

Saliency modulates global perception in simultanagnosia

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Abstract Patients with parieto-occipital brain damage may show simultanagnosia, a selective impairment in the simultaneous perception and integration of multiple objects (global perception) with normal recognition of individual objects. Recent findings in patients with simultanagnosia indicate improved global perception at smaller spatial distances between local elements of hierarchical organized complex visual arrays. Global perception thus does not appear to be an all-or-nothing phenomenon but can be modified by the spatial relationship between local elements. The present study aimed to define characteristics of a general principle that accounts for improved global perception of hierarchically organized complex visual arrays in patients with simultanagnosia with respect to the spatial properties of local elements. In detail, we investigated the role of the number and size of the local elements as well as their relationship with each other for the global perception. The findings indicate that global perception increases independently of the size of the global object and depends on the spatial relationship between the local elements and the global object. The results further argue against the possibility of

a restriction in the attended or perceived area in simultanagnosia, in the sense that the integration of local elements into a global scene is impaired if a certain spatial “field of view” is exceeded. A possible explanation for these observations might be a shift from global to local saliency in simultanagnosia.

Keywords Vision · Global · Saliency · Simultanagnosia · Perception

Introduction

Mechanisms that allow the efficient and coherent perception of our visual surround have been extensively investigated over the past twenty years. Patients with simultanagnosia following bilateral brain damage of the parieto-occipital cortex show a ‘piecemeal’ perception of their visual surround and lack the integration of individual objects into a complex array or are able to report the presence of only one object at a time (Luria 1959). Simultanagnosia is thus characterized by disturbed global perception, while the recognition of individual objects remains intact (Balint 1909; Wolpert 1924; Luria 1959; Rizzo and Hurtig 1987; Friedman-Hill et al. 1995; Rafal 1997). The disorder has been discussed in the context of visuo-spatial attention. The restriction of global processing in simultanagnosia typically results in an advantage for local perception (Rizzo and Robin 1990; Friedman-Hill et al. 1995; Karnath et al. 2000). Theories of spatial attention emphasize selection processes of spatially restricted areas together with the ability to shift spatial attention to another location (Posner 1980; Coull and Nobre 1998; Di Russo et al. 2003; de-Wit et al. 2008). Independent elements that lie within such an area are

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processed more efficiently than elements located outside. In contrast to theories of spatial attention, object-based approaches focus on the idea that attention selects a perceptual object rather than a spatial area (Duncan 1984; McMains et al. 2007; Shomstein and Behrmann 2008; Olson 2001).

Interestingly, spatial-attentional mechanisms allow healthy observers to turn their typically observed global precedence into a local advantage, which depend on the spatial properties of the local elements including the distance between individual elements and changes in the number of individual elements (Kimchi and Palmer 1982; Lamb and Robertson 1988; Hughes et al. 1990). In a recent study, we observed a similar behaviour by investigating the role of the spatial distance between the individual elements of hierarchically organized complex visual arrays such as Navon letter stimuli, in which a global letter is constructed of multiple local letters (Navon 1977; Huberle and Karnath 2006). In detail, patients with simultanagnosia showed improved global perception at decreased spatial distances between the individual letters at the local level indicating that global perception in patients with simultanagnosia can be modulated by the spatial distance between local elements. Global and local perception can be manipulated not only in patients with simultanagnosia but also in healthy observers and is strongly dependent on the spatial properties of the local elements of hierarchically organized complex visual arrays. However, little is known about these properties in patients with simultanagnosia. Besides smaller spatial distances between the local elements, other spatial properties of the local elements (e.g. size of the local element) and their relation to the global object might influence global perception in these patients.

In order to define a general principle that accounts for improved global perception of hierarchically organized complex visual arrays, the present study aimed to investigate conditions under which the local dominance in patients with simultanagnosia can be manipulated to enable an improved perception of a global gestalt. We thus applied Navon hierarchical letter stimuli in one patient with simultanagnosia as well as healthy controls and increased the size of the local letter, while the distance between adjacent elements and their number remained unchanged (Experiment 1), manipulated the size of the local letter and the inter-element distance using a constant number of elements (Experiment 2), or varied the number of local letters, while their size and the inter-element distance remained unchanged (Experiment 3).

Materials and methods

Subjects

Patient HW

HW, a 71-year-old, right-handed woman, was admitted to our department with a history of unspecific progressive ‘visual impairment’ for several years affecting a number of activities of daily living such as visual orienting, reading abilities and other daily activities such as counting coins, descending stairs and cooking. Standard neurological examination was normal, while ophthalmologic examination showed reduced visual acuity of the right eye (near 0.5/far 0.6) in the context of a beginning glaucoma. Visual acuity for the left eye (near 0.9/far 0.9) was normal, and standard Goldmann-Perimetry detected no visual field deficits.

