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Preattentive surface and contour grouping in Kanizsa figures: Evidence from parietal extinction

Markus Conci[a,*], Eva Böbel[a], Ellen Matthias[a], Ingo Keller[b], Hermann J. Müller[a], Kathrin Finke[a]

[a] Department of Psychology, Ludwig-Maximilians-University, Munich, Germany
[b] Neurological Clinic Bad Aibling, Germany

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ABSTRACT

Visual extinction commonly occurs after unilateral, parietal brain damage and manifests in a failure to identify contralesional stimuli when presented simultaneously with other, ipsilesional stimuli – but full awareness for single stimulus presentations. However, extinction can be substantially reduced when preattentive grouping operations link fragmentary items across hemifields into a coherent object. For instance, one study demonstrated preserved access to bilateral stimulus segments when these could be grouped to form a Kanizsa square [Mattingley, J. B., Davis, G., & Driver, J. (1997). Preattentive filling-in of visual surfaces in parietal extinction. *Science*, *275*, 671–674]. Here, we investigated the relative contributions of distinct object attributes to the spared access in Kanizsa figure completion in extinction, by systematically varying the degree to which bilateral surface filling-in and contour interpolations group disparate items. We demonstrate that surface information can substantially reduce extinction, whereas contour completions showed comparably smaller influences. In summary, such graded influences of object attributes support recurrent models of grouping, first, linking fragmentary parts into coherent surfaces and, second, interpolating the precise boundaries.

1. Introduction

Natural ambient arrays confront the visual system with a series of computationally demanding operations in order to achieve a consistent representation of the external world. Given our complex environment, visual processing appears to be surprisingly effortless, with the integration of fragmentary information into coherent wholes ('objects') performed seemingly automatically. Nevertheless, theories of visual perception suggest that only a subset of primitive features is encoded automatically at preattentive stages of processing, whereas mechanisms that subserve object integration are only available at later, attentive stages of processing (e.g., Treisman & Gelade, 1980).

A powerful means to test whether selective attention is required for processes of object integration can be provided by the study of brain-damaged patients that show a selective impairment of attentional mechanisms. For instance, discrete lesions predominantly located in the right inferior parietal lobe have led to attentional deficits of hemispatial neglect and extinction (Karnath, Milner, & Vallar, 2002; Kerkhoff, 2001). Neglect and extinction result in a profound loss of perceptual awareness, albeit with, in general, preserved low-level visual processing (Driver & Vuilleumier, 2002, for review). Neglect and extinction frequently co-occur. Neglect is characterized by the failure to perceive or orient towards stimuli that are presented in the contralesional field. Patients with extinction are capable of detecting single stimuli, but they tend to miss contralesional stimuli if these are presented together with ipsilesional stimuli. Importantly, several cases suggest that neglect and extinction do not only, or simply, result from a deficit in spatial orienting. Rather, they indicate a competitive disadvantage for selection from the contralesional field due to disrupted processes of selective attention (Baylis, Driver, & Rafal, 1993; Humphreys, Romani, Olson, Riddoch, & Duncan, 1994; Ward and Goodrich, 1996).

Despite of impaired mechanisms of attentional selection, patients with neglect or extinction have shown largely preserved access to integrated object information (Driver, 1995, for review). For instance, residual processing has been demonstrated for object groupings and basic processes that subserve figure-ground segmentation (e.g., Brooks, Wong, & Robertson, 2005; Driver, Baylis, & Rafal, 1992; Gilchrist, Humphreys, & Riddoch, 1996; Marshall & Halligan, 1994; Pavlovskaya, Sagi, Soroker, & Ring, 1997; Robertson, Eglin, & Knight, 2003; Ward, Goodrich, & Driver, 1994). The typical finding of these studies was that perceptual groupings strongly modulated the severity of the attentional deficit. When fragmentary items could be grouped into a coherent representation, neglect and extinction are less profound than when a corresponding

* Corresponding author at: Allgemeine und Experimentelle Psychologie, Department Psychologie, Ludwig-Maximilians-Universität, Leopoldstr. 13, D-80802 München, Germany. Tel.: +49 89 2180 2975; fax: +49 89 2180 5211.
E-mail address: conci@psy.uni-muenchen.de (M. Conci).

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ungrouped stimulus is presented. This suggests that mechanisms responsible for the integration of discrete items into coherent entities may operate even though attentional processing is clearly impaired.

A particularly strong case for the preattentive encoding of integrated object information can be demonstrated in experiments that investigate how visual illusions are perceived subsequent to the development of neglect. For instance, in line bisection tasks, illusory stimuli such as Müller-Lyer figures, Judd figures (Ro & Rafal, 1996), or Kanizsa figures (Vuilleumier & Landis, 1998; Vuilleumier, Valenza, & Landis, 2001; see Fig. 1A-2 for an example of a Kanizsa square; Kanizsa, 1955) typically lead to bisection errors that indicate an unimpaired access to complete-object representations, comparable to real (i.e., unbiased) configurations. Similarly, Kanizsa figures have been shown to substantially reduce extinction in a visual detection task (Mattingley, Davis, & Driver, 1997). In these experiments, a patient (V. R.) with parietal extinction was presented with a sequence of displays that consisted of four circles arranged to form a square, centered around fixation. On each trial, quarter-segments were briefly removed from the circles, either from the left, from the right, from both sides, or not at all, and V. R.'s task was to detect and report the side(s) of the offsets (see Fig. 1A for an example trial and Fig. 1B for examples of possible stimulus configurations). When the segments were arranged such that no grouping emerged (e.g., with segments faced outwards, see Fig. 1A1), the bilateral removal of quarter-segments showed extinction, that is, a strong increase of errors for offset detections on the left side when presented together with right-sided offsets, relative to unilateral left presentations. However, these typical signs of extinction vanished when V. R. was presented with a stimulus configuration that could be grouped to form a Kanizsa square (as in Fig. 1A2). In this case, no sign of extinction was observable, suggesting that V. R. had access to an integrated illusory object representation. Thus, not only basic perceptual groups seem to be preserved in extinction or neglect, but also item arrangements that induce a strong, illusory object. These results suggest that Kanizsa figures are integrated at preattentive stages of processing.

