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ORIGINAL ARTICLE

The role of temporo-parietal junction (TPJ) in global Gestalt perception

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Abstract Grouping processes enable the coherent perception of our environment. A number of brain areas has been suggested to be involved in the integration of elements into objects including early and higher visual areas along the ventral visual pathway as well as motion-processing areas of the dorsal visual pathway. However, integration not only is required for the cortical representation of individual objects, but is also essential for the perception of more complex visual scenes consisting of several different objects and/or shapes. The present fMRI experiments aimed to address such integration processes. We investigated the neural correlates underlying the global Gestalt perception of hierarchically organized stimuli that allowed parametrical degrading of the object at the global level. The comparison of intact versus disturbed perception of the global Gestalt revealed a network of cortical areas including the temporo-parietal junction (TPJ), anterior cingulate cortex and the precuneus. The TPJ location corresponds well with the areas known to be typically lesioned in stroke patients with simultanagnosia following bilateral brain damage. These patients typically show a deficit in identifying the global Gestalt of a visual scene. Further, we found the closest relation between behavioral performance and fMRI activation for the TPJ. Our data thus argue for a significant role of the TPJ in human global Gestalt perception.

Keywords fMRI · Global/Local · Perception · Simultanagnosia · Temporal cortex · Parietal cortex · Human

Introduction

Several decades ago, Gestalt psychologists (Wertheimer 1923; Koffka 1935) suggested that grouping processes enable the intact perception of our environment. Meanwhile, perceptual grouping has been accepted as a main principle in object recognition. Early work by Treisman and Gelade (1980) suggested that beneath conscious awareness, individual objects (so-called ‘features’) are represented in a master map and features such as proximity, motion and orientation group together (Kramer and Jacobsen 1991; Kapadia et al. 1995; Ferber et al. 2003). Numerous studies have focused on the ability of a coherent representation of objects and shapes, especially in the context of integration mechanisms along the ventral visual pathway (e.g., Malach et al. 1995; Gilbert et al. 1996; Lerner et al. 2001; Altmann et al. 2003; Kourtzi et al. 2003; Altmann et al. 2003). It has been assumed that integration processes follow a ‘hierarchical axis’ of object processing that extends from the analysis of local features in early visual areas to the representation of global shapes in higher processing areas of the ventral visual pathway (Lerner et al. 2001). In addition, a rather lateralized fashion of local and global processing has been suggested: Impaired Gestalt perception might follow right hemispheric brain damage (Delis et al. 1986) in the context of a functional predominance of the right hemisphere over the left hemisphere for Gestalt perception (Martin 1979; Alivisatos and Wilding 1982; Robertson et al. 1988; Fink et al. 1997; Yamaguchi et al. 2000). In detail, stronger activation for global than local processing was found in the right hemisphere, while the left hemisphere

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showed stronger involvement for local processing. In contrast, a right hemispheric specialization for local and a left hemispheric specialization for global processing were also reported suggesting a reversed pattern (Fink et al. 1999).

However, integration is not only required for the perception of individual objects, but also for the representation of more complex visual arrays consisting of several different objects and shapes. Previous studies have suggested an involvement of the parietal and temporal lobe in such integration processes (Friedman-Hill et al. 1995; Shafritz et al. 2002; Weissman and Woldorff 2005; but also see Rees et al. 1997). Supporting evidence has been reported from patients with simultanagnosia (Bálint 1909; Wolpert 1924; Luria 1959) following bilateral parieto-temporal brain damage (Rizzo and Hurtig 1987; Friedman-Hill et al. 1995; Rafal 1997; Karnath et al. 2000; Valenza et al. 2004; Tang-Wai et al. 2004; Huberle and Karnath 2006, 2010; Chechlacz et al. 2011). These patients show a specific deficit in identifying the global Gestalt of a visual scene, while recognition of individual objects remains unaffected that allows the perception of only one object at a time (Rafal 1997; Karnath and Zihl 2003). In detail, these patients are typically capable of identifying the letter at the local scale of Navon hierarchical letter stimuli (Navon 1977)—a letter at the global level constructed of multiple letters at the local level—while recognition of the letter at the global level is disturbed (Rafal 1997; Karnath et al. 2000; Huberle and Karnath 2006, 2010).

Taken together, recent work has focused on the ability of a coherent representation of objects and shapes in the context of integration mechanisms along the ventral visual pathway with an unclear hemispheric specialization, while evidence from patients with simultanagnosia indicated a bilateral involvement of the temporal-parietal cortex in the perception of global Gestalt. A number of cortical areas thus appear to be possible candidates to be involved in the global Gestalt perception of a complex visual array consisting of multiple objects. The present fMRI experiments addressed this question by applying hierarchically organized stimuli in healthy observers, which consisted of circles or squares (global level) rendered by smaller images of the same shapes (circles, squares). Recognition of the shape at the global level was enabled by the integration of several individual objects at the local level. Global Gestalt perception was modulated by parametrical degrading of the object at the global level, while perception at the local level remained unaffected.

Materials and methods

Subjects

The same 13 subjects (4 males/9 females; mean age 23.8 years, $SD \pm 0.9$ years) participated in Experiment 1 (psychophysical study) and Experiment 2 (fMRI study). A

subset of 11 subjects (3 males/8 females; mean age 24.6 years, $SD \pm 0.7$ years) also participated in Experiment 3 (fMRI study). Subjects had normal or corrected to normal vision and reported no history of neurological impairment affecting their visual capacity. They were paid for participation and gave their informed consent before the participation in the study, which has been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Visual stimuli and presentation procedure

Subjects were presented with hierarchically organized stimuli, in which a global Gestalt is perceived by the integration of local elements (Navon 1977; Costen et al. 1994, 1996). The stimuli displayed a circle or square (global level) that was constructed from several smaller images of circles or squares (local level). Figure 1 illustrates examples from our set of stimuli which were created from four different, two congruent and two incongruent, combinations of objects at the local and global level: (a) circle at the global level rendered of smaller circles at the local level; (b) global circle of local squares; (c) global square of local circles; and (d) global square of local squares.