Neuropsychological testing revealed severe simultanagnosia. The patient was not able to identify the letter at the global level of each of ten Navon hierarchical letter stimuli (Navon 1977), while the recognition of the letter at the local level was intact, and the patient was able to report the presence of multiple objects. Reading of three-letter-words was also impaired, and HW could only report the identity of the individual letters. In parallel to recent findings in other patients with simultanagnosia (Huberle and Karnath 2006), HW showed increased performance for global shape recognition at smaller inter-element distances of the letters at the local level, that exceeded chance level significantly at close distances, while recognition of the local level was close to perfect independent of the inter-element distance (Fig. 1b, global letter: $10.9^\circ \times 10.9^\circ$; local letter $0.35^\circ \times 0.35^\circ$; visual angle between local letters 0.64° – 2.56° ; for a detailed description of the stimuli and procedure, see Huberle and Karnath 2006). Further, she was not able to detect the general context of complex images of the type of the Broken Window Picture from the Stanford Binet Intelligence Test (Binet and Simon 1905; Roid 2003), while she was able to describe individual parts or objects of these images. In addition to simultanagnosia, HW showed signs of constructive apraxia that did not allow her to copy objects with increasing complexity. No signs of spatial neglect, visual agnosia, visual extinction or visual field defects were observed. In the Mini-Mental State Examination, HW reached 21 of 30 points indicating moderate cognitive impairment.

T1- and T2-weighted magnetic resonance imaging of HW showed no pathological results. An 18-fluorodeoxyglucose positron emission tomography (FDG-PET)

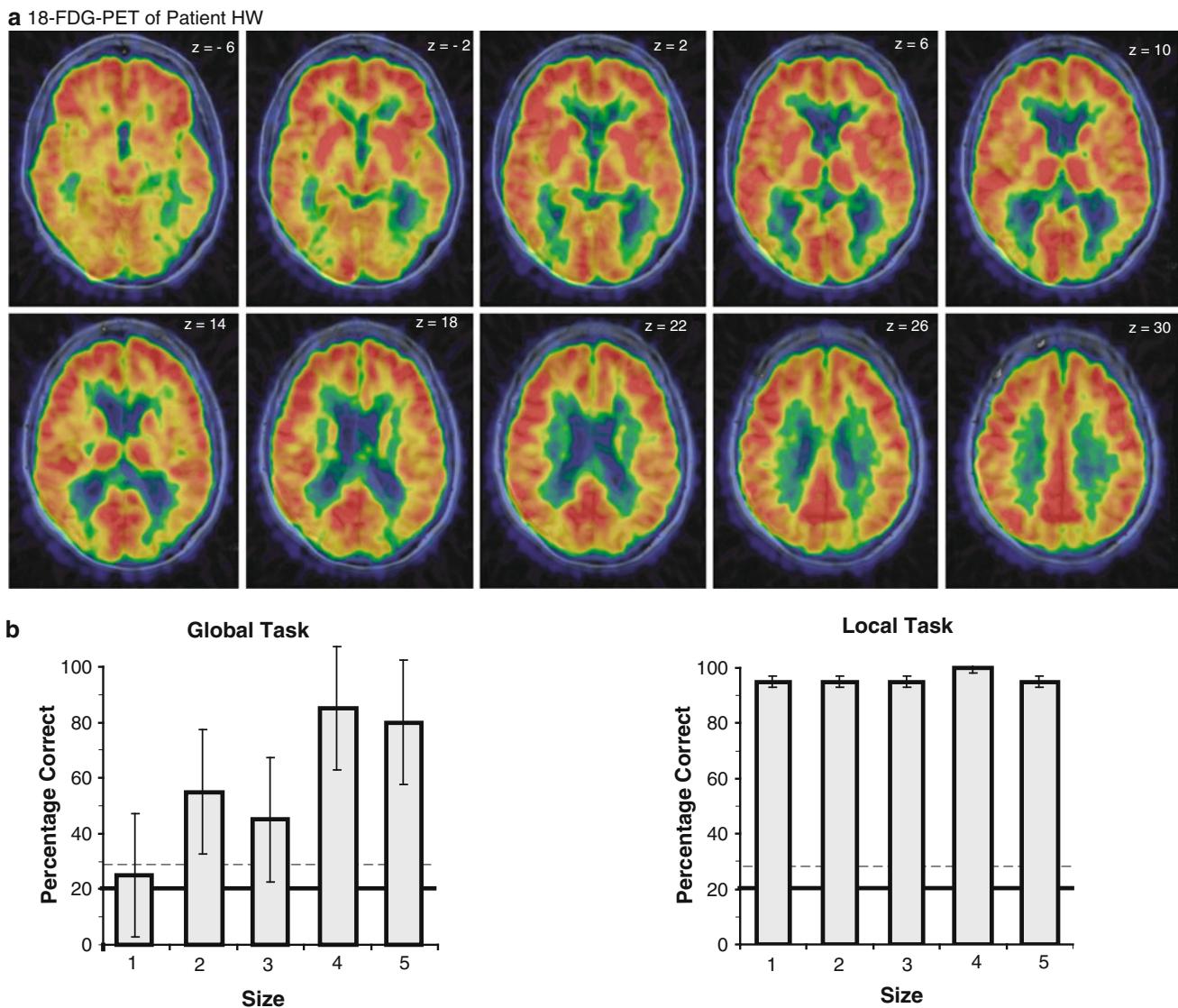


Fig. 1 **a** 18-Fluorodeoxyglucose positron emission tomography (FDG-PET) scans overlaid with the magnetic resonance imaging (MRI) scans revealed reduced metabolism in the parieto-occipital cortex bilaterally for patient HW. **b** In parallel to earlier findings