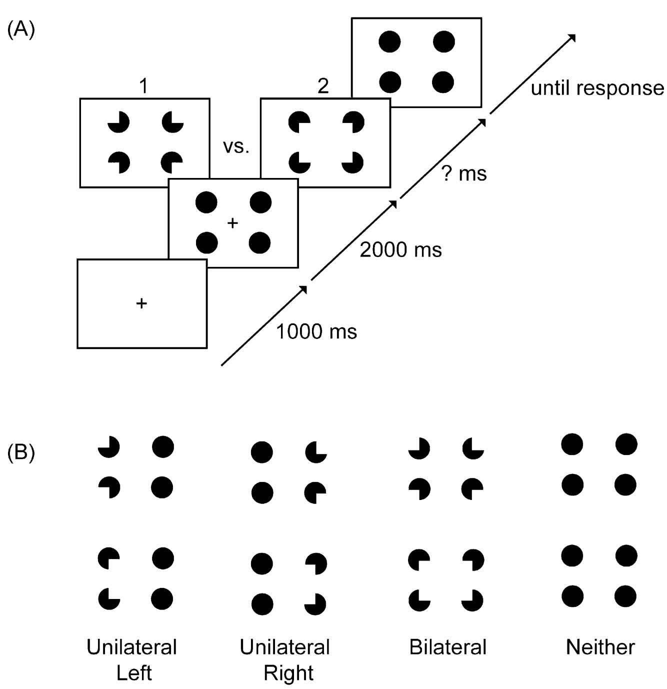

Fig. 1. (A) Schematic example of a trial sequence in the experiment. Each trial started with the presentation of a fixation cross for 1000 ms, followed by a premask display of four placeholder circles presented for 2000 ms. Subsequently, for a short period (specified on an individual basis in a pretest) quarter-segments were removed from the circles. Finally, a postmask containing four placeholder circles was presented until response. In the example sequence, quarter-segments were removed on both sides either presenting a configuration without a centrally grouped shape (1), or a Kanizsa figure (2) that induces an illusory square. (B) Examples of the target display types with quarter-segments removed either at unilateral left, unilateral right, bilateral, or neither side(s). For the different types of targets, a verbal response was required indicating the sides at which quarter-segments were removed (left, right, both, or none).

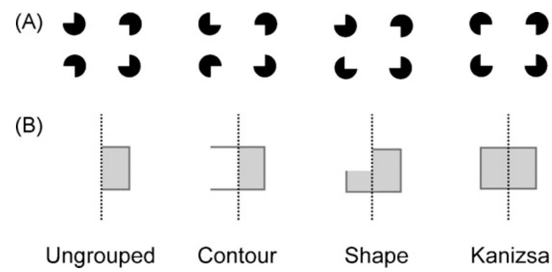

Fig. 2. Examples of the different types of object groupings tested in the experiment. For each stimulus configuration, the local arrangement of inducers (A) is shown together with the representation of the global object (B), illustrating the respective contour and surface stimulation (in dark and light gray, respectively) with relation to the (dashed) vertical midline. Four types of grouping were employed: for Kanizsa stimuli, a complete global square was induced. By contrast, Shape stimuli presented a partial global grouping that consisted of incomplete bilateral surface and contour groupings. Contour stimuli consisted of bilateral illusory contours without corresponding surface portions. Finally, Ungrouped configurations did not exhibit any bilateral contour- or surface-based groupings.

However, neglect studies that report efficient and preattentive completion processes in Kanizsa figures (Mattingley et al., 1997; Vuilleumier & Landis, 1998; Vuilleumier et al., 2001) do not necessarily elucidate the specific processes involved, since contour completions and surface filling-in could both provide sufficient information on their own in order to bind bilateral stimulus-segments into a coherent object representation. For instance, results from neuroimaging studies suggest that the percept of an illusory figure is generated in multiple specialized regions along the ventral stream (Seghier & Vuilleumier, 2006, for review). In addition, computational models (Grossberg & Mingolla, 1985) propose (in agreement with the neuroanatomical findings) that distinct global attributes of an illusory figure are computed by independent and segregated subsystems: on the one hand, cells in V1 and V2 code illusory contours comparable to real contours (Lee & Nguyen, 2001; von der Heydt, Peterhans, & Baumgartner, 1984). On the other hand, processes responsible for the filling-in of the illusory surface have been located in the lateral occipital complex (LOC) and the fusiform gyrus (e.g., Stanley & Rubin, 2003; Abu Bakar, Liu, Conci, Elliott, & Ioannides, 2008). Thus, contours and surfaces of a Kanizsa figure are completed by separable and independent subsystems that both operate at hierarchical levels below inferior parietal regions.

