Exp Brain Res
DOI 10.1007/s00221-007-0939-7

RESEARCH ARTICLE

The contribution of prefrontal cortex to global perception

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Received: 20 September 2006 / Accepted: 10 March 2007

Abstract Recent research suggests a role of top-down modulatory signals on perceptual processing, particularly for the integration of local elementary information to form a global holistic percept. In this study we investigated whether prefrontal cortex may be instrumental in this top-down modulation in humans. We measured detection thresholds for perceiving a circle defined by a closed chain of grating patches in 6 patients with prefrontal lesions, 4 control patients with temporal lesions and 17 healthy control subjects. Performance of patients with prefrontal lesions was worse than that of patients with temporal lesions and normal controls when the patterns were sparse, requiring integration across relatively extensive regions of space, but similar to the control groups for denser patterns. The results clearly implicate the prefrontal cortex in the process of integrating elementary features into a holistic global percept, when the elements do not form a "pop-out" display.

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Keywords Prefrontal cortex · Global perception · Pattern integration

Introduction

In order to perceive the world as a coherent global percept, the brain needs to integrate elementary sensory information, initially analysed in parallel in a visuotopic fashion. Although the problem of integration has been extensively studied in recent times (e.g. Robertson and Lamb 1991; Field et al. 1993; Kovacs and Julesz 1993), the mechanisms and neural substrates for global perception are far from well-understood.

Neurophysiological and psychophysical research frame the problem of global perception in terms of perceptual grouping, meaning the emergence of a meaningful stimulus clearly segregated from a coherent set of local elements within an otherwise incoherent background (Palmer 1999). Perceptual grouping has been investigated in multiple-choice detection tasks in which a chain of spatial curtailed gratings, or gabor patches (that model the receptive field structure of V1 cells), has to be segregated from a noisy background (Field et al. 1993; Kovacs and Julesz 1993). In such tasks there is no global cue such as colour or texture to allow segregation of the elements of the chain from the background (see Fig. 2 for example). The global pattern seems to emerge from local interactive processes, which are influenced by local perceptual variables, such as the relative orientation and position of nearby cues (Field et al. 1993). Psychophysical evidence, derived for example within the lateral masking paradigm, has suggested that long-range facilitatory interactions linking cells with similar orientation preferences as early as in V1 may be instrumental in contour integration and figure-ground segregation (e.g. Kovacs and Julesz 1993; Polat and Sagi 1993).

Other research, however, indicates that contour integration may also be mediated by top-down modulation from higher areas. Piccini et al. (2003) described a patient (MC) with a marked atrophy of the right temporo-parietal junction who showed a deficit in integrating visual local information in a coherent whole (i.e. integrative agnosia; see also Humphreys 1987). In order to provide some constraint to the limits of perceptual grouping in MC, the authors measured thresholds for detection of a circle defined by a chain of gabor patches in MC, as a function of background noise. The patient was required to detect the appearance of the circle on the screen and to report its position. Crucially, the number of local elements composing the circle was varied across experimental conditions, thereby varying inter-element distance values (see also Field et al. 1993; Kovacs and Julesz 1993). It was found that MC was able to identify the stimuli with small inter-element distance values (which induced a "pop-out" perception), but failed in identifying sparser stimuli (Piccini et al. 2003). The authors thus argued that top-down neural mechanisms, involving the temporo-parietal junction, may be necessary to achieve the segregation of a target from background when global perception cannot be entirely supported by local cortico-cortical integration rules (Piccini et al. 2003; see also Fink et al. 1997; Robertson and Lamb 1991). Accordingly, a PET study demonstrated that attending to a predetermined target (i.e. a letter) that could appear either at the local or the global level in a Navon task engaged the temporo-parietal junction, which, in turn, modulated the sensory neural responses in prestriate cortex (Fink et al. 1997; see also Yamaguchi et al. 2000).