(Huberle and Karnath 2006), HW showed increased global gestalt perception at decreased inter-element distances (Sizes 1 to 5) of Navon hierarchical letter stimuli (*left*), while the recognition of the letter at the local scale remained intact (*right*)

revealed reduced metabolism in the parieto-occipital cortex bilaterally (Fig. 1). Cerebrospinal fluid analysis showed normal results for cell count and protein, but indicated decreased β -amyloid-peptide 1–42 and increased hyperphosphorylated tau-protein. This finding is frequently seen in patients with Alzheimer's disease (Jensen et al. 1995, Motter et al. 1995). In accordance with the clinical presentation and recent findings (Tang-Wai et al. 2004), which suggested a high incidence of atypical Alzheimer's disease (up to 80%) in the cortex of hypometabolism in the parieto-occipital cortex bilaterally, posterior cortical atrophy (PCA) was diagnosed.

Control subjects

In addition to HW, four healthy subjects (mean age 64 years, range 61–68 years; three males and one female) without a history of brain damage were tested to exclude the possibility of a general difficulty with the performance of the task and the stimulus parameters.

All subjects (HW & control subjects) gave their informed consent before the participation in the study that has been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and was approved by the local ethics committee.

Visual stimuli

In three experiments, Navon hierarchical letter stimuli (Navon 1977) that consist of a global letter (global level) constructed of several local letters (local level) were applied. In parallel to an earlier study (Huberle and Karnath 2006), five different letters (A, B, E, H, and N) were used for the global and the local levels. The letters at the local level were black and presented on a white background. All possible combinations of incongruent stimuli (different letters at the global and local scale) were applied resulting in a total number of 20 different combinations.

The same procedure was used for HW and the healthy control subjects. Prior to all experiments, the subjects were familiarized with the stimuli. Each trial was initiated by the experimenter when the participants indicated readiness. After a delay of 600 ms, the stimulus appeared at the center of the monitor for a presentation duration of 5,000 ms. HW and the healthy control subjects were instructed to identify the letter at the global level, while the experimenter coded the verbal responses. For all experiments, 20 repetitions per

conditions were used resulting in a total number of 60 trials. The stimuli were presented on a monitor placed 50 cm in front of them at daylight condition in an order that balanced for the letter at the global level, the letter at the local level, and the different experimental conditions. In order to ‘quantify’ spatial properties of the stimuli at the local and global level, we calculated an ‘Integration-by-Size-Index’ (IS-Index), which was defined as the ratio between the size of the local letter and the size of the global letter multiplied by 100%, an ‘Integration-by-Distance-Index’ (ID-Index) as the ratio between the distance between the center of two individual letters at the local level and the size of the global letter multiplied by 100% and used the percentual ratio between the size of the local letter and the inter-element distance as ‘Local-Integration-Index’ (LI-Index).

Experiment 1

We manipulated the size of the local letters, while the number and the distance between the center of adjacent elements remained unchanged (Fig. 2a, Table 1). The size

Fig. 2 Sample stimuli of the three experiments. Stimuli consisted of Navon hierarchical letter stimuli where a global letter is constructed of multiple letters at the local level. Five different letters were used for the global as well as local letter (A, B, E, H, N). The global letter was always different from the letter at the local level