In the current study, we set out to explore the specific impact of illusory contours and illusory surfaces in completion of Kanizsa figures in neglect and extinction by using the paradigm introduced by Mattingley et al. (1997). As in their study, we compared offset detection for ungrouped control configurations (that do not induce a bilateral global object grouping, see Experiment 2 in Mattingley et al., 1997; Fig. 2, Ungrouped) with performance when presented with a Kanizsa square (Fig. 2, Kanizsa). Moreover, two 'intermediate' configurations were displayed that varied in the extent to which contour and surface information could be completed across hemispheres (see Conci, Gramann, Müller, & Elliott, 2006, and Conci, Müller, & Elliott, 2007, for a comparable approach): for one configuration, the quarter-segments were arranged such that elements integrated to induce bilateral illusory contours (Fig. 2, Contour). In addition, a second configuration was arranged such that a partial

Table 1
Clinical and demographic data of patients and control subjects.

	Sex	Hand	Age	Education (years)	Infarction type	VF deficit	BIT score	TSI (weeks)
Patients								
A. L.	m	r	52	10	MCA	Q, l. s.	102	2
E. G.	m	r	65	10	MCA	–	126	7
E. K.	m	r	72	10	MCA	–	119	9
F. P.	f	r	79	10	MCA	H, l.	127	9
O. B.	m	r	71	10	SC	–	124	8
P. B.	m	r	72	13	MCA	–	123	25
R. A.	m	r	67	9	MCA	Q, l. i.	(47)	8
Controls								
H. S.	f	r	66	10	–	–	–	–
H. D.	m	r	70	13	–	–	–	–
I. R.	f	r	69	10	–	–	–	–
K. M.	m	r	74	13	–	–	–	–
R. F.	f	r	64	10	–	–	–	–
W. G.	m	r	72	13	–	–	–	–
W. H.	m	r	66	13	–	–	–	–

Abbreviations: VF, visual field; BIT, behavioral inattention test; TSI, time since injury; m, male; f, female; r, right; MCA, medial cerebral artery; SC, striato capsular; Q, quadrantanopia; H, hemianopia; l, left; s, superior; I, inferior.

contour-plus-surface arrangement (referred to as a partial 'shape') emerged into the contralesional field (Fig. 2, Shape). Thus, presenting these four types of configuration permits the relative impact of specific figural attributes (global contours or global surfaces) to preattentive illusory figure completion to be established.

Extrapolating from previous studies (in particular, Mattingley et al., 1997), we expected that no (or only modest) signs of extinction should be evident with bilateral stimuli that could be grouped to form a coherent Kanizsa square. By contrast, a relatively strong decline of performance was expected with the ungrouped configurations. In addition, previous results from a series of visual search studies (Stanley & Rubin, 2003) suggest that, for the intermediate stimuli, partial surface information (in shape configurations) should be as efficient as the complete Kanizsa square in guiding attention and, thus, reducing extinction. In contrast, for contour configurations, extinction should be present, given that visual search experiments provide no evidence for preattentive guidance of attention on the basis of illusory contours (Li, Cave, & Wolfe, 2008).

2. Methods

Subjects. Seven right-handed patients (six male, one female; mean age: 68.3 years; mean education: 10.3 years) who had a stroke in the right hemisphere and clinical signs of left-sided visual hemi-neglect were recruited from the Neurological Clinic Bad Aibling, Germany, and tested within 2–25 weeks post-injury. Three patients (E. K., E. G., F. P.) received medical treatment for high blood pressure, and one patient (R. A.) suffered from diabetes mellitus type II. All patients had normal or corrected-to-normal visual acuity and were tested for visual-field deficits (see Table 1). Visuospatial neglect was diagnosed on the basis of neurological examinations and neuropsychological assessments using the Behavioural Inattention Test (BIT; Wilson, Cockburn, & Halligan, 1987). Patients were tested with cancellation, visual search, line bisection, figure copying, and representational drawing tasks. Spatial neglect was ascertained when a minimum of two tests revealed the typical symptoms of left-sided visual hemi-neglect. All patients obtained test-scores slightly below the cut-off value of 129, supporting the diagnosis of a mild neglect (see Table 1 for the individual BIT sum-scores; note that one patient, R. A., obtained a much lower score of 47, as he was assessed only with two subtests due to long-lasting motor impairments of the right dominant hand and an acquired hemiparesis of the left hand). Finally, inspection of lesion locations (see Fig. 3) showed that these were confined to the right hemisphere including inferior-parietal and temporo-parietal areas.

In addition, an age- and education-matched healthy control group of seven right-handed subjects (four male, three female; mean age: 68.8 years; mean education: 11.7 years) was tested. All subjects had normal or corrected-to-normal vision. None of them reported any history of neurological or psychiatric disease. Controls did not differ significantly from the patient group with respects to age [$t(12) = 0.12$, $p = .91$] or years of education [$t(12) = 1.73$, $p = .09$].

Informed consent according to the Declaration of Helsinki II was obtained from all participants. Demographic and clinical data of all patients and controls are summarized in Table 1.

Apparatus and stimuli. The experiment was controlled by an IBM-PC compatible computer using Matlab routines and Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997), and stimuli were presented on a 17-in. monitor (1024 × 768 pixel screen resolution, 70 Hz refresh rate). Observers viewed the monitor from a distance of 57 cm, with head position maintained by the use of a head and chin rest. To control for eye movements, a light-sensitive web-camera was used, with maintenance of fixation monitored by the experimenter. In case of a loss of central fixation, the experimenter verbally instructed the observer to refixate at the screen center. The experiment was conducted in a sound-attenuated room that was dimly lit.