Each stimulus consisted of 900 small elements organized in 30 columns and 30 rows covering an area of $21.0^\circ \times 18.0^\circ$ (width \times height) in all experiments. The local elements had a size of $0.7^\circ \times 0.6^\circ$. A similar number of local elements was used to represent the objects at the global level, that were similar in perimeter and area. In order to minimize learning mechanisms as a result of acquired spatial certainty during the experiments, all global objects were presented at one of four different positions within an individual stimulus (left top, right top, left bottom, right bottom; see also Fig. 1). Further, luminance and contrast were varied between the objects and their background (e.g., dark objects presented in light background and vice versa, see Fig. 1). All changes in the stimulus parameters were controlled across the four combinations of circles and squares. As a result of this procedure, 192 different stimuli were created (4 combinations of objects at the global and local level, 48 stimuli per combination differing in luminance and position of the global objects).

Finally, we parametrically degraded the objects at the global level in steps of 10% by exchanging the small images of objects at the local level with each other. The number of percentage indicated hereby the percentage of relocated local elements in relation to their total number of 900. This procedure led to 11 different versions of each stimulus (0-, 10-, 20-, 30-, 40-, 50-, 60-, 70-, 80-, 90- and 100%-scrambled objects) and a total number of 2,112 different stimuli. Examples are illustrated in Fig. 2.

Fig. 1 Examples for the four categories of stimuli used in the present study. The hierarchically organized stimuli showed a *circle* or *square* (global level) that were constructed from 900 (30×30) smaller images of *circles* or *squares*. The objects were displayed at four different positions and varied in contrast and luminance. All objects were similar in perimeter and size. Stimuli consisted of four different possible combinations of objects at the local and global level

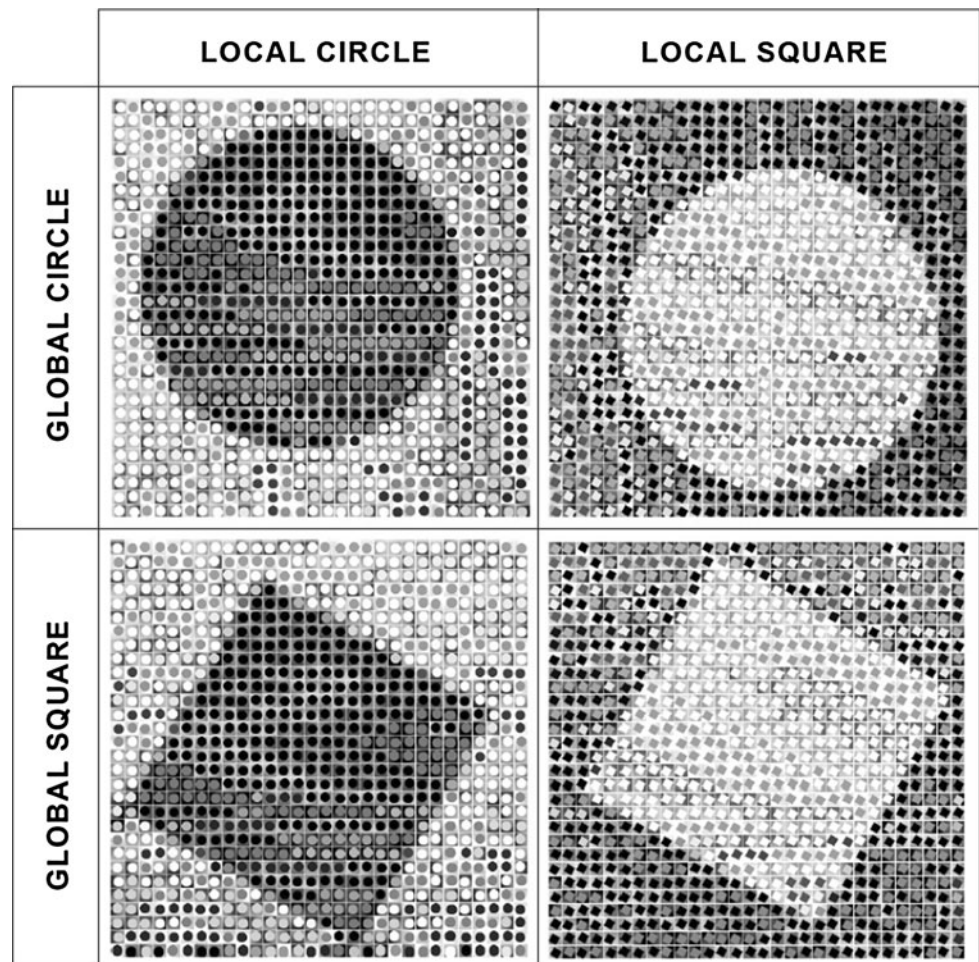
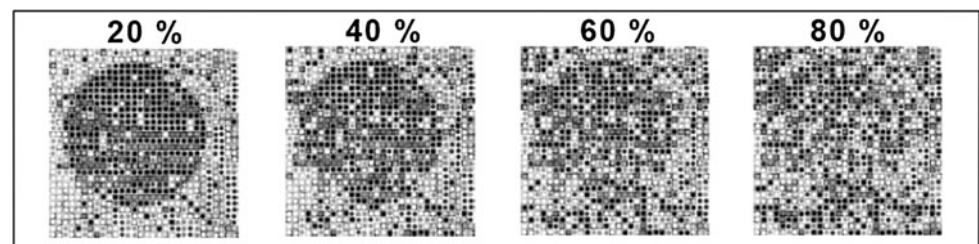


Fig. 2 Sample stimuli of the different levels of degradation. The objects at the global level were parametrically degraded by exchanging the objects at the local level with each other. Illustrated are stimuli with 20-, 40-, 60-, and 80%-scrambled objects at the global level



The stimuli were centrally displayed on a PC monitor for Experiment 1 and a translucent screen for Experiments 2 and 3 in a darkened environment. Each stimulus appeared for 300 ms followed by a blank period of 2,700 ms with only the fixation dot at the center of the display. During the blank period, subjects were required to give a response by pressing one of two buttons positioned in their right and left hand with balanced key presses for the expected responses. Prior to the onset of all three experiments, subjects participated in a short practice session during which they were familiarized with the types of stimuli and the tasks used in the respective experiment.

