification* of the stimulus, in about a fifth of the trials the patients actually reported the identity of the (extinguished) left sound, while detecting explicitly only a right sound. Considering the number of possible identification answers, the rate of this report was well above what could be expected by chance. Therefore, the processing of spatial attributes of the stimuli was more impaired than the processing of non-spatial attributes. Further support for this conclusion was recently provided by Pavani, Ladavas, and Driver (2002), who compared the ability of patients with unilateral auditory neglect to identify spatial (elevation) and non-spatial (pitch) attributes of auditory stimuli. Pavani et al. found side differences (in favor of the ipsilesional side) in regard to the spatial but not to the non-spatial task.

Mislocalization of sounds towards the ipsilesional side may in fact provide a compensatory mechanism, allowing better awareness of the stimuli. Soroker, Calamaro, and Myslobodsky (1995; Calamaro, Soroker, & Mislobodsky, 1995) also asked UN patients to identify consonant–vowel syllables played by loudspeakers. The patients performed worse when the stimuli were on their left, consistent with left auditory UN. However, in the critical condition, the true loudspeakers were concealed, and a “dummy” loudspeaker was placed either on the left or on the right of the patient, making the patient believe that this was the active source (reminiscent of a “ventriloquism” effect). The critical result of this study within the present context was that the performance of the patients depended on the location of this dummy speaker; placing the dummy speaker on the right of the patients when the stimuli were actually played from the left, improved performance. In view of the ERP and behavioral results described above, it is possible that overt responses to the left sided stimuli were originally hindered in the patients by lack or disruption of spatial information regarding the stimuli. In contrast, providing a spatial anchor in the form of the dummy speaker on the right allowed the implicitly processed information to access CA and effect behavior. The important implication is that a spatial “tag”, even an erroneous one, may be needed for CA to arise.

The “ventriloquist” manipulation described in the previous paragraph may work particularly for the auditory modality because localization of sound is computed on the basis of several cues, rather than being directly encoded on the receptor surface

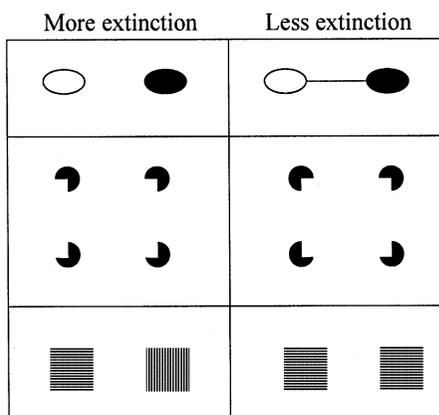


Fig. 1. Illustration of grouping that ameliorates extinction. In these cases (see Humphreys, 1999; Mattingley, Davis, & Driver, 1997; Pavlovskaya, Sagi, Soroker, & Ring, 1997) there was less extinction for grouped stimuli (right column) than for non-grouped stimuli.

(as in the case of retinotopic mapping), and especially because in the case of audio-visual stimuli, the localization of the visual stimulus dominates (e.g., Driver, 1996a; McGurk & MacDonald, 1976; Recanzone, 1998). We (Deouell et al., 2000a) have previously argued that this intrinsic “vulnerability” of sound localization may be one reason why auditory neglect is clinically harder to detect than visual or tactile neglect. In vision, spatial positions are coded directly on the retina and later in the visual cortex. Even though the neglected/extinguished section of space is relative, rather than fixed to specific retinotopic locations (see Kinsbourne, 1993), relative positions are also directly coded at any given moment on the retina. Retinotopic primary visual cortex seems to be activated even in imagery, so that small imagined objects activate the foveal representation and larger objects activate more peripheral parts of the retinotopic map in V1 (e.g., Kosslyn, Thompson, Kim, & Alpert, 1995; see Bisiach & Luzatti, 1978 for a classical description of neglect in imagery). The availability of a source of unequivocal information regarding the location of the stimulus in the visual field, in the form of the pattern of neuronal firing in the retina or in the striate cortex, would make an erroneous visual localization less plausible than in audition.<sup>2</sup>