Stimulus configurations were composed of four gray circles (luminance: 3.81 cd/m^2) of a diameter of 1.6° of visual angle, presented on a black background (luminance: 0.01 cd/m^2). Each stimulus configuration of circles was arranged in rectangular form subtending 2.1° × 3.4° of visual angle. The distance of each circle from the central fixation cross (0.6° × 0.6°) was 2° of visual angle on a diagonal. There were four different types of target display: Unilateral Left displays presented the two circles left of fixation with quarter-segments removed from the circles. Conversely, for Unilateral Right displays, quarter-segments from the circles right of fixation were removed. In Bilateral displays, all four circles were presented with quarter-segments removed. Finally, on catch trials ('Neither'), four full circles were presented (to provide a measure for guessing). Examples for all four types of target display are presented in Fig. 1B.

To induce different types of global groupings in bilateral stimuli, the orientations of the quarter-segments were varied systematically. Ungrouped configurations were arranged such that no bilateral global groupings were induced (see Fig. 2, left). By contrast, for the Kanizsa figure configuration, the segmented circles were arranged such that a complete illusory square was elicited by means of inward-facing quarter-segments (see Fig. 2, right). For the Contour configuration (see Fig. 2, middle left), the quarter-segments were arranged such that illusory contours were induced extending across the horizontal borders of the rectangle. Finally, for the Shape configuration (see Fig. 2, middle right), the quarter-segments integrated to form a partial global grouping consisting of an illusory contour extending horizontally with its corresponding partial surface portions (either extending along the top- or bottom-horizontal borders of the figure). Fig. 2A presents examples of all four types of local stimulus arrangement together with illustrations of corresponding global objects (see Fig. 2B). For unilateral target displays, the spatial arrangement of the circles with removed quarter-segments corresponded to the spatial arrangement in the bilateral target displays.

Procedure and design. Each trial started with the presentation of a central fixation cross-presented for 1000 ms at the center of the screen. The subsequent premask display presented four circles in rectangular arrangement around fixation for 2000 ms. Next, the target display was presented with quarter-segments removed from the circles on either left or right side, both sides, or neither side (relative to fixation). The duration of the removal was based on results of individually performed pretests (see below). Finally, a postmask of complete circles reappeared until the observer responded verbally, indicating the number and location of the removed segments in the display (left, right, both, or none). The experimenter recorded the response by typing a corresponding key on the keyboard. Subsequently, the experimenter initiated a new trial by pressing the space bar. Each trial was separated from the next by an inter-trial-interval of 1000 ms. Fig. 1A shows an example of a trial sequence.

At the beginning of the experiment, each observer was required to complete a pretest in order to determine the individual target display duration at which unilateral left trials could be detected with an accuracy of ~85% correct responses. The sequence of displays in the pretest was similar to the experiment itself, except that only ungrouped stimulus configurations were presented. Stimulus duration was determined by means of an adaptive staircase procedure. The starting duration was