The first part of Experiment 1 (psychophysical study) aimed to identify the conditions in a ‘global attention’ task in which healthy subjects showed ‘intact’ or ‘disturbed’ perception of the global Gestalt of our hierarchical stimuli. The 11 conditions of parametrically degraded versions of the stimuli (0-, 10-, 20-, 30-, 40-, 50-, 60-, 70-, 80-, 90- and 100%-scrambled objects) were presented randomly in two blocks of 264 trials each resulting in a total number of 528 trials. The randomization procedure controlled for a balanced presentation of all 2,112 stimuli (including luminance and the location of the global object) across the subjects. Furthermore, the design balanced for an equal presentation of ‘circles’ or ‘squares’ at the global and local

level across subjects. Subjects had to perform a two-alternative forced choice (2AFC) task and were instructed to report the category of the object at the global level (global attention: ‘global circle’ vs. ‘global square’). Each condition (0-, 10-, 20-, 30-, 40-, 50-, 60-, 70-, 80-, 90- and 100-scrambled objects) was repeated 48 times in the ‘local’ as well as the ‘global attention’ task. In the second part of Experiment 1, subjects were instructed to report the category of the object at the local level (local attention: ‘local circle’ vs. ‘local square’), while the design and procedure was identical with the first part.

The aim of Experiment 2 (fMRI study) was to identify the neuronal correlates involved in the perception of the global Gestalt in a complex visual scene. Based on the results obtained in Experiment 1, we employed a subset of 768 stimuli at scrambled levels of 20-, 40-, 60- and 80% (Fig. 2). The 20%-scrambled condition represented ‘intact’ perception of the global Gestalt and the 80%-scrambled condition ‘disturbed’ perception. The experiment consisted of four event-related scans of 100 experimental trials (25 experimental trials per condition and scan with a controlled number of stimuli for the possible combinations of luminance and position across subjects that allowed an equal number of presentations across subjects while an individual subject was presented with a subset of all 768 stimuli) and 25 fixation trials interleaved. Additionally, a 16-second fixation epoch at the beginning and an 8-second fixation epoch at the end of the scan were added for each event-related scan. The order of trials was counterbalanced so that trials from each condition, including the fixation condition, were preceded (two trials back) equally often by trials from each of the other conditions (Friston et al. 1995; Buckner et al. 1998; Burock et al. 1998). Each stimulus appeared for 300 ms followed by a blank period of 2,700 ms with only the fixation dot at the center of the display. During the blank period, subjects were engaged in a 2AFC task and instructed to report the category of the object at the global level (global attention: ‘global circle’ vs. ‘global square’). Key responses were balanced across subjects.

The aim of Experiment 3 (fMRI study) was to investigate the attentional modulation of fMRI responses in the perception for an unattended global Gestalt. Design, procedure, and stimuli were identical with Experiment 2. In contrast, subjects were now instructed to report the category of the object at the local level (local attention: ‘local circle’ vs. ‘local square’).

Data acquisition and analysis of fMRI experiments

Experiments 2 and 3 were conducted at a 3.0 Tesla Siemens TRIO scanner located at the University Hospital in Tübingen. Data were collected with a head coil from 24

axial ($3 \times 3 \times 5 \text{ mm}^3$, 320×320 matrix) slices covering the entire cortex. Blood oxygenation level dependent (BOLD) contrast for the functional scans was obtained by using a T2*-weighted gradient echo pulse sequence (TR = 2 s, TE = 90 ms). Additionally, high-resolution T1-weighted anatomical images ($1 \times 1 \times 1 \text{ mm}^3$) were acquired from each subject.

fMRI data were processed using the ‘BrainVoyager®’ software package. Preprocessing of all the functional data included slice scan time correction, head movement correction, temporal filtering of high frequencies and removal of linear trends. The functional images were aligned to anatomical data and the complete data set was transformed to Talairach coordinates. No functional scans were excluded from the final analysis due to excessive head movement or poor psychophysical performance. Finally, all data were analyzed by applying a general linear model (GLM; $\beta > 0$) with separate predictors (random effects) for each subject and experimental condition (20-, 40-, 60- and 80%-scrambled objects) convolved with the hemodynamic response function and contrast (+, – and 0) between predictors. Clusters of significant activation were identified by applying a cluster criterion of $p < 0.05$ (corrected for multiple comparisons) and a minimum cluster size of 50 voxels. These areas were labeled based on standard Talairach coordinates and the individual anatomical structure of the subjects’ brains.

Results

Experiment 1 (psychophysical study)

Figure 3a shows the mean performance of correct responses across subjects while Fig. 3b illustrates the mean reaction time for the ‘global attention’ and ‘local attention’ task.