Still, visual extinction can be reduced by grouping the left and right stimuli according to various Gestalt rules (Fig. 1; see review by Humphreys, 1999). This advantage of grouped objects has been attributed to a preserved within-object spatial coding in the context of disrupted between-object spatial coding (Humphreys, 1999) and to the fact that attention may spread across continuous surfaces, allowing more

<sup>2</sup> However, not all spatial information is directly coded even in vision. For example, retinotopic information has to be combined with eye-in-head and head-on-trunk information in order to determine the location of an object relative to the body axis and to the limbs, and these computations are manipulable in a way that affects UN (see, e.g., Karnath, 1997).

attention to be allocated to the left stimuli within a grouped context (Mattingley et al., 1997). Nevertheless, in the vein of the argument for the “ventriloquism” results, is it possible that perceptually anchoring a previously ignored left stimulus to a right stimulus provides the missing ‘location tag’ for the stimulus and therefore allows CA? In other words, connecting an extinguished left side ellipsoid to an ellipsoid on the right by a line or a common frame (see current Fig. 1 and Humphreys, 1999, Fig. 10.1), making two side by side gratings collinear (Pavlovskaya et al., 1997), or creating an illusion of an occluding object overlapping left and right stimuli (Mattingley et al., 1997) robustly reduce extinction perhaps because the previously extinguished stimuli are now associated with the spatial representation of the stimuli on the ipsilesional side.

#### 4. Multiple spatial codes

The use of “spatial information processing” as a unitary entity that might be impaired in UN is probably too crude however. Ro and Rafal (1996) tested a patient with UN using the Judd and Müller–Lyer illusions. In their version of these famous illusions, the perceptual midline of a line is biased (in normal individuals) by the existence of arrowhead ‘fins’ attached to the edges of a line (Fig. 2). The direction and extent of this bias is determined by the spatial configuration of the fins, i.e., the direction in which the arrowheads point. Ro and Rafal’s patient was influenced by this spatial configuration although she was explicitly unaware of the orientation (or existence) of the left fins. This supports implicit processing of spatial information,

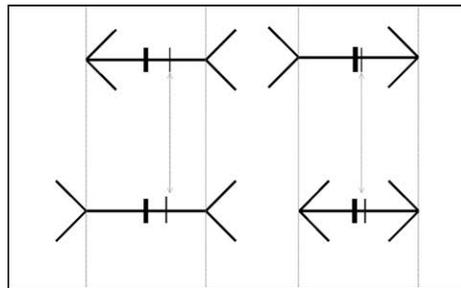


Fig. 2. The Judd illusion (top row) and the Müller–Lyer illusion (bottom row) used by Ro and Rafal (1996). All the horizontal lines are of equal length, but the fins bias perception. The patient was required to mark the midline in each case. The thick vertical lines are at the objective midline (which was not marked of course on the original stimuli). The thin verticals are the midline judgment of a unilateral neglect patient that was unaware of the left fins. In the Judd illusion (top row) normal observers judge the midline to the right of the true midline when the arrowheads point left (top left) and vice versa when the arrowheads point right (top right). As this figure shows, although the patient bisected always to the right of the true midline (consistent with left unilateral neglect), her bisection judgment was influenced by the illusion in the same direction as in normal observers. This is evident especially by the difference between the top and bottom figure in each column, where the only difference is on the (neglected) left.

and could be viewed as an example of unawareness despite *preserved* spatial processing, inconsistent with the above postulated relationship between *lack* of spatial encoding and unawareness in UN.