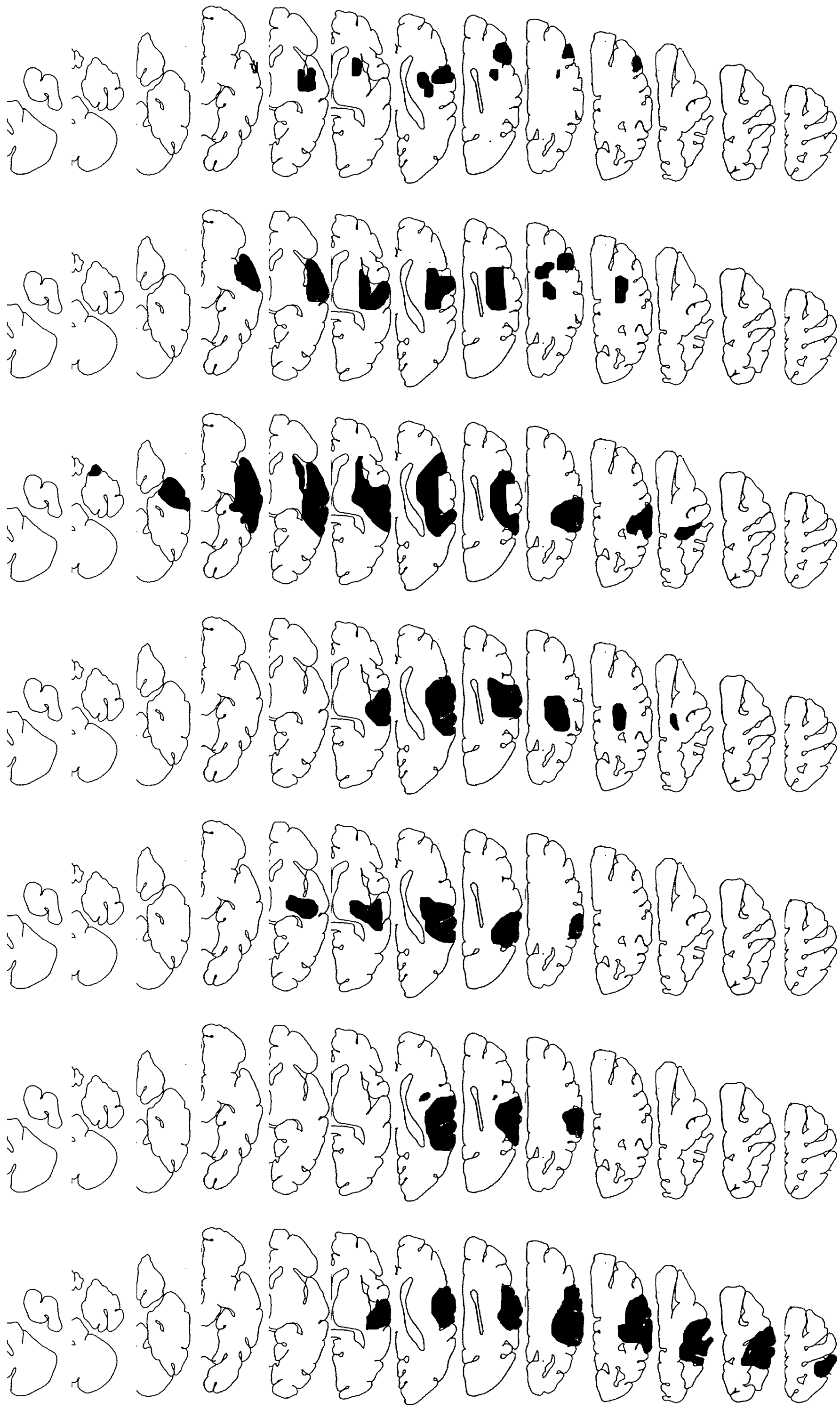

Fig. 3. Reconstruction of the brain lesions in each patient according to the method described by Damasio and Damasio (1989).

200 ms and was adjusted according to the level of correct responses until the performance criterion (~85% correct unilateral left detections) was reached. Presentation durations were estimated on the basis 20 randomized trials (with 10, 5, 3, and 2 trials presenting unilateral left, unilateral right, bilateral, and catch target displays, respectively). The mean presentation durations derived from the pretests were 21 ms for the controls (range: 20–25 ms) as compared to 409 ms for the patient group (see Table 2 for individual presentation times), showing a large and significant increase of the required presentation duration for the neglect patients [$t(12) = -1.98$, $p < .05$].

The experiment consisted of 144 experimental trials, presented in four blocks of 36 trials each, with a break after each block. Each block presented one type of global object (Kanizsa, Shape, Contour, or Ungrouped) and consisted of 8 unilateral left, 8 unilateral right, 16 bilateral, and 4 catch trials that were presented in randomized order. Blocks were administered in random order on an observer-by-observer basis. In summary, the experiment varied two factors, *object type* (Kanizsa, Shape, Contour, Ungrouped) and *target type* (Unilateral Left, Unilateral Right, Bilateral, Neither).

3. Results

Performance for unilateral right target presentations was high for both patients and controls (83.1% and 94.7% correct detections,

Table 2
Presentation times, average detection rates for unilateral left targets, and relative differences of left target detections for the different types of bilateral groupings, for the individual patients and for both patient and control group averages. The relative difference denotes the individual increase of left detections (in %) for the different types of bilateral grouping relative to the averaged performance for unilateral left targets.

	Presentation time (ms)	Uni. Left (%)	Relative difference (%)			
			Ungrouped	Contour	Shape	Kanizsa
Patients						
A. L.	25	53	0	47	141	141
E. G.	200	97	19	103	97	97
E. K.	40	94	7	47	73	100
F. P.	1300	59	32	63	84	84
O. B.	100	47	13	107	213	187
P. B.	200	78	64	96	96	104
R. A.	1000	75	83	58	117	125
Group average						
Patients	409	72	31	74	117	120
Controls	21	94	91	100	100	103

respectively), and levels of accuracy did not differ significantly between the two groups [$t(12) = 1.98$, $p = .07$]. Similarly, all participants were highly accurate in identifying catch trials (94.7% and 100% of correct detections for patients and controls, respectively), without significant differences between both groups [$t(12) = 1.44$, $p = .18$]. This pattern of results indicates that observers were, in principle, able to correctly perform the required task, without any indication of a tendency to guess the response.

Of most importance for the purpose of the current experiment is the comparison of trials that presented targets within the neglected (left) hemifield. Consequently, the correct detection of quarter-segments removed left from fixation was analyzed for unilateral left and bilateral target displays. Fig. 4 presents the correct left detections as a function of target type, separately for all four object types in the control and patient groups (Fig. 4A and B, respectively). In addition, Table 2 provides the relative differences between bilateral and unilateral left targets for each individual patient and for both group averages. Correct left detections were compared by means of a mixed-design analysis of variance (ANOVA), with the between-subjects factor group (patients, controls) and the within-subject factors object type (Kanizsa, Shape, Contour, Ungrouped) and target type (Unilateral Left, Bilateral). This analysis revealed significant main effects of group [$F(1, 12) = 21.10$, $p < .01$] and object type [$F(3, 36) = 16.81$, $p < .01$], and a marginally significant main effect of target type [$F(1, 12) = 4.58$, $p = .053$]. In addition, the group × object type interaction [$F(3, 36) = 7.02$, $p < .01$], the object type × target type interaction [$F(3, 36) = 7.23$, $p < .01$], and the three-way interaction [$F(3, 36) = 5.12$, $p < .01$] were significant. The latter indicates that patients and controls exhibited substantial differences in the pattern of performance. Next, to decompose the three-way interaction, the data sets for both groups of participants were analyzed separately by two repeated-measures ANOVA with the factors target type and object type.