We hypothesize that the prefrontal cortex may also be a crucial component in a system that provides top-down attentional control for global perception. Recent evidence suggests that the prefrontal cortex may be implicated in the control of perceptual processes. For example, in a study investigating perceptual reversals, Windmann and colleagues found a reduced ability to switch between the two competing representations in patients with prefrontal lesions compared to normal controls, which suggests that the prefrontal cortex can bias the selection of visual representations in accordance with current goals (Windmann et al. 2006). Moreover, in a visual search task requiring detection of inverted triangles embedded in a rapid train of upright ones, patients with damage to prefrontal cortex were impaired for contralateral targets compared with normal controls (Barcelò et al. 2000). Event-related potentials revealed that this behavioural deficit was accompanied by reduced post-selection target-related neuronal activity in ipsilesional inferior temporal cortex neurons that are specialized in the early analysis of object features (e.g. Desimone and Duncan 1995).

This evidence has suggested that the prefrontal cortex might be necessary to activate and maintain a representation of the relevant stimuli in extrastriate areas (Barcelò et al. 2000; Windmann et al. 2006), that could be used to guide top-down selection of task-relevant object features (Desimone 1998; Miller and Cohen 2001; Miyashita and Hayashi 2000). Studies using single-cell recordings have indeed shown that working memory-related activity can significantly influence the deployment of attention, so as to contribute to the selection of appropriate visual information (Desimone 1998; Duncan and Humphreys 1989). For example, Chelazzi and colleagues presented monkeys with a cue image, followed by a search array containing two or more objects after an appropriate delay. The monkey was required to saccade to the object that matched the cue (target). About 90–120 ms before the onset of the eye movement to the target, responses in the inferior temporal neurons to non-targets were suppressed, and the neural response was dominated by the target (Chelazzi et al. 1993; Tomita et al. 1999; Miyashita and Hayashi 2000). Importantly, it seems that the contents of working memory are in turn controlled by the prefrontal cortex: in monkeys, prefrontal neurons exhibit object-specific delay-period activity that is robust to distraction (Miller et al. 1996). Moreover, a disruption of top-down inputs from the prefrontal cortex to the inferotemporal cortices prevents the activation of stored task-relevant information (Tomita et al. 1999; see also Rainer et al. 1998).

In the present study we investigate whether prefrontal cortex may play a role in global perception in humans. If the prefrontal cortex modulates extrastriate responses to attended sensory events, then this brain region might be crucial in segregating a desired target from background under difficult or noisy conditions. In contrast, the prefrontal cortex is not expected to be necessary to perceive high-salient stimuli, which may induce a pop-out perception. To verify our hypothesis, we measured thresholds for detecting a circle defined by a closed chain of gabor patches in 6 patients with prefrontal lesions, 4 control patients with temporal lesions and 17 normal controls. The number of patches defining the circle was manipulated across experimental conditions, hence varying the inter-element distance values. The results show that patients with prefrontal lesions perform well in detecting stimuli with small inter-element distances, but are impaired in perceiving sparse patterns with large inter-element distance values compared to patients with temporal lesions and normal controls.

Methods

Participants

Three groups of participants took part in the study (see Table 1): a group of patients with lesions in the prefrontal

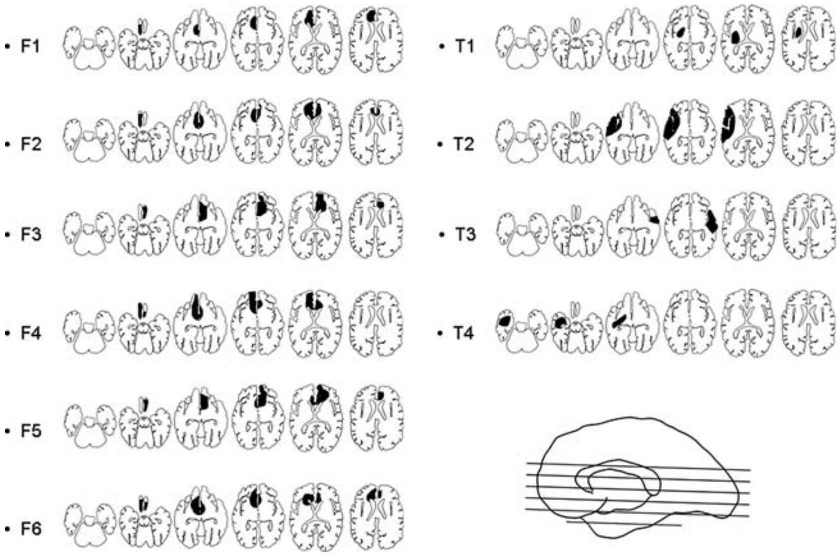

Fig. 1 Location of brain lesions according to the templates developed by Damasio and Damasio (1989)