However, this apparent contradiction may be resolved by examining the case of another patient. Robertson and her colleagues extensively investigated a patient (R.M.) with bilateral parietal lesions following repeated embolic strokes, who could not acknowledge more than one item in his visual field at a time (simultanagnosia), and had no conscious awareness of its spatial location (Friedman-Hill, Robertson, & Treisman, 1995; Phan, Schendel, Recanzone, & Robertson, 2000; Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997). Although R.M. could not explicitly report the location of detected single feature targets, information about the spatial relationship between all the items in a small array were encoded and implicitly effected behavior (Kim & Robertson, 2001). Based on the distribution of R.M.'s lesions, this finding suggests that intact ventral structures can support the processing of spatial relationships among parts of a structured array or an object, but do not afford conscious awareness of the occurrence of sensory events in a coherent space<sup>3</sup> (Kim & Robertson, 2001). This covert spatial processing may have also supported the Judd and Müller-Lyer illusion in Ro and Rafal's patient. This is consistent with the notion of two spatial representations (cf. Humphreys, 1999; Milner & Goodale, 1995), one which supports explicit egocentric and between-object spatial information and has a possible role in motor planning and locomotion, and the other, which supports implicit within-object spatial information for the purpose of identification.<sup>4</sup>

The case of patient D.F., studied by Milner and Goodale (summarized by Milner (1999); Milner & Goodale (1995)), also appears to be relevant here. This patient suffered diffuse brain damage due to carbon monoxide poisoning and lost her ability to recognize form, shape, and orientation. This kind of visual form agnosia is typically associated with damage to the ventral temporal lobe (Farah, 1990). Whereas D.F. fails to recognize shape and orientation, her motor behavior reflects knowledge of the size and orientation of objects. For example, she is able to quite accurately 'post' a plaque through a slanted slot despite being unable to accurately recognize the orientation of the slot. This led Milner and Goodale (1995) to propose that the ventral visual areas are essential for conscious perception, whereas the dorsal areas largely support an unconscious on-line system for motor control (see updated discussion in Milner, 1999).

Milner and Goodale's position seems to be the exact opposite of the idea expressed above, namely that egocentric spatial information, which most likely relates

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<sup>3</sup> Kim and Robertson discussed the unawareness of the patient only to the location of the target; however, the hit rate in fact was quite poor (28%; false alarm: 15%), so that in fact, the patient should be considered unaware not only of the location of the target, but also of the existence of the target, in most trials. The patient was tested however with brief presentations (60 ms) and perhaps with longer exposure more information could have reached CA (L. Robertson, personal communication).

<sup>4</sup> Here again, the way these two systems map into the classical view of dorsal and ventral systems is controversial, and depends on the way these two divisions of the visual system are defined (Milner & Goodale, 1995).

to spatial motor planning, is essential for CA, whereas the domain-specific visual processing areas (e.g., in and near the fusiform gyrus) support the *implicit* processing seen in UN. The contradiction may be resolved if the content of CA is considered. With lesions of the ventral temporal areas (and area V5/MT), patients may lose conscious awareness of specific attributes of the visual scene, which may include the form of shapes and identity of objects (form agnosia), faces (prosopagnosia), color (achromatopsia), and motion (akinetopsia) (Farah, 1990). Zeki and Bartels (1999) maintain that each of the sub-areas specialized for some dimension of visual processing supports a “microconsciousness” for that dimension, which is lost if that particular area is damaged. However, the patients with lesions to the ventral temporal areas are aware of the *existence* of the sensory stimulus (i.e., they know an object is present, only it is not familiar anymore). In contrast, patients with damage to more dorsal areas, like the majority of the UN patients described above, and also like the patients with bilateral parietal lesions, are unaware (or their awareness is unstable) of the mere existence of some sensory events. It is for this kind of CA that the egocentric and between-object (Humphreys, 1999) spatial information might be an essential pre-requisite. This type of explicit spatial information could be based on the ‘dorsal stream’ proper in posterior parietal and frontal cortex (cf. Snyder, Batista, & Andersen, 2000),<sup>5</sup> but possibly also on multi-modal spatial representation in the temporo-parietal junction (Mattingley, Husain, Rorden, Kennard, & Driver, 1998), which is not clearly an exclusive part of either ventral or dorsal stream (cf. Milner & Goodale, 1995).