For the control group, the target type by object type ANOVA revealed a significant main effect of object type [$F(3, 18) = 3.57$, $p < .04$], but no effects involving target type (all p's > .18). The object type effect was due to a reduction in detection accuracy for the ungrouped stimulus configurations relative to all other object types (mean correct left detections were 88%, 94%, 93%, and 96% for Ungrouped, Contour, Shape, and Kanizsa stimulus configurations, respectively; p's < .05 for all comparisons involving ungrouped configurations). This finding indicates that normal observers were able to exploit the global groupings in order to achieve an increased accuracy of target detection. However, importantly, there was no influence of stimulus laterality on performance for the control group (see Fig. 4A).

By contrast, for the patient group, an identical ANOVA revealed clear indications of lateral differences in performance. As for the control group, the main effect of object type [$F(3, 18) = 13.53$, $p < .01$] was significant, with performance being reduced for ungrouped

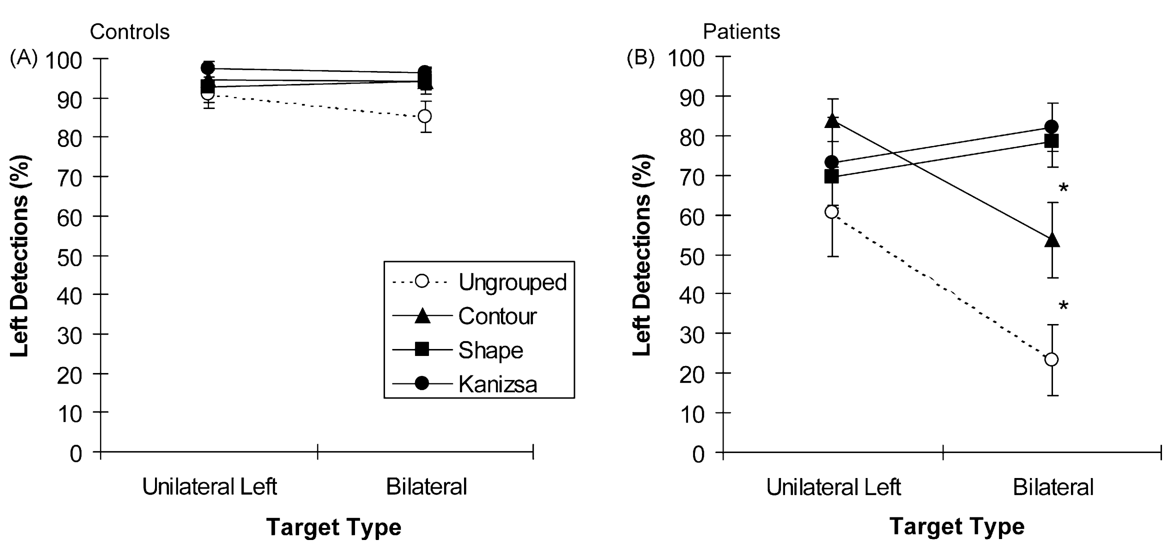

Fig. 4. Mean percentage (and associated standard errors) of correct left detections in the control (A) and patient (B) groups. Data are plotted as a function of target type (unilateral left or bilateral), separately for the four different object types (Kanizsa, Shape, Contour, or Ungrouped). Significant differences in the pairwise comparisons are indicated by an asterisk.

configurations relative to all other types of object (mean correct left detections were 41%, 68%, 74%, and 77% for Ungrouped, Contour, Shape, and Kanizsa stimulus configurations, respectively; p's < .003 for all comparisons involving ungrouped configurations). However, in addition, the significant interaction between object type × target type [$F(3, 18) = 6.95$, $p < .004$] indicated substantial differences in processing displays that contained either unilateral left or bilateral targets (see Fig. 4B). For unilateral left target types, a one-way repeated-measures ANOVA revealed no significant differences among object types [$F(3, 18) = 2.29$, $p = .12$]. In contrast, for bilateral target types, a significant main effect was obtained [$F(3, 18) = 17.16$, $p < .001$]. Subsequent post hoc comparisons revealed that presenting bilateral grouped objects (i.e., Kanizsa, Shape, or Contour) significantly increased the mean correct left detections as compared to bilateral ungrouped configurations (all p's < .05). Furthermore, for grouped objects, correct left detections were more accurate for Kanizsa and Shape configurations than for the bilateral Contour grouping (all p's < .05). In addition, a comparable outcome was also obtained in an analysis of the relative differences between bilateral and unilateral left detections (see Table 2): a one-way repeated measures ANOVA again revealed a significant main effect of object type [$F(3, 18) = 12.51$, $p < .001$], showing substantial differences between Ungrouped and Contour configurations and between Contour and Shape configurations (all p's < .05), but not between Shape and Kanizsa configurations ($p = .7$). Thus, to summarize, patients were impaired in general in detecting bilateral – relative to unilateral left targets. However, when the bilateral stimulus could be grouped, performance accuracy was increased. This was the case when contours were displayed, but, in addition, a substantially larger benefit in performance was obtained when the contour information was accompanied by corresponding surface portions.