Table 1 Demographic, clinical and lesion data of patient groups

Prefrontal patients	Sex	Age (years)	Education (years)	Etiology	Side of lesion	Description of lesion	MMSE	WMS	SRM*	WCST* (perseverative errors)
F1	F	61	8	AcoA Aneurysm	L	Vm PFC	26	84	50	9
F2	F	56	18	AcoA Aneurysm	B	Vm PFC	27	97	5	5
F3	M	45	8	AcoA Aneurysm	R	Vm PFC	28	94	50	30
F4	M	65	5	AcoA Aneurysm	L	Vm PFC	26	92	50	18
F5	M	48	8	AcoA Aneurysm	R	Vm PFC	27	93	5	5
F6	M	56	13	AcoA Aneurysm	L	Vm PFC	25	82	19	5
Temporal patients										
T1	F	59	13	Infarction	L	Temporal white matter	28	40	50	10
T2	M	70	8	Infarction	L	Lateral temporal	n.a.	n.a.	25	30
T3	M	56	5	Infarction	L	Lateral temporal	27	82	55	70
T4	M	49	10	Infarction	L	Basal ganglia/internal capsule	n.a.	n.a.	50	50

M male, *F* female, *L* left, *R* right, *B* bilateral, *ACoA* anterior communicating artery, *Vm PFC* ventromedial prefrontal cortex, *MMSE* mini-mental state examination (cut-off = 24); *WMS* weschler memory scale (normal mean = 100, SD 15); *SRM* standard raven matrices; *WCST* Wisconsin Card Sorting Test

Scores in percentile value are indicated with a *. Percentile values ≤5 are indicative of impaired performance. *n.a.* non-applicable due to the presence of aphasia

cortex ($n = 6$), a control group of patients with lesions in the temporal cortex ($n = 4$), and a control group of healthy individuals ($n = 17$). Patients were all more than 8 months post-onset. Frontal patients were selected on the basis of lesion restricted to the frontal lobe, as documented on CT or MRI scans (see Fig. 1). They had a mean age of 55.1 years (SD 7.5), a mean of 10 years of education (SD 4.6), and presented lesions mainly involving the ventromedial prefrontal cortex (BA 10, 12, 24, 32). Temporal patients were selected on the basis of lesion restricted to the temporal lobe, as documented on CT or MRI scans (see Fig. 1). They had a mean age of 58.5 years (SD 7.5), a mean of 9.8 years of education (SD 3.3).

Patients were matched to a group of 17 healthy individuals with a mean age of 60.2 years (SD 6.4) and a mean education of 9.4 years (SD 3.1). No significant differences in age [Kruskal–Wallis $\chi^2(2) = 0.03$; $P = 0.8$] or education [Kruskal–Wallis $\chi^2(2) = 0.02$; $P = 0.9$] emerged across participant groups.

Participants were included who had no other diagnosis likely to affect cognition or interfere with the participation in the study (e.g. psychiatric disease, alcohol abuse, history of cerebrovascular disease, etc.). Before commencing the main experiment, we first measured contrast sensitivity of all groups by means of the Vistech tables. All patients and controls were within the normal range both for low and for high-spatial frequencies, showing that there were no major deficits in basic visual function. All subjects had vision corrected for 57 cm viewing. Participants gave informed consent to participate in the study according to the Declaration of Helsinki (International Committee of Medical Journal Editors, 1991) and the Ethical Committee of the Department of Psychology, University of Bologna.