Since this review emphasized data from the auditory modality, it is important to note that the existence of a dorsal stream, representing auditory spatial information, has been substantiated by recent studies (Alain, Arnott, Hevenor, Graham, & Grady, 2001; Bushara et al., 1999; Lewald, Foltys, & Töpper, 2002; Romanski et al., 1999, 2000). That this pathway overlaps to a great extent the distribution of the visual dorsal pathway may be an anatomical realization of the cross-modal nature of space, especially as it is translated towards controlling action.

## 5. Discussion

In an attempt to explain the paradox of implicit processing of extinguished information, Berti and Rizzolatti speculated that “without spatial encoding and related preparation to act—...—the stimuli do not reach consciousness even when processed to a semantic level” (Berti & Rizzolatti, 1992, p. 349; cf. Driver, 1996b). However, direct evidence for a deficit of spatial encoding was lacking. The ERP and behavioral data described in this paper now give support to this conjecture. Processing spatial and non-spatial attributes of auditory and visual stimuli are differentially affected in UN. Processing of information about space, at a pre-attentive and automatic level is disrupted. Initial encoding of spatial coordinates of an external

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<sup>5</sup> Interestingly, the immediate spread of activity along the dorsal pathway from the occipital to the frontal cortex precedes the spread via the ventral pathway (Foxe & Simpson, 2002).

event may be a critical stage for establishing CA of a sensory event. In the absence of sufficient (but not necessarily veridical or precise) spatial information sensory events may be extensively processed to a semantic level and implicitly effect behavior, but with the exception of some information on single non-localizable features (Friedman-Hill et al., 1995), these events are precluded from CA.

There are several reasons why spatial information might be so critical for awareness of an external event. Kant (1787) argued that space and time are a priori intuitions or concepts of the perceiving mind and that they are preconditions for consciously knowing the world. Only with these concepts is it possible for us to be aware of ourselves (mainly through the concept of time), to differentiate ourselves from the outer world (which is impossible without the concept of space), and therefore to acquire knowledge about the external world. Kant proposed that we cannot know “things in themselves” but only the impressions of these things on our senses, an argument that is consistent with a cognitive neuroscience approach. Kant went on to argue that space and time cannot, in fact, be intrinsic attributes of objects because, unlike intrinsic features such as color or pitch, they would continue to exist in our minds even if all objects were suddenly annihilated (but see Humphreys, 1999 for apparent evidence against this last point). Whether space is a subjective mental construct as Kant proposed or an objective attribute of the world, our cognitive system has evolved in a world in which each external event must happen somewhere. Hence “spaceless” events cannot be acknowledged and may be filtered out at some stage as “noise.”

As exemplified by the cases of auditory neglect described herein, the spatial representation or ‘tag’ linked to the sensory event need not be veridical or precise to support awareness. In some cases (non-visual mainly), external sensory events may be actually perceived when their spatial origin is underdetermined, such as in a case of smell, or some auditory events like a thunder or continuous rumble. I would argue however that in these cases, neural circuits of spatial representation are still invoked normally, if in a very distributed way. The case of real lack of spatial representation (and hence unawareness) is hard to conceive therefore for individuals with intact brains and is seemingly unveiled only in brain-damaged patients. However, anecdotal evidence suggests that even in normal individuals, information emanating from physically “impossible” (and therefore not neurally represented) positions in space is rejected from CA even if it excites sensory system: Hayhoe and Williams (1984) reported that eccentric visual afterimages disappear as eye movements bring the receptive field of the previously stimulated retinal cells to regions blocked by the orbit (and thus outside the visual field), and this has been recently confirmed by stimulating the peripheral retina through the sclera (Cavanagh & Barton, 2001).