4. Discussion

The present study was designed to assess the relative contributions of preattentive, illusory contour and surface information on completion of Kanizsa figures in a group of seven patients with neglect or extinction. Our results clearly replicated a previous single-case study (Mattingley et al., 1997) and demonstrate that these results can be generalized to a group of patients with heterogeneous neglect forms of varying severity. Our results revealed strong signs of extinction for bilateral stimuli that cannot be grouped to form an illusory square. By contrast, when quarter-segments of the stimulus configurations were arranged such that an illusory figure was induced, performance improved and extinction was less severe. Moreover, our results revealed that shape configurations (presenting only partial surface and contour information) were as efficient as complete Kanizsa squares in improving performance: with both Kanizsa and shape configurations, extinction was less severe for bilateral stimulus presentations. In contrast, when the quarter-segments induced bilateral illusory contours only, the level of extinction was intermediate, that is: performance was significantly better relative to ungrouped configurations, but detection of offsets on the left side was substantially worse compared to Kanizsa and shape configurations. Finally, comparisons of the two groups of participants showed that modulations in the severity of 'extinction' with the type of grouping were evident only for the neglect patients (but not the control group). Despite a slight decrease of left-sided offset detections for the ungrouped configurations, no differences between lateralized stimulus configurations was obtained, suggesting an unspecific effect of grouping on performance.

Taken together, these results are in line with a number of studies that have reported influences of low-level grouping and segmentation operations on the strength of extinction and neglect (e.g., Marshall & Halligan, 1994; Pavlovskaya et al., 1997; Robertson et al., 2003; Ward et al., 1994). In addition, our findings replicate previous studies reporting preserved access to visual illusions despite of neglect (Ro & Rafal, 1996; Vuilleumier & Landis, 1998; Vuilleumier et al., 2001). Consequently, preattentive mechanisms of figure-ground segmentation can, in general, have a profound influence on how information in the contralesional field is processed.

More specifically, our results support the view that attention is primarily guided by surface information (e.g., Nakayama & Shimojo, 1992). Thus, the extraction of salient regions in Kanizsa figures (Stanley & Rubin, 2003) determines the allocation of spatial attention, with preattentive mechanisms subserving surface filling-in and region extraction in Kanizsa and shape configurations. However, in extension to the predominant role of global surfaces in Kanizsa figures, the preattentive interpolation of illusory contours also showed a (somewhat smaller) influence on offset detections: as with surface stimuli, configurations that presented contour information improved detection of quarter-segments presented in the contralesional field. Thus, the contribution of surface- and contour-based completion appears to be graded: surfaces maximally reduce signs of extinction, whereas for contours, a smaller but nevertheless substantial reduction of extinction is observable.

A comparable, graded outcome has also been reported in studies that investigated visual search for Kanizsa figures (Conci et al., 2006, 2007). Surface information was found to determine the efficiency of search (modulating the slope of the RT/set-size functions). By contrast, no comparable effect on the search slopes has been reported for illusory contours. Rather, illusory contours were found to specifically influence the base reaction times (the y-intercept of the set-size function). This finding indicates that contours are processed in search, however, only surfaces exert a major influence on the efficiency of target detection. In general agreement with these findings, for the neglect patients, surface information more strongly influenced extinction than the completion of shape-defining illusory contours.

An alternative to the predominant role of surface information in guiding attention (as proposed above) could be an explanation according to which both contours and surfaces influence performance to an equal extent. In this view, extinction would be more strongly reduced in shape than in contour configurations because shape stimuli contain both contour and surface information, permitting their effects to be combined (relative to contour configurations that do not possess comparable surface portions). However, visual search studies have revealed that illusory contours do not guide search (Li et al., 2008) while surfaces do, even if the surface lacks a bounding contour (Conci et al., 2007; Stanley & Rubin, 2003). This pattern of results lends support to a predominant role of surface information, rather than an equal contribution of surface and contour completion mechanisms.

Could an influence other than global contour and surface processing in Kanizsa figures explain the current results? One potential factor which has been shown to influence the severity of extinction of contralesional stimuli could be the overall complexity of the stimulus configurations. For instance, one study (Driver et al., 1992) reported preserved symmetry perception in neglect. However, in the current study, an explanation of the results in terms of symmetry (or stimulus complexity) is unlikely, as the level of extinction did not vary with the degree of symmetry or complexity (see also Conci et al., 2007, for a comparable finding): Kanizsa figures and shape configurations yielded near-identical outcomes, even though their rotational and reflectional properties clearly differ (see Fig. 2). Thus, factors other than overall stimulus complexity appear to affect processing, suggesting that global surface and contour information modulated the severity of extinction.

The observed graded influence of distinct object attributes in Kanizsa figure completion is difficult to explain in terms of sequential processing stages. If one assumes that, first, illusory contours are interpolated in early visual areas (V1 and V2) and only subsequently, the surface is filled-in at a hierarchically higher level of processing (in LOC; Seghier & Vuilleumier, 2006, for review), then it would not be clear why the completed surface has a stronger effect on the level of extinction as the (previously) interpolated contour boundaries – as both processes would make an equal contribution to the formation of the illusory figure. Instead, a potential explanation for this graded influence of grouping could be in terms of models that assume a crucial role for recurrent processing in grouping (e.g., Roelfsema, Lamme, Spekreijse, & Bosch, 2002; Stanley & Rubin, 2003). According to this view, the visual system first extracts salient regions by means of surface filling-in in LOC. Only subsequently, the surface is matched with the precise illusory contours by means of feedback connections to earlier, retinotopically organized visual areas. Such a recurrent network could more readily explain why surface information decreases extinction to a larger extent than contour information, as the former is available earlier during processing and appears to be essential for attentional selection (Conci et al., 2007). Nevertheless, reduced (but reliable) access to the illusory contour suggests that both processes of surface and contour grouping are available preattentively.

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References

Abu Bakar, A., Liu, L., Conci, M., Elliott, M. A., & Ioannides, A. A. (2008). Visual field and task influence illusory figure responses. *Human Brain Mapping*, *29*, 1313–1326.