The subjects’ performance in the ‘global attention’ task decreased with an increasing percentage of scrambled elements (Fig. 3a). The highest performances, close to the maximum of 100% correct, were observed for 0%- (96.8% correct), 10%- (97.0% correct) and 20%-scrambled objects (96.6% correct). In contrast, the lowest performances, close to the chance level of 50% correct, were observed for 80%- (54.2% correct), 90%- (48.7% correct) and 100%-scrambled objects (52.4% correct). The opposite pattern was observed for the reaction times that increased with the percentage of scrambled elements (Fig. 3b). A repeated measures ANOVA with ‘Stimulus Condition’ as independent factor revealed a main effect for the performance ($F > 1,000$, $p < 0.0001$) and the reaction times ($F > 1,000$, $p < 0.0001$). Contrast analysis did not indicate a significant difference between 0- and 10%-, 0- and 20%-

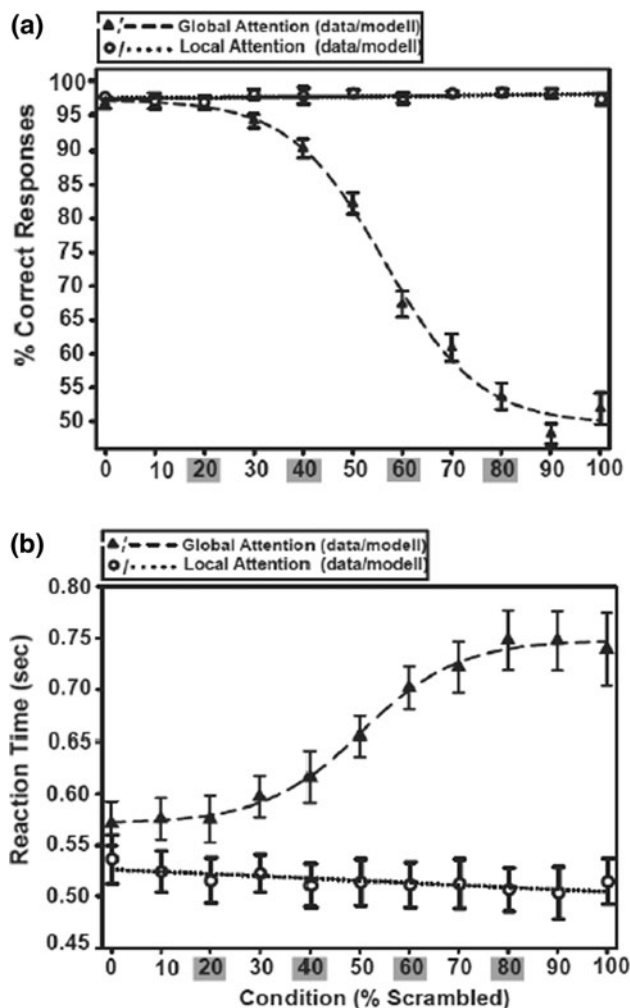


Fig. 3 Results of Experiment 1. Displayed is the mean performance (a) and the mean reaction time (b) across subjects in the ‘global’ (filled triangle) and ‘local’ (open circle) attention’ task. Fitting a psychometric function to the observed data suggested a sigmoidal function with four parameters for the ‘global attention’ task (dashed line) and a linear function with two parameters for the ‘local attention’ task (dotted line). The detection threshold for the intact perception of the global Gestalt was defined as the 75% correct point according to the suggested fitted function of the “global attention” task. Error bars indicate the standard error across subjects. The conditions that were applied in the subsequent fMRI studies are marked in dark gray. The performance decreased for highly degraded objects at the global level in the ‘global attention’ task from the maximal performance of 100% to chance level of 50%, but not in the ‘local attention’ task. In parallel, the reaction times increased for highly degraded stimuli in the ‘global attention task’, but not in the ‘local attention’ task

as well as 10- and 20%-scrambled objects for the performance and the reaction times. Fitting a psychometric function to the observed data revealed a sigmoidal function for the performance and the reaction times.

In the ‘local attention’ task, the subjects’ performance was close to ceiling (100% correct) with no differences across conditions (Fig. 3a). In parallel, differences in

reaction times were not observed (Fig. 3b). A repeated measures ANOVA with ‘Stimulus Condition’ as independent factor did not reveal a main effect for the performance ($F = 1.13$, $p = 0.65$) and the reaction times ($F = 0.45$, $p = 0.49$). In addition, contrast analysis did not indicate a significant difference between 0- and 10%-, 0- and 20%- as well as 10- and 20%-scrambled objects for the performance and the reaction times. Fitting a psychometric function to the observed data revealed a linear function for the performance and reaction times.

Experiment 2 (fMRI study)

Subjects showed a behavioral performance similar to Experiment 1, that is—in the ‘global attention’ task—they responded correctly in 97.4% (20%-scrambled objects), 88.9% (40%-scrambled objects), 67.4% (60%-scrambled objects) and 52.0% (80%-scrambled objects). Paired t tests with the averaged performance for each subject comparing the data of Experiment 1 and Experiment 2 for individual conditions revealed no differences across experiments (20%-scrambled objects: $T = -1.03$, $p = 0.325$; 40%-scrambled objects: $T = 0.88$, $p = 0.397$; 60%-scrambled objects: $T = 0.10$, $p = 0.919$; and 80%-scrambled objects: $T = 0.93$, $p = 0.368$).