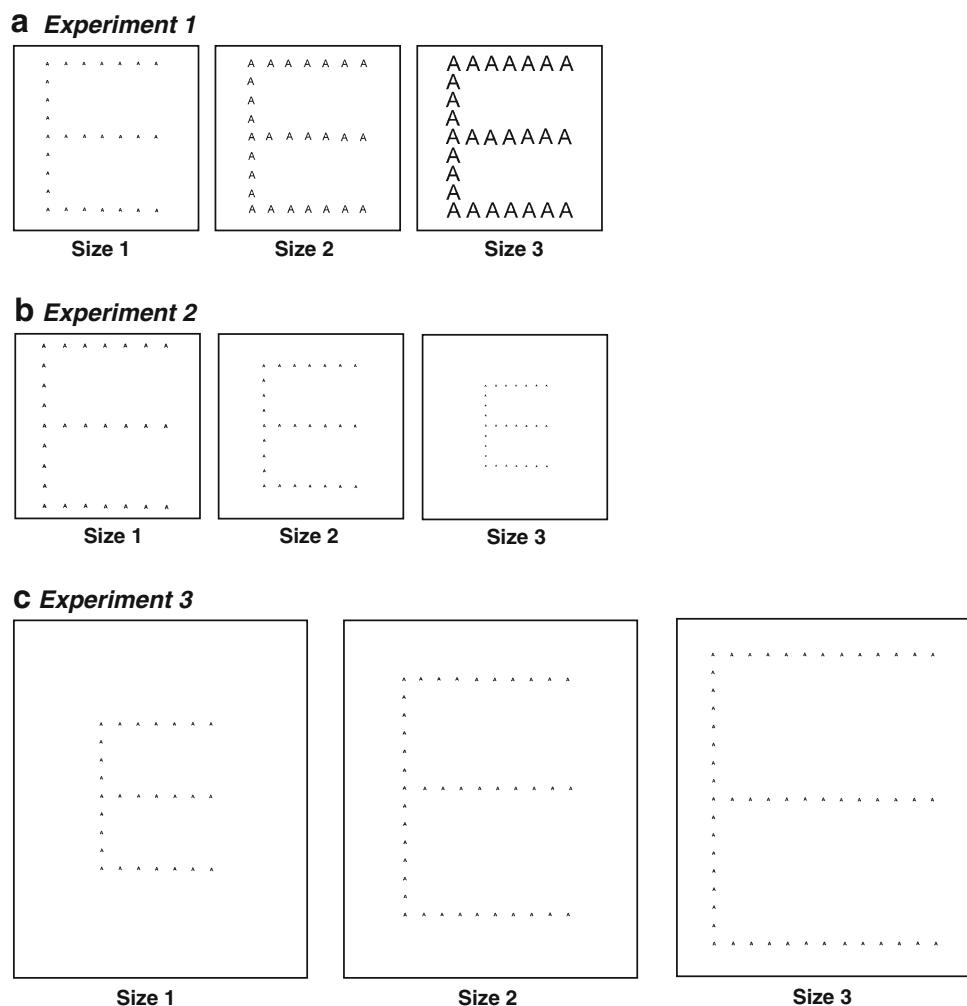


Table 1 Displayed are the stimulus parameters for Experiments 1 to 3

	Experiment 1	Experiment 2	Experiment 3
Size of local letter (°)	0.35 (Size 1)	0.35 (Size 1)	0.35 (Size 1)
	0.70 (Size 2)	0.26 (Size 2)	0.35 (Size 2)
	1.40 (Size 3)	0.17 (Size 3)	0.35 (Size 3)
Size of global letter (°)	10.90 (Size 1)	10.90 (Size 1)	10.90 (Size 1)
	10.90 (Size 2)	8.12 (Size 2)	16.35 (Size 2)
	10.90 (Size 3)	5.45 (Size 3)	21.80 (Size 3)
VA (°)	1.28 (Size 1)	1.28 (Size 1)	1.28 (Size 1)
	1.28 (Size 2)	0.96 (Size 2)	1.28 (Size 2)
	1.28 (Size 3)	0.64 (Size 3)	1.28 (Size 3)
IS-Index (%)	3.20 (Size 1)	3.20 (Size 1)	3.20 (Size 1)
	6.40 (Size 2)	3.20 (Size 2)	2.40 (Size 2)
	12.80 (Size 3)	3.20 (Size 3)	1.60 (Size 3)
ID-Index (%)	11.70 (Size 1)	11.70 (Size 1)	11.70 (Size 1)
	11.70 (Size 2)	11.70 (Size 2)	8.80 (Size 2)
	11.70 (Size 3)	11.70 (Size 3)	5.80 (Size 3)
LI-Index (%)	27.30 (Size 1)	27.30 (Size 1)	27.30 (Size 1)
	54.60 (Size 2)	27.30 (Size 2)	27.30 (Size 2)
	109.20 (Size 3)	27.30 (Size 3)	27.30 (Size 3)

VA, visual angle between the centres of two adjacent letters at the local level; IS-Index ('Integration-by-Size-Index'), ratio between the size of the local letter and the size of the global letter multiplied by 100%; ID-Index ('Integration-by-Distance-Index'), ratio between the distance between the center of two individual letters at the local level and the size of the global letter multiplied by 100%; LI-Index ('Local-Integration-Index'), ratio between the size of the local letter and the inter-element distance multiplied by 100%

of the letters at the local level was $0.35^\circ \times 0.35^\circ$ (Size 1), $0.70^\circ \times 0.70^\circ$ (Size 2), $1.40^\circ \times 1.40^\circ$ (Size 3), while the letters on the global scale always covered an area of $10.9^\circ \times 10.9^\circ$. The visual angle between letters at the local level was 1.28° . These parameters resulted in an IS-Index of 3.2% (Size 1), 6.4% (Size 2) and 12.8% (Size 3), while the ID-Index of 11.7% was constant across conditions. The LI-Index was 27.3% (Size 1), 54.6% (Size 2), and 109.2% (Size 3). The complete stimulus set consisted of 60 different stimuli (five letters at the global level each rendered of four letters at the local level and presented at three different sizes).

Experiment 2

In this experiment, the size of the local letters and the distance between adjacent elements were manipulated, while the number of local letters remained unchanged (Fig. 2b, Table 1). As a result, the stimulus appeared as if it was presented at different distances from the observer. The following parameters were used: the global letter covered an area of $10.9^\circ \times 10.9^\circ$ and the local letter of

$0.35^\circ \times 0.35^\circ$, while the visual angle (VA) between the local letters was 1.28° (Size 1); global letter 8.12° , local letter 0.26° , VA 0.96° (Size 2); global letter 5.45° , local letter 0.17° , VA 0.64° (Size 3). These parameters resulted in an IS-Index of 3.2%, an ID-Index of 11.7%, and an LI-Index of 27.3%; each independent of the condition. A total number of 60 stimuli was used for Experiment 2 (five letters at the global level constructed of four letters at the local level that were presented at three different sizes).