Table 1 shows demographic data, lesion side, etiology, lesion description, as well as the results each patient obtained in neuropsychological tests commonly used in clinical practice (see Spinnler and Tognoni 1987 for normative data). Patients with prefrontal lesions were mostly impaired in tests tapping executive functions, such as the Wisconsin Card Sorting Test, where three of the six patients showed impaired performance, and the Standard Raven Matrices, where two patients showed impaired performance. In contrast, their memory performance at the Wechsler Memory Scale was close to normal (as a group they scored 90, where normal mean and standard deviation are 100 and 15, respectively). On the other hand, two of the four temporal patients showed a severe aphasia that precluded the administration of some neuropsychological tests. Moreover, of the two non-aphasic patients, one showed severely impaired memory at the Wechsler Memory Scale (score = 40). In contrast, temporal patients' performance in executive tests was within the normal range.

Stimuli

Sensitivity for integration of local elements into a global pattern was measured by testing the ability of the subjects to detect a target circle embedded in noise (see Fig. 2), where both the circle and noise elements were sinusoidal grating patches (Field et al. 1993; Kovacs and Julesz 1993). Grating patches of the target were distributed equally around and oriented parallel to the circumference of a virtual circle of radius of 4.3°. The position and orientation of noise elements were distributed randomly. Spatial frequency of grating patches was 1.75 cycles per degree, each patch subtended 0.57° of visual angle. Inter-element spacing of the patches was 4.3°, 3.1° and 2.1°, corresponding to 6, 10 and 14 patches in the target (see also Piccini et al. 2003). Stimuli were presented on a 60 Hz frame-rate LCD display driven by a PC laptop. Distance of subjects from the screen was 57 cm. The whole stimulus had mean luminance 20 cd/m^2, subtended 20° × 20° of visual angle and was displayed for 1 s. All measurements were made in a darkened room.

Fig. 2 Example of the stimulus used to explore visual integration ability. The circular target is located in the lower right quadrant. The number of noise elements shown here are below threshold for all subjects

Procedure

Subjects were required to identify in the quadrant where the grating patch was displayed (four-alternative forced choice) by reporting to the experimenter. Subjects had no time limit for response and no feedback was given. The number of random elements was varied by the adaptive QUEST procedure (Watson and Pelli 1983), and the psychometric functions fitted by a Weibull function (with asymptotes of 0.25 and 1), to calculate threshold as 75% correct. Sensitivity is defined as $(S + N)/S$ where S is the number of patches in the target, and N is the number in the background at threshold. To reduce fatigue, data were generally collected in three sessions, carried out on different days. In total three blocks of 30 trials were measured for each condition.

Results

Figure 3 shows example psychometric curves for two representative subjects, one with prefrontal lesions (patient F3: filled symbols) the other with temporal lesions (patient T3: open symbols). Squares show results for fairly dense gabor chains (inter-stimulus spacing 2°), and circles those for sparse chains (inter-stimulus spacing 4.3°). All four curves show the same general pattern, going from perfect performance for low-noise levels to chance (25%) at high noise levels. Sensitivity is defined as the noise level at which performance is 75% correct. For the dense gabor chains, the functions for the two patients are similar. For the sparse chain, however, the performance of the patient with prefrontal lesions (filled symbols) was considerably worse than the patient with temporal lesions (open symbols).

Figure 4 shows average sensitivities for detecting the patch-defined circles, as a function of inter-stimulus