Baylis, G. C., Driver, J., & Rafal, R. D. (1993). Visual extinction and stimulus repetition. *Journal of Cognitive Neuroscience*, *5*, 453–466.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.

Brooks, J. L., Wong, Y., & Robertson, L. C. (2005). Crossing the midline: Reducing attentional deficits via interhemispheric interactions. *Neuropsychologia*, *43*, 572–582.

Conci, M., Müller, H. J., & Elliott, M. A. (2007). The contrasting impact of global and local object attributes on Kanizsa figure detection. *Perception & Psychophysics*, *69*, 1278–1294.

Conci, M., Gramann, K., Müller, H. J., & Elliott, M. A. (2006). Electrophysiological correlates of similarity-based interference during detection of visual forms. *Journal of Cognitive Neuroscience*, *18*, 880–888.

Damasio, H., & Damasio, A. R. (1989). *Lesion analysis in neuropsychology*. New York: Oxford University Press.

Driver, J. (1995). Object segmentation and visual neglect. *Behavioral Brain Research*, *71*, 135–146.

Driver, J., Baylis, G. C., & Rafal, R. D. (1992). Preserved figure-ground segregation and symmetry perception in visual neglect. *Nature*, *360*, 73–75.

Driver, J., & Vuilleumier, P. (2002). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*, *79*, 39–88.

Gilchrist, I., Humphreys, G. W., & Riddoch, M. J. (1996). Grouping and extinction: Evidence for low-level modulation of selection. *Cognitive Neuropsychology*, *13*, 1223–1256.

Grossberg, S., & Mingolla, E. (1985). Neural dynamics of form perception: Boundary completion, illusory figures and neon colour spreading. *Psychological Review*, *92*, 173–211.

Humphreys, G. W., Romani, C., Olson, A., Riddoch, M. J., & Duncan, J. (1994). Non-spatial extinction following lesions of the parietal lobe in humans. *Nature*, *372*, 257–259.

Kanizsa, G. (1955). Margini quasi-percettivi in campi con stimolazione omogenea. *Rivista di Psycologia*, *49*, 7–30.

Karnath, H.-O., Milner, A. D., & Vallar, G. (2002). *The cognitive and neural bases of spatial neglect*. Oxford: Oxford University Press.

Kerkhoff, G. (2001). Spatial hemineglect in humans. *Progress in Neurobiology*, *63*, 1–27.

Lee, T. S., & Nguyen, M. (2001). Dynamics of contour formation in the early visual cortex. *Proceedings of the National Academy of Science, USA*, *98*, 1907–1911.

Li, X., Cave, K., & Wolfe, J. M. (2008). Kanisza-style subjective contours do not guide attentional deployment in visual search but line-termination contours do. *Perception & Psychophysics*, *70*, 477–488.

Marshall, J. C., & Halligan, P. W. (1994). The yin and yang of visuo-spatial neglect: A case study. *Neuropsychologia*, *32*, 1037–1057.

Mattingley, J. B., Davis, G., & Driver, J. (1997). Preattentive filling-in of visual surfaces in parietal extinction. *Science*, *275*, 671–674.

Nakayama, K., & Shimojo, S. (1992). Experiencing and perceiving visual surfaces. *Science*, *257*, 1357–1363.

Pavlovskaya, M., Sagi, D., Soroker, N., & Ring, H. (1997). Visual extinction and cortical connectivity in human vision. *Cognitive Brain Research*, *6*, 159–162.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.

Ro, T., & Rafal, R. D. (1996). Perception of geometric illusions in hemispatial neglect. *Neuropsychologia*, *34*, 973–978.

Robertson, L. C., Eglin, M., & Knight, R. (2003). Grouping influences in unilateral visual neglect. *Journal of Clinical and Experimental Neuropsychology*, *25*, 297–307.

Roelfsema, P. R., Lamme, V. A. F., Spekreijse, H., & Bosch, H. (2002). Figure-ground segregation in a recurrent network architecture. *Journal of Cognitive Neuroscience*, *14*, 525–537.

Seghier, M. L., & Vuilleumier, P. (2006). Functional neuroimaging findings on the human perception of illusory contours. *Neuroscience and Biobehavioral Reviews*, *30*, 595–612.

Stanley, D. A., & Rubin, N. (2003). fMRI activation in response to illusory contours and salient regions in the human lateral occipital complex. *Neuron*, *37*, 323–331.

Treisman, A. M., & Gelade, G. (1980). A feature integration theory of attention. *Cognitive Psychology*, *12*, 97–136.

von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science*, *224*, 1260–1262.

Vuilleumier, P., & Landis, T. (1998). Illusory contours and spatial neglect. *NeuroReport*, *9*, 2481–2484.

Vuilleumier, P., Valenza, N., & Landis, T. (2001). Explicit and implicit perception of illusory contours in unilateral spatial neglect: Behavioural and anatomical correlates of preattentive grouping mechanisms. *Neuropsychologia*, *39*, 597–610.

Ward, R., & Goodrich, S. (1996). Differences between objects and nonobjects in visual extinction: A competition for attention. *Psychological Science*, *7*, 177–180.

Ward, R., Goodrich, S., & Driver, J. (1994). Grouping reduces visual extinction: Neuropsychological evidence for weight-linkage in visual selection. *Visual Cognition*, *1*, 101–130.

Wilson, B. A., Cockburn, J., & Halligan, P. (1987). *Behavioral Inattention Test (BIT)*. Titchfield: Thames Valley Test Company.