Experiment 3

In parallel to an earlier study (Huberle and Karnath 2006), we manipulated the number of letters at the local level. However, in contrast to that study, the inter-element distance now remained unchanged (Fig. 2c, Table 1). As a result of this procedure, the size of the letter at the global level varied across conditions. Specifically, the size of the global letter was $10.9^\circ \times 10.9^\circ$ (Size 1), $16.35^\circ \times 16.35^\circ$ (Size 2), and $21.8^\circ \times 21.8^\circ$ (Size 3), while the letters at the local level had a constant size of $0.35^\circ \times 0.35^\circ$. The visual angle between letters at the local level was also constant with 1.28° . These parameters resulted in an IS-Index of 3.2% (Size 1), 2.4% (Size 2), and 1.6% (Size 3), while the ID-Index was 11.7% (Size 1), 8.8% (Size 2) and 5.8% (Size 3). The LI-Index of 27.3% was constant between conditions. The complete stimulus set consisted of 60 different stimuli (five letters at the global level, each rendered of four letters at the local level and presented at three different sizes).

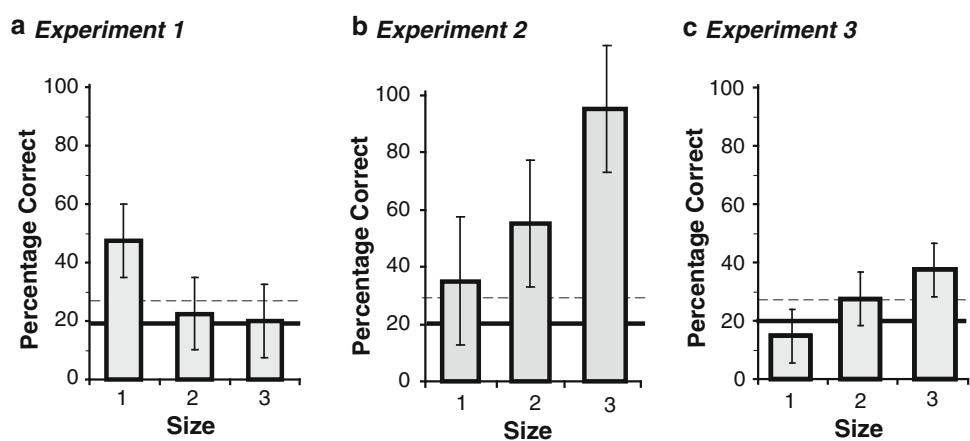
The number of trials presented in the three experiments did not allow us to complete the investigation of HW's global perception within one day. For HW, the three experiments thus were conducted over a period of several days, while the healthy control subjects participated in the next experiment immediately after the end of an experiment.

Results

We computed the percent of correct responses (CR) for each experiment and condition. Performance above chance level was defined by applying the 95% confidence interval (95% CI) for the binomial distribution for each experiment. Due to the possibility of larger fluctuations in performance of neurological patients from one day to the next, 'Size 1' was identical across experiments and was used as a baseline condition in the different experiments.

The performance of the four healthy controls was at ceiling, reaching 100% correct responses in all experiments. Figure 3 illustrates the average percent of correct

Fig. 3 Average percentage of correct responses for global gestalt perception by patient HW in the three experiments with respect to the different conditions ('Sizes 1 to 3'). The solid horizontal line indicates chance level and the dashed line the 95% confidence interval of the binomial distribution for the chance level. Error bars indicate the standard error across conditions



responses across conditions in the three experiments for patient HW.

Global perception was manipulated varying the size of the local letters in Experiments 1 and 2 as well as the distance between adjacent elements in Experiment 2. In Experiment 1, HW's global recognition performance decreased with an increasing size of the letters at the local level, reaching chance level at Sizes 2 and 3 (Fig. 3a). Interestingly, a smaller IS-Index and LI-Index indicated improved performance, while no relation with the ID-Index was observed. In parallel to Experiment 1, smaller sizes of the global letter facilitated global perception together with decreased inter-element distances in Experiment 2, reaching almost perfect performance for the smallest size and closest distance of the local letters (Fig. 3b). Interestingly, differences in the performance were observed at a constant IS-/ID- or LI-Index. HW's global perception thus was varied with the number of letters at the local level and the size of the global letter but independently from the inter-element distance between adjacent letters at the local level. In Experiment 3, HW's global recognition performance increased with the number of letters at the local level (Fig. 3c). Chance level was exceeded for the highest number of local letters (Size 3). A smaller IS-Index indicated improved performance, while a smaller ID-Index showed decreased performance. No relation with the LI-Index was found.

Discussion

Global perception in simultanagnosia is not an all-or-nothing phenomenon, but can be modulated by the spatial properties of complex visual arrays consisting of multiple independent objects (Huberle and Karnath 2006). In order to define a general principle that accounts for improved global perception of hierarchically organized complex visual arrays in patients with simultanagnosia, the present

study investigated conditions under which the local dominance in patients with simultanagnosia can overcome to enable global gestalt perception. We systematically varied the size of the local letters (Experiment 1) or the size of the local letters together with the inter-element distance (Experiment 2). In addition, we presented stimuli that differed in the number of local elements, while the inter-element distance and the size of the local letters remained constant (Experiment 3). We observed an increase in global perception in patient HW at smaller sizes of the local letters that reached almost perfect performance for small inter-element distances (Experiment 1 and 2). Finally, improved performance was observed in conditions with a higher number of local elements (Experiment 3).