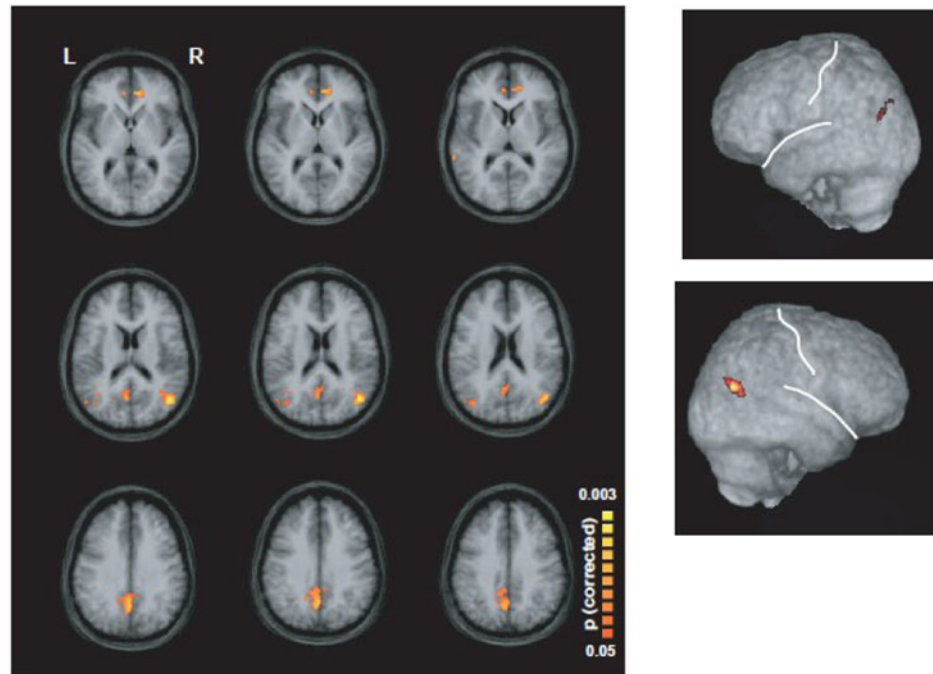
Areas involved in the intact perception of global Gestalt were identified as those voxels that showed significantly stronger activation for 20%-scrambled objects (intact global perception) compared to 80%-scrambled objects (disturbed global perception). Statistical analysis revealed a network of cortical areas involved in the intact perception of global Gestalt of a complex visual array. This network included the temporo-parietal junction (TPJ) bilaterally with larger extent in the right hemisphere, the precuneus (PC) predominantly in the left hemisphere, and the anterior cingulate cortex (ACC) bilaterally (Fig. 4a; Table 1). The TPJ activation of the left hemisphere suggested two foci, while the TPJ activation of the right hemisphere clustered in one focus that covered the combined area of activation of the opposite hemisphere. At lower significance thresholds, the two foci of the left hemisphere grouped together, so that one focus of activation remained.

A similar network was obtained when the fMRI responses for mild disturbed global perception (40%-scrambled objects) were compared to disturbed global perception, which included the TPJ, PC and ACC (Fig. 4b). Comparison with medium disturbed global perception (60%-scrambled objects) revealed stronger activation mainly in the PC and to a limited extent in the TPJ and ACC.

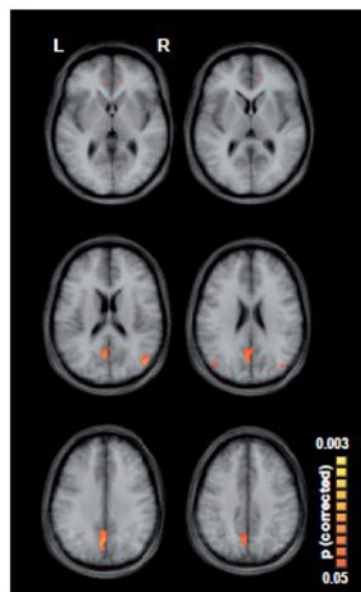
No differences in activation between intact and disturbed global perception were observed along areas of the ventral visual pathway. However, stronger activation was

Fig. 4 Results of Experiment 2. **a** Displayed are the results of intact global Gestalt perception (20%-scrambled stimuli) versus disturbed perception (80%-scrambled stimuli) on the mean anatomical brain averaged over all subjects for the relevant slices (*left*) and projected on to the mean 3D-reconstruction (*right*; white lines indicate here central sulcus and lateral fissure). A cortical network including the temporo-parieto junction (TPJ) junction bilaterally, the precuneus (PC) predominantly on the left hemisphere, and the anterior cingulate cortex (ACC) bilaterally were found to be involved in the perception of global Gestalt. **b** A similar network was revealed for mild (40%-scrambled stimuli) and severe (60%-scrambled stimuli) disturbed global perception versus disturbed perception (*left*). **c** Displayed are the results of visual stimulation versus fixation baseline for the ‘global attention’ task on the mean anatomical brain averaged over all subjects for the relevant slices. Early and higher visual areas along the ventral pathway were found to be involved in the general analysis of visual information. A similar network was obtained for the ‘local attention’ task. **d** The selective activation found for the TPJ is located within the lesions of the initial reports by Bálint (1909) on simultanagnosics (image adapted from Bálint 1909)