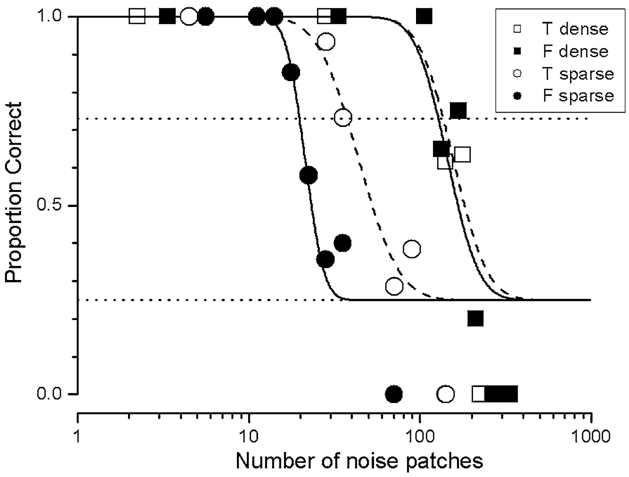

Fig. 3 Example psychometric curves for one patient with prefrontal lesions (*F*) and one patient with temporal lesions (*T*). *Squares* show results with dense patterns (inter-stimulus spacing 2°) and *circles* for sparse patterns (inter-stimulus spacing 4.3°). The data are fitted by cumulative Gaussian functions, and sensitivity is given by the noise level at which performance is 75% correct. The *dotted horizontal lines* show chance and threshold performance

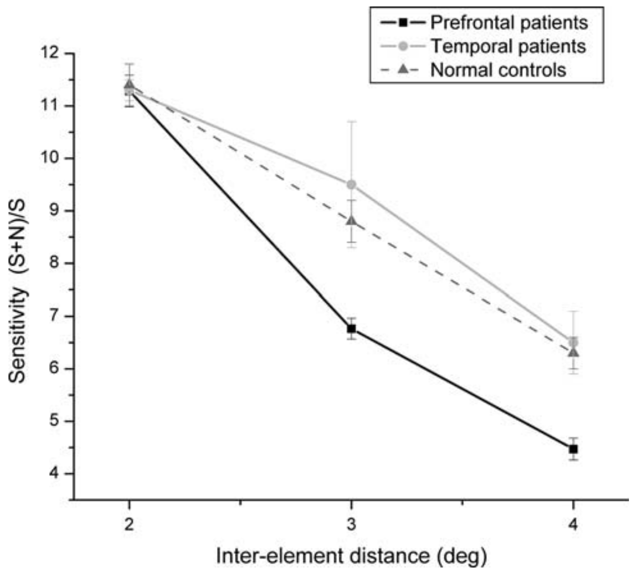

Fig. 4 Mean sensitivity for detecting the patch-defined *circles*, as a function of inter-stimulus interval, for patients with prefrontal lesions, control patients with temporal lesions, and normal controls. The means are geometric means, with the *bars* representing 1 standard error of the mean

spacing, for patients with prefrontal lesions, control patients with temporal lesions, and normal controls. For each subject and experimental condition, curves like those of Fig. 3 were fitted to the data to yield estimates of sensitivity (at 75% performance), and these sensitivities were averaged across subjects. For all subjects performance decreased with increasing inter-stimulus distance: stimuli with high inter-element distance values were more difficult to detect than low distances, consistent with previous evidence (Field et al. 1993; Kovacs and Julesz 1993; Piccini et al. 2003). However, for patients with prefrontal lesions the dependence on inter-stimulus distance was greater than for controls. Thus, while their sensitivity to dense patterns was as good as the controls, both in mean and in spread, sensitivity to sparse patterns was consistently lower in prefrontal patients compared to normal controls. The patients with temporal damage behaved quite differently: sensitivity was as good as for controls under all conditions (see Fig. 4).

Performance of patients with prefrontal lesions was contrasted to that of the control groups by using non-parametric tests. For the dense patterns (2° inter-stimulus spacing, no significant difference in sensitivity was detected across participant groups [Kruskal–Wallis $\chi^2(2) = 1$; $P = 0.6$]: sensitivity of patients with prefrontal lesions was statistically indistinguishable from that of patients with temporal lesions (Mann–Whitney $U = 11$; $P = 0.8$) and normal controls (Mann–Whitney $U = 47$; $P = 0.8$).

For stimuli with inter-stimulus spacing of 3° (10 Gabors per circle), there was a significant difference in sensitivity across groups [Kruskal–Wallis $\chi^2(2) = 7.5$; $P < 0.05$]: prefrontal patients showed lower sensitivity compared to normal controls (Mann–Whitney $U = 20$; $P < 0.05$), whereas temporal patients showed comparable sensitivity to normal controls (Mann–Whitney $U = 50$; $P = 0.6$). The difference in sensitivity between prefrontal and temporal patients did not reach statistical significance (Mann–Whitney $U = 6$; $P = 0.2$).