The perception of hierarchically organized visual stimuli can be manipulated not only in patients with simultanagnosia but also in healthy observers (Kimchi and Palmer 1982; Lamb and Robertson 1988; Hughes et al. 1990). Visual processing within an attended area of space has also been investigated in healthy individuals and patients with simultanagnosia in the context of grouping mechanism and the 'binding-problem' (Treisman and Gelade 1980; Coslett and Saffran 1991; Fox et al. 1998; Kim and Cave 2001; Han et al. 2005a, b; Han and Humphreys 2005; Bhatt et al. 2007; von der Malsburg and Willshaw 1981; von der Malsburg 1995; Roelfsema 2006). The perception of hierarchically organized visual stimuli can be manipulated not only in patients with simultanagnosia but also in healthy observers (Kimchi and Palmer 1982; Lamb and Robertson 1988; Hughes et al. 1990). Experimental data (Fox et al. 1998; Kim and Cave 2001; Han et al. 2005a, b; Han and Humphreys 2005) as well as computational models (Mozer 1991, 1998) indicated a relation between spatial attention and grouping mechanisms (Goldberg and Segraves 1987; Corbetta et al. 1993). Grouping of individual and independent objects (so-called 'features') is facilitated if features share similar attributes (Treisman and Gelade 1980). Behavioral data (Coslett and Saffran 1991; Ben-Av and

Sagi 1995; Han and Humphreys 1999; Han et al. 1999a, b; Demeyere and Humphreys 2007) suggest a dominance of proximity over similarity in perceptual grouping tasks if both grouping principles are used within the same stimulus with shorter latencies for proximity-related grouping (Han 2004). Early activity for proximity-based grouping mechanisms might thus reflect bottom-up processing (Han 2004). In line with earlier findings in healthy observers (e.g. Kimchi and Palmer 1982; Lamb and Robertson 1988; Hughes et al. 1990), the results of Experiment 2 emphasize the role of proximity as a major grouping principle in patients with simultanagnosia. Global perception increased at closer distances of adjacent elements independently of the number of local elements. However, the results of the Experiment 3 do not support the idea, that proximity is the only pronounced grouping principle in simultanagnosia. The inter-element distance and the size of the local letters remained identical across conditions, while the number of letters at the local level was manipulated. As a result of this procedure, the size of the global letter increased with an increasing number of local letters.

It has been proposed that restrictions in global perception can be mediated by spatially constricted vision in the way that a restricted spatial window of attention does not allow the integration of individual objects over a larger spatial scale (e.g. Dalrymple et al. 2010). In contrast to these suggestions, the results of the present experiments argue against the possibility to interpret simultanagnosia as a restriction in the attended and perceived area. If spatially constricted vision is critical for the restricted global perception in patients with simultanagnosia, decreased global perception shall be expected with an increase in the size of the global letter. However, the opposite pattern was observed: The present findings rather demonstrate that global perception might even increase with the size of the global letter that required a larger “field of view” (Experiments 3).

Our findings also support skepticism against the hypothesis of a restriction in the capacity of visual working memory, which has been suggested to be a major mechanism underlying the disturbed global perception in simultanagnosia (Coslett and Saffran 1991; Friedman-Hill et al. 1995). If this is the critical mechanism underlying simultanagnosia, improved global perception at an increased number of local elements appears unlikely. But the latter was observed in Experiment 3, in which Navon hierarchical letter stimuli were used that varied in their number of local elements at a constant inter-element distance.

Is there a possibility to integrate the findings from the three experiments into a common hypothesis? A solution may be found in the term ‘saliency’, which aims to describe the relative importance of an object for a certain

visual percept. Objects with a high saliency are more pronounced or prominent compared to the remaining objects. For example, saliency increases with the increase in contrast between an object and its visual surround. The saliency of a hierarchically organized complex visual array and the connectivity of its elements underlie the Gestalt rule of good continuation (Field et al. 1993). Global saliency decreases not only with increased inter-element distances but also with decreasing density of the local elements and is thus based in local integration mechanisms of intermediate spatial extent (Li and Gilbert 2002). Spatial attention may be a major mechanism for saliency detection by focusing limited perceptual resources on the most salient subset of the visual surround in the way that stimuli with stronger saliency attract more attention (Lee et al. 2002). Mevorach et al. (2006a) use the term ‘relative saliency’ to determine local over global saliency and *vice versa*. Parieto-occipital cortex and its connections to dorsolateral prefrontal cortex are associated with saliency maps (Bichot and Schall 1999; Colby and Goldberg 1999; Gottlieb et al. 1998; Schall and Thompson 1999; Koch and Ullman 1985; Niebur and Koch 1996; Constantinidis and Steinmetz 2005; Mevorach et al. 2006a, b; Riddoch et al. 2010). Disturbed global perception in simultanagnosia following parieto-occipital brain damage could thus be regarded as a shift of relative saliency towards local processing compared to healthy observers (Shalev et al. 2007). If so, one can assume that deficits in global perception of patients with simultanagnosia can be overcome by high global saliency.