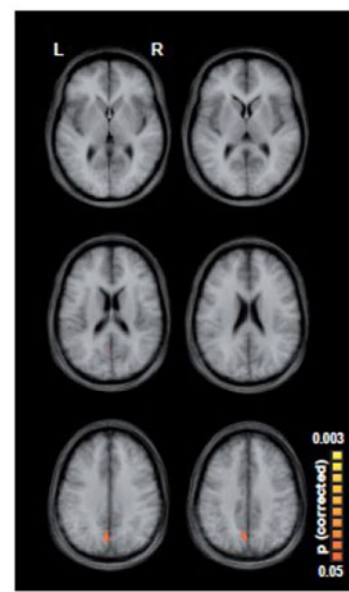
(a) 20% Scrambled > 80% Scrambled



(b) 40% Scrambled > 80% Scrambled



60% Scrambled > 80% Scrambled



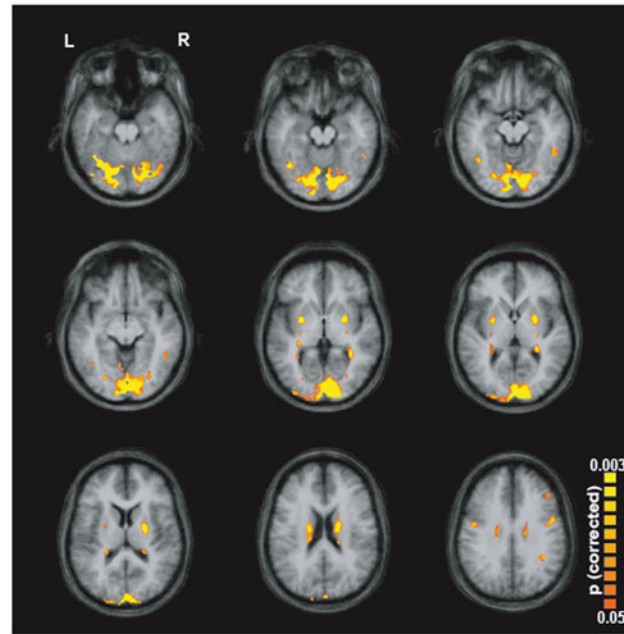
here revealed when the experimental conditions (20-, 40-, 60- and 80%-scrambled objects) were contrasted to the fixation condition indicating neuronal selectivity in early and higher object-selective areas to our stimuli (Fig. 4c). Thus, activation in the aforementioned areas including the TPJ, the precuneus, and the ACC is dependent on the perception of global Gestalt and does not show an unselective involvement in the processing of visual processing.

Finally, we computed an index that improved the compatibility between fMRI responses and psychophysical

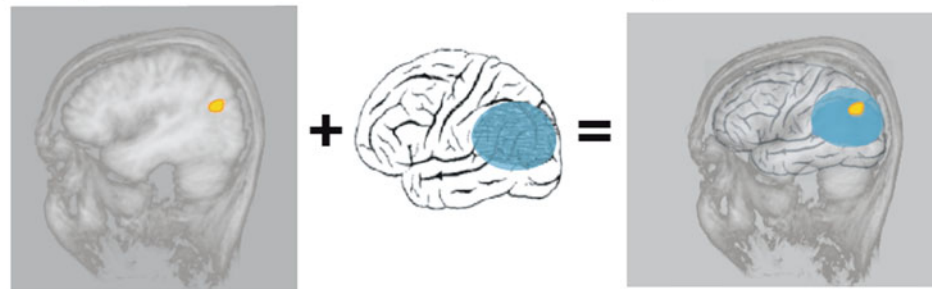
performance to better understand the role of the different areas in the perception of global Gestalt. This analysis was performed for different levels of significance for the fMRI data ($p = 0.1$, $p = 0.05$, $p = 0.01$, $p = 0.001$). Data from 80%-scrambled objects (disturbed global perception) was used as baseline and set to a value of 0. The difference in the number of voxels of both hemispheres (TPJ, PC, ACC) as well as the performance to the baseline was calculated for all conditions and normalized so that the index for 20%-scrambled objects (intact global perception) had a value of

Fig. 4 continued

(c) visual stimulation > fixation baseline



(d) overlap of fMRI-activation and lesion location of simultanagnosics

**Table 1** Extensions of areas involved in global Gestalt perception (Experiment 2)

Area	<i>x</i>			<i>y</i>			<i>z</i>		
	Left	Right	Avg (\pm SD)	Ant	Post	Avg (\pm SD)	Low	High	Avg (\pm SD)
PC	-16	9	-3.86 (3.74)	-36	-65	-51.02 (6.57)	13	46	30.03 (7.20)
ACC right	4	15	10.55 (2.88)	41	31	37.51 (2.18)	2	16	8.24 (3.51)
ACC left	-9	-3	- 6.11 (1.57)	38	33	36.30 (1.33)	1	11	6.26 (2.41)
TPO right	29	52	41.74 (4.48)	-47	-73	-61.88 (4.66)	10	26	17.24 (3.51)
TPO left1	-38	-31	-34.78 (1.52)	-54	-59	-56.33 (1.05)	13	21	16.64 (1.99)
TPO left2	-50	-34	-40.32 (4.70)	-64	-74	-67.80 (2.26)	13	27	19.50 (2.57)

Displayed are the maximal extensions (in Talairach coordinates) along the *x*-, *y*- and *z*-axis of the areas that showed an involvement in global Gestalt perception for each hemisphere (20%-scrambled stimuli vs. 80%-scrambled stimuli; $p = 0.05$). Additionally, the mean values for the three axes and their standard deviation are plotted. *PC* precuneus, *ACC* anterior cingulate cortex, *TPO* temporo-parieto-occipital region

1.0 (Fig. 5). Closest relation between cortical activation and psychophysical performance was observed for the TPJ, while the index for the PC reached values that exceeded the indices for the performance as well as the remaining areas for mild and severe disturbed global perception. The result

for the ACC showed a marked reduction compared to the performance and the remaining areas. Similar results were found with higher variance, when this index was calculated for each hemisphere for the ACC and TPJ (PC activation was found mainly in the left hemisphere).

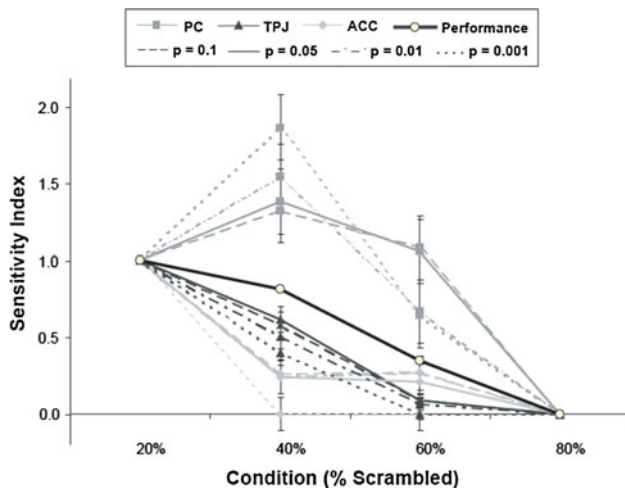


Fig. 5 Displayed are the results from the Index analysis (for further information see “Results”) for the TPJ, PC and ACC of both hemispheres at the different stimulus conditions as well as the performance. Closest relation between fMRI activity and performance was found for the TPJ

No differences in activation between intact and disturbed global perception were observed along areas of the ventral visual pathway. However, stronger activation was here revealed when the experimental conditions (20-, 40-, 60- and 80%-scrambled objects) were contrasted to the fixation condition indicating neuronal selectivity in early and higher object-selective areas to our stimuli. Additional analysis revealed no differences between congruent (identical categories at the local and global level) and incongruent (different categories at the local and global level) stimuli across conditions. Finally, no differences across conditions were observed for stimuli showing a global circle compared to those with a global square.