From an evolutionary point of view, it seems also plausible that at least part (if not all) of our awareness of external events and objects serves motor planning. Crick and Koch (1995) proposed that “. . . the biological usefulness of visual awareness. . . is to produce the best current interpretation of the visual scene, in the light of past experience either of ourselves or of our ancestors. . . and to make it available, for a sufficient time to the parts of the brain that contemplate, plan and execute voluntary motor outputs” (p. 121). Arguably, there is no survival advantage in being aware of

anything if the organism is not to do something about it, be it escaping, fighting, grasping, or chasing (or the sophisticated elaboration of these actions seen in primates). Clearly, any motor planning requires, primarily, the spatial and temporal attributes of the target, and encoding space and time should, under this premise, be inseparable from any conscious perception. Data from intracranial recording in awake monkeys suggest an overlap of spatial and motor maps (of, e.g., saccades and reach movements) in the parietal and premotor regions and, moreover, show that mapping of external space is neurally dynamic and targeted towards action (Fadiga, Fogassi, Gallese, & Rizzolatti, 2000; Fogassi et al., 1992; Rizzolatti, Fogassi, & Gallese, 1997; Snyder et al., 2000). For example, the visual receptive field of neurons in the monkey's ventral premotor area is locked to the position of the moving hand and moves with it, rather than being locked to fixed retinal coordinates (Graziano, Hu, & Gross, 1997). According to these studies much of space representation in parieto-frontal circuits is linked to moving body parts like the hand, head, eyes, and the mouth (Colby & Goldberg, 1999; Graziano & Gross, 1998). Of course, it cannot be ruled out that some of the spatially tuned neurons in the parietal lobe serve purely perceptual purposes.

From the perceptual side, space and time are necessary for conscious awareness because they are organizing dimensions. Being extrinsic features, as Kant noted, and also being a-modal dimensions, space and time conceivably form the basis for the solution of the binding problem—the problem of putting in register the different features of a perceived object, within and across modalities, to create the normal perception of a whole. According to the influential feature-integration theory (Treisman & Gelade, 1980), individual visual features, such as the color and orientation of a presented stimulus, are encoded pre-attentively and in parallel, but in order to individuate, be aware of, and respond to a visual object, the features need to be bound together. This process is mediated by attention, and relies on cross-referencing the different features through their spatial coordinates (Treisman, 1999). R.M., the patient with simultanagnosia due to bilateral parietal lesions described above, could not bind features of objects in free viewing (Friedman-Hill et al., 1995). Thus, either the spatial information used for binding is of the “dorsal” egocentric type, or this type of spatial information is required for shifting spatial attention to the location of an object that need to be “bound.” In either case, spatial information is critical for binding.

In contrast to vision, the formation of objects in audition (also known as “streaming”) may occur to a great extent automatically and pre-attentively, so that selective attention may be directed to preformed objects, rather than to individual acoustic features (Bergman, 1990; see Alain & Arnott, 2000 for a review of recent supportive evidence). Spatial location may not even be the most salient cue for streaming (e.g., Deutsch, 1975). However, if “properties have to belong to something” (Bergman, 1990, p. 11), and the definition of an auditory object is a mental description of a “physical happening” (ibid), then all the features of a real auditory object (e.g., its pitch, timbre, etc.) must co-occur in space and co-vary in time, as they do in every other modality. Nevertheless, the intrinsic complexity and fuzziness of auditory localization makes the auditory system more lenient to partial ablation of spatial representation.

## 6. Conclusions

The aim of this review was to address the question of the pre-requisites for conscious awareness of external events, using a combination of electrophysiological and behavioral data in the context of the neuropsychological phenomena of unilateral neglect and extinction. Specifically, this selective review examined the relevance of early processing of physical attributes of visual and auditory stimuli to conscious awareness. As in most cases in the domain of the cognitive neuroscience of consciousness, the evidence needs to be corroborated by converging information from other sources. Nevertheless, the studies reviewed revealed important clues. In particular, I highlighted evidence suggesting that a deficit in initial encoding of spatial information may be a fundamental determinant in UN, and therefore that spatial encoding may be necessary (but not sufficient in most likelihood) for conscious awareness of the occurrence of external events.

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