Although it has been shown that global perception improves for smaller inter-element distances in patients with acute stroke as well as with PCA (Huberle and Karnath 2006; Huberle et al. 2010), we would like to point out that the type of brain damage (PCA in the present case) and stimulus (Navon letter stimuli in the present case) might have a different impact on global perception. It thus remains an issue of future projects to verify the present findings in subjects with acute brain lesions and vary the type of stimulus.

In conclusion, our results argue against the possibility to interpret simultanagnosia as a restriction of spatial perception in the way that the integration of local elements into a global scene is impaired if a certain spatial “field of view” is exceeded. They rather extend previous findings and indicate that global perception can be manipulated independently of the number of local letter and the distance between adjacent elements of Navon hierarchical letter stimuli. In addition, global perception in simultanagnosia can be increased independently of the size of the global letter. A possible explanation for these observations might be a shift from global to local saliency in simultanagnosia.

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References

- Balint R (1909) Seelenlähmung des Schauens, optische Ataxie, räumliche Störung der Aufmerksamkeit. *Monatsschr Psychiatr Neurol* 25:51–181
- Ben-Av MB, Sagi D (1995) Perceptual grouping by similarity and proximity: experimental results can be predicted by intensity autocorrelations. *Vision Res* 35:853–866
- Bhatt R, Carpenter GA et al (2007) Texture segregation by visual cortex: perceptual grouping, attention, and learning. *Vision Res* 47:3173–3211
- Bichot NP, Schall JD (1999) Effects of similarity and history on neural mechanisms of visual selection. *Nat Neurosci* 2:549–554
- Binet A, Simon T (1905) Méthodes nouvelles pour le diagnostic du niveau intellectuel des anormaux. *Année Psychol* 11:191–337
- Colby CL, Goldberg ME (1999) Space and attention in parietal cortex. *Annu Rev Neurosci* 22:319–349
- Constantinidis C, Steinmetz MA (2005) Posterior parietal cortex automatically encodes the location of salient stimuli. *J Neurosci* 25:233–238
- Corbetta M, Miezin FM et al (1993) A PET study of visuospatial attention. *J Neurosci* 13:1202–1226
- Coslett HB, Saffran E (1991) Simultanagnosia. To see but not two see. *Brain* 114:1523–1545
- Coull JT, Nobre AC (1998) Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *J Neurosci* 18:7426–7435
- Dalrymple KA, Buschow WF, Cameron D, Barton JJ, Kingstone A (2010) Simulating simultanagnosia: spatially constricted vision mimics local capture and the global processing deficit. *Exp Brain Res* 202:445–455
- Demeyere N, Humphreys GW (2007) Distributed and focused attention: neuropsychological evidence for separate attentional mechanisms when counting and estimating. *J Exp Psychol Hum Percept Perform* 33: 1076–1088
- de-Wit LH, Kentridge RW et al (2008) Object-based attention and visual area LO. *Neuropsychologia* 47:1483–1490
- Di Russo F, Martinez A et al (2003) Source analysis of event-related cortical activity during visuo-spatial attention. *Cereb Cortex* 13:486–499
- Duncan J (1984) Perceptual selection based on alphanumeric class: evidence from partial reports. *Percept Psychophys* 33:533–547
- Field DJ, Hayes A et al (1993) Contour integration by the human visual system: evidence for a local association field. *Vision Res* 33:173–193
- Fox GB, Fan L et al (1998) Effect of traumatic brain injury on mouse spatial and nonspatial learning in the Barnes circular maze. *J Neurotrauma* 15:1037–1046
- Friedman-Hill SR, Robertson LC et al (1995) Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions. *Science* 269:853–855
- Goldberg ME, Segraves MA (1987) Visuospatial and motor attention in the monkey. *Neuropsychologia* 25:107–118
- Gottlieb JP, Kusunoki M et al (1998) The representation of visual salience in monkey parietal cortex. *Nature* 391:481–484
- Han S (2004) Interactions between proximity and similarity grouping: an event-related brain potential study in humans. *Neurosci Lett* 367:40–43
- Han S, Humphreys GW (1999) Interactions between perceptual organization based on Gestalt laws and those based on hierarchical processing. *Percept Psychophys* 61:1287–1298
- Han S, Humphreys GW (2005) Perceptual organization at attended and unattended locations. *Sci China C Life Sci* 48:106–116
- Han S, Humphreys GW et al (1999a) Parallel and competitive processes in hierarchical analysis: perceptual grouping and encoding of closure. *J Exp Psychol Hum Percept Perform* 25:1411–1432
- Han S, Humphreys GW et al (1999b) Uniform connectedness and classical Gestalt principles of perceptual grouping. *Percept Psychophys* 61:661–674
- Han S, Jiang Y et al (2005a) Attentional modulation of perceptual grouping in human visual cortex: functional MRI studies. *Hum Brain Mapp* 25:424–432
- Han S, Jiang Y et al (2005b) Attentional modulation of perceptual grouping in human visual cortex: ERP studies. *Hum Brain Mapp* 26:199–209
- Huberle E, Karnath HO (2006) Global shape recognition is modulated by the spatial distance of local elements—evidence from simultanagnosia. *Neuropsychologia* 44:905–911
- Huberle E, Driver J, Karnath HO (2010) Retinal versus physical stimulus size as determinants of visual perception in simultanagnosia. *Neuropsychologia* 48:1677–1682
- Hughes H, Fendrich R et al (1990) Global versus local processing in the absence of low spatial frequencies. *J Cogn Neurosci* 2:272–282
- Jensen PH, Sorensen ES et al (1995) Residues in the synuclein consensus motif of the alpha-synuclein fragment, NAC, participate in transglutaminase-catalysed cross-linking to Alzheimer-disease amyloid beta A4 peptide. *Biochem J* 310:91–94
- Karnath HO, Ferber S et al (2000) The fate of global information in dorsal simultanagnosia. *Neurocase* 6:295–306
- Kim MS, Cave KR (2001) Perceptual grouping via spatial selection in a focused-attention task. *Vision Res* 41:611–624
- Kimchi R, Palmer SE (1982) Form and texture in hierarchically constructed patterns. *J Exp Psychol Hum Percept Perform* 8:521–535
- Koch C, Ullman S (1985) Shifts in selective visual attention: towards the underlying neural circuitry. *Hum Neurobiol* 4:219–227
- Lamb M, Robertson L (1988) The processing of hierarchical stimuli: effects of retinal locus, locational uncertainty, and stimulus identity. *Percept Psychophys* 44:172–181
- Lee TS, Yang CF et al (2002) Neural activity in early visual cortex reflects behavioral experience and higher-order perceptual saliency. *Nat Neurosci* 5:589–597
- Li W, Gilbert CD (2002) Global contour saliency and local colinear interactions. *J Neurophysiol* 88:2846–2856
- Luria AR (1959) Disorders of simultaneous perception in a case of bilateral occipitoparietal brain injury. *Brain* 82:437–449
- McMains SA, Fehd HM et al (2007) Mechanisms of feature- and space-based attention: response modulation and baseline increases. *J Neurophysiol* 98:2110–2121
- Mevorach C, Humphreys GW et al (2006a) Effects of saliency, not global dominance, in patients with left parietal damage. *Neuropsychologia* 44:307–319
- Mevorach C, Humphreys GW, Shalev L (2006b) Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nat Neurosci* 9:740–742
- Motter R, Vigo-Pelfrey C et al (1995) Reduction of beta-amyloid peptide42 in the cerebrospinal fluid of patients with Alzheimer's disease. *Ann Neurol* 38:643–648
- Mozer M (1991) The perception of multiple objects. MIT Press, Cambridge
- Mozer M (1998) Computational modeling of spatial attention. Psychology Press, Erlbaum