Experiment 3 (fMRI study)

Subjects showed a behavioral performance similar to Experiment 1, i.e., they responded correctly in the ‘local attention’ task in 98.64% (20%-scrambled objects), 98.35% (40%-scrambled objects), 98.54% (60%-scrambled objects) and 98.09% (80%-scrambled objects). Paired *t* tests with the averaged performance of eleven subjects comparing the behavioral data of Experiments 1 and 3 revealed no differences (20%-scrambled objects: $t = -1.54$; $p = 0.16$; 40%-scrambled stimuli: $t = -0.38$; $p = 0.71$; 60%-scrambled stimuli: $t = -1.67$; $p = 0.13$; and 80%-scrambled stimuli: $t = 0.01$; $p = 0.99$).

The areas involved in the global Gestalt perception of a complex visual array (observed in Experiment 2) showed no selective activation at varied levels of significance in a whole brain analysis when subjects performed the ‘local attention’ task. In parallel to Experiment 2, significantly

stronger activation was observed in early and higher object-selective areas contrasting the experimental conditions to the fixation condition.

Discussion

Our experiments investigated the neural substrates underlying global Gestalt perception. Hierarchical stimuli allowed parametrical modulation of the global perception while the local perception remained unaffected. The results suggested an involvement of the TPJ bilaterally (right stronger than left), the ACC bilaterally and the precuneus in the left hemisphere for the perception of the global Gestalt of a complex visual scene. In addition, significant differences in all three regions were no longer present, when the subjects attended the local features of the same stimuli.

Integration theories of perceptual grouping (von der Malsburg and Willshaw 1981; for review: von der Malsburg 1995; Roelfsema 1998; Singer 2001) have been extensively studied in the context of integration processes of the ventral visual pathway (Kovacs and Julesz 1993; Riesenhuber and Poggio 1999a; Altmann et al. 2003; for review: Riesenhuber and Poggio 1999b). Consistent with computational models (Mozer 1991; Mozer and Sitton 1998), integration processes were linked to visuo-spatial attention and the arrangement of individual visual features (Kimchi and Palmer 1982; Lamb and Robertson 1988; Hughes et al. 1990; Shafritz et al. 2002). Processing of global shapes consisting of collinear oriented Gabor elements has not only been observed in higher visual areas, but also at early stages of cortical processing, especially in area V1 (Gilbert et al. 1996; Altmann et al. 2003; Kourtzi et al. 2003). It is widely accepted that early visual areas with their retinotopic arrangement and small receptive field sizes show a strong involvement in the local processing of visual information. In addition, recent studies also suggested an involvement of early visual areas, especially V1, in the integration of local elements into a global shape that exceeded the size of classical receptive fields (Ito et al. 1995; Altmann et al. 2003; Kourtzi et al. 2003). These findings might be explained by reentrant connections from higher to early visual areas (Sporns et al. 1991; Freeman et al. 2003). In the present study, the low-level features of our hierarchical stimuli were kept similar. Differential processing across conditions in early visual areas thus appears unlikely. In accordance, we did not observe significant differences in fMRI activation in these areas across conditions in Experiments 2 and 3.

Secondly, object-selective neurons in the lateral-occipital and temporal cortex (Malach et al. 1995; Grill-Spector et al. 1999; Lerner et al. 2001; Grill-Spector et al. 2001;

Kourtzi and Kanwisher 2001) that show significantly stronger activation to ‘intact’ than ‘scrambled’ images of familiar as well as novel objects (Malach et al. 1995) need to be regarded in more detail. Our data did not reveal significantly stronger fMRI responses for intact (20%-scrambled objects) compared to disturbed (80%-scrambled objects) global Gestalt perception of complex visual arrays in object-selective areas, while these voxels showed selectivity to our stimuli (higher fMRI responses were observed for experimental stimulation than the fixation condition). What could be the mechanisms underlying these findings? fMRI adaptation (Buckner et al. 1998; Grill-Spector and Malach 2001; Altmann et al. 2003; Kourtzi et al. 2003; for review see: Schacter and Buckner 1998) focuses on decreased fMRI responses for repeated stimulus presentation. That is, the BOLD signal for consecutively identical stimuli is lower than for different stimuli. In parallel, a decrease following repetition of visual stimuli is also observed in the neural firing, especially of object-selective neurons in the inferotemporal (IT) cortex of the Macaque (Wiggs and Martin 1998; for review see: Desimone 1996). Our set of stimuli consisted of not more than two different objects—a circle or a square. This limited number most likely accounted for extensive adaptation in neuronal populations corresponding to higher visual areas. Furthermore, the stimuli allowed intact recognition of the object at the local level independent of the percept of the global level. That is, for any of our stimuli object-selective areas, which process objects independent of their size (Grill-Spector et al. 1999) would show an increased firing rate compared to fixation, but no difference across the experimental conditions.