- Navon D (1977) Forest before trees: the precedence of global features in visual perception. *Cognit Psychol* 9:353–383
- Olson CR (2001) Object-based vision and attention in primates. *Curr Opin Neurobiol* 11:171–179
- Posner MI (1980) Orienting of attention. *Q J Exp Psychol* 32:3–25
- Rafal R (1997) Balint syndrome. Behavioral neurology and neuropsychology. In: Feinberg T, Farah M (ed) McGraw-Hill, New York
- Riddoch MJ, Chachlacz M, Mevorach C, Mavritsaki E, Allen H, Humphreys GW (2010) The neural mechanisms of visual selection: the view from neuropsychology. *Ann NY Acad Sci* 1191:156–181
- Rizzo M, Hurtig R (1987) Looking but not seeing: attention, perception, and eye movements in simultanagnosia. *Neurology* 37:1642–1648
- Rizzo M, Robin DA (1990) Simultanagnosia: a defect of sustained attention yields insights on visual information processing. *Neurology* 40:447–455
- Roelfsema PR (2006) Cortical algorithms for perceptual grouping. *Annu Rev Neurosci* 29:203–227
- Schall JD, Thompson KG (1999) Neural selection and control of visually guided eye movements. *Annu Rev Neurosci* 22:241–259
- Shomstein S, Behrmann M (2008) Object-based attention: strength of object representation and attentional guidance. *Percept Psychophys* 70:132–144
- Shalev L, Mevorach C, Humphreys GW (2007) Local capture in Balint's syndrome: effects of grouping and item familiarity. *Cogn Neuropsychol* 24:115–127
- Tang-Wai DF, Graff-Radford NR et al (2004) Clinical, genetic, and neuropathologic characteristics of posterior cortical atrophy. *Neurology* 63:1168–1174
- Treisman AM, Gelade G (1980) A feature-integration theory of attention. *Cognit Psychol* 12:97–136
- Von der Malsburg C (1995) Binding in models of perception and brain function. *Curr Opin Neurobiol* 5:520–526
- Von der Malsburg C, Willshaw DJ (1981) Cooperativity and brain organization. *Trends Neurosci* 4:80–83
- Wolpert I (1924) Die Simultanagnosie. *Z. Gesamte. Neurol Psychiatr* 93:397–415