Evidence for the functional role of the TPJ in global Gestalt perception was recently observed in an fMRI study investigating a patient with posterior cortical atrophy, who suffered from intermittent simultanagnosia (Himmelbach et al. 2009). This patient allowed the comparison within the same subject of brain activation during successful global Gestalt perception (identification of Navon hierarchical letter stimuli) and when global recognition failed. Bilateral activity on the rostral and caudal banks of the sulcus separating angular and supramarginal gyri was observed. Thus, the present data is not only in agreement with the anatomical findings of patients with simultanagnosia (see also Fig. 4d), but also functional investigation of the TPJ in simultanagnosia and supports further the role of the TPJ in global Gestalt perception of complex visual arrays.

The role of the TPJ in global Gestalt perception was further strengthened by the close relation between the psychophysical data and cortical activation at different degrees of global Gestalt perception, while the activation of the ACC and PC was found to be rather independent. Interestingly, selective activation was exclusively observed

for the investigation of perceptual manipulations while attentional modulations (local attention vs. global attention) did not reveal a cortical specialization as suggested by others (e.g., Weissman and Woldorff 2005).

Thus, the present data is not only in agreement with the anatomical findings of patients with simultanagnosia but also functional investigation of the TPJ and supports further its role in global Gestalt perception of complex visual arrays. Our results possibly suggest an extension of the ‘hierarchical axis’ of object processing proposed for the ventral visual pathway (Lerner et al. 2001) to areas in the temporo-parietal cortex that is required for the global Gestalt perception of complex visual arrays consisting of multiple objects or shapes. However, the present findings support the role of a hemispheric specialization to a limited degree. TPJ activation was stronger in the right than in the left hemisphere, while PC showed a strong left hemispheric dominance. Several authors reported impaired Gestalt perception following right hemispheric brain damage (Delis et al. 1986) and a functional predominance of the right hemisphere over the left hemisphere for global Gestalt perception (Martin 1979; Alivisatos and Wilding 1982; Robertson et al. 1988; Fink et al. 1997; Yamaguchi et al. 2000). In detail, stronger activation was found, when attention was focused on a global object rather than its local features in the right hemisphere. Interestingly, the reversed pattern was also reported with stronger involvement of the left hemisphere (Fink et al. 1999). While these studies investigated rather attentional mechanisms, the present work focused on grouping mechanisms independent of attention. The design did not allow us direct comparison of attentional mechanisms across the two fMRI experiments.

Besides theories of perceptual grouping, several approaches have been discussed over the past years underlying global Gestalt perception that could serve as alternative explanations for the present findings: First, form discrimination might be mediated mainly by local features and high-frequency spatial components, whereas recognition is mediated mainly by global features and low-frequency spatial components (Uttal et al. 1995; Dakin and Bex 2001). Second, global Gestalt perception has been suggested to be modified by the size of an attentional window (Robertson et al. 1993). A number of studies also suggested an influence of task difficulty on the fMRI activation in the visual domain as well as other modalities (Gerlach et al. 1999; Sunaert et al. 2000; Gould et al. 2003; Assmus et al. 2005; Livesey et al. 2007). These studies observed a positive correlation between task difficulty and fMRI activation in extrastriate visual areas (Gerlach et al. 1999; Sunaert et al. 2000) as well as parietal and frontal areas (Sunaert et al. 2000; Gould et al. 2003; Assmus et al. 2005; Livesey et al. 2007). In contrast to these findings, our

experiments revealed stronger fMRI activation for intact compared to disturbed global Gestalt perception (Experiment 2), while the data of Experiment 1 likely indicated increased task difficulty with an increase in the percentage of degradation. Although we cannot exclude the possibility that the task difficulty might have influenced the fMRI activation of Experiment 2, such an interpretation does not appear convincing since in that case we would have expected stronger fMRI activation for disturbed compared to intact global Gestalt perception.

Besides the involvement of the occipital, temporal and parietal cortex in visual processing, increased cortical activation has also been observed for the frontal lobe (Pouget et al. 2005; Green et al. 2005). However, the role of the ACC in vision remains under debate. An earlier study suggested an involvement in visual discrimination (Nishijo et al. 1997), while recent studies discussed the function of the ACC in the context of spatial working memory (Inoue et al. 2004) as well as goal-directed attentional processes (Danckert et al. 2000). In contrast to findings by Lux and colleagues (Lux et al. 2004), our data revealed no advantage for local processing in the right ACC as a result of global suppression. The present findings rather showed an involvement of the ACC bilaterally for the perception of global Gestalt but not local processing. The data thus argue against a role of the ACC in local processing and favour a function possibly related to attentional and/or working memory mechanisms in global Gestalt perception.

Previous studies investigating local and global processing mechanisms in the human brain noted an involvement of the precuneus (Heinze et al. 1998; Wilkinson et al. 2001; Rao et al. 2003) while others failed to show such a role (Fink et al. 1997). The mechanisms underlying the activation of the precuneus remain largely under debate. Some studies (e.g., Heinze et al. 1998; Rao et al. 2003) suggested a role of sustained attention. In contrast, other investigators related these results to switches in the judgment of the global and local level of hierarchically organized stimuli (Wilkinson et al. 2001). Further studies suggested an involvement of the precuneus in working memory processes due to visual (Cornette et al. 2004) and non-visual phonological and spatial stimulus processing (Zurowski et al. 2002). Finally, some studies proposed that the right precuneus (amongst other areas) might play a critical role in spatial as well as non-spatial shifts of attention, including those in long-term memory (Nagahama et al. 1999; Pathel and Sathian 2000; Ruby et al. 2002). At the present stage of investigation, the role of the precuneus in global shape recognition remains largely open. Future work will have to address this issue.

Conclusion

The data of the present study indicate a significant role of the tempo-parietal junction in human global Gestalt

perception of complex visual arrays consisting of multiple objects that exceeds the level of early visual areas located around the calcarine fissure as well as the higher visual areas along the ventral visual pathway. The result is in agreement with the finding of a specific defect to identify the global Gestalt of visual scenes following brain damage at the temporoparietal junction in stroke patients.

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