For the sparse stimuli with inter-stimulus spacing of 4.3° (6 Gabors per circle) there was a significant difference in sensitivity across groups [Kruskal–Wallis $\chi^2(2) = 7.4$; $P < 0.05$]. Sensitivity of prefrontal patients was significantly lower than that of normal controls (Mann–Whitney $U = 9$; $P < 0.005$), and temporal patients (Mann–Whitney $U = 0.5$; $P < 0.05$). In contrast, temporal patients' performance was comparable with normal controls (Mann–Whitney $U = 44$; $P = 0.9$).

Figure 5 shows individual results for the two patient groups and normal controls, plotting sensitivity to sparse patterns (inter-stimulus separation 4.3°) against that to dense patterns (2° separation). While the scatter distributions for dense patterns are very similar for the three groups, both in mean and in spread, sensitivity for the prefrontal patients to sparse patterns was consistently lower than that of the control and temporal groups. This shows that the results were a general trend across subjects and not just due to a few atypical outliers.

Discussion

This study investigated perceptual grouping in patients with lesions in prefrontal cortex, control patients with lesions in

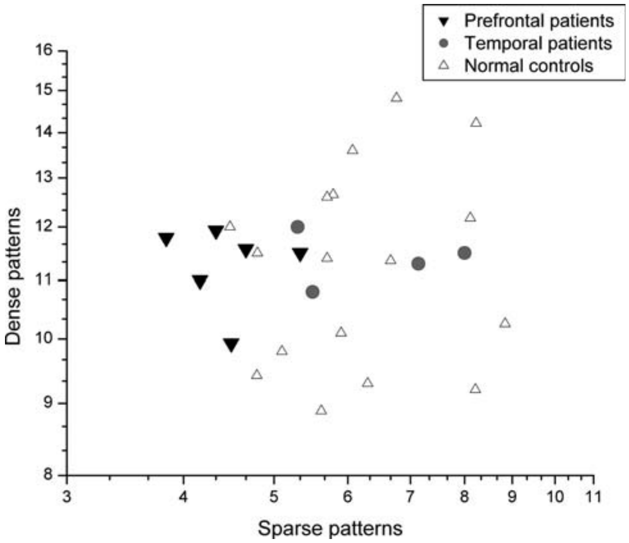

Fig. 5 Sensitivity of individual prefrontal patients (*filled triangles*), temporal patients (*filled circles*), and their age-matched controls (*open triangles*) represented as a scatterplot, with sensitivity to dense patterns (inter-stimulus distance of 2°) shown on the ordinate and that to sparse patterns (inter-stimulus distance of 4.3°) on the abscissa

temporal cortex, and normal controls. Compared with the control groups, patients with prefrontal lesions were impaired in perceiving stimuli with high inter-element distance values (with 4.3° separation). The deficit was specific for sparse patterns, and therefore cannot be ascribed to scarce motivation, failure to maintain attention on the task, or other non-specific reasons. It cannot be put down to a difference in task difficulty, as we adjusted the noise levels to calculate thresholds at constant task difficulty, yielding 75% performance. In any event, no comparable deficit was observed in patients with lesions to the temporal cortex, who may also be expected to show task-difficulty related effects. Finally, it is improbable that the deficit resulted from reduced contrast sensitivity, as this was shown to be normal over a wide range of spatial frequencies.

Thus, our findings point to a perceptual deficit in patients with prefrontal lesions for integrating relatively sparse elements into a global percept. Many have argued that spatial integration of local elements could be determined by a series of local rules (e.g. orientation, colinearity) within a spatially limited region of the visual space surrounding each local element, the "association field" (Field et al. 1993). These interactions could well be implemented at an early level of visual processing, possibly V1 (Polat and Sagi 1993; Cass and Spehar 2005; Das and Gilbert 1995). The finding that the prefrontal patients of this study, who have no occipital damage, showed no reduction in sensitivity to dense targets (2° inter-element separation) supports the notion that integration between elements can occur at a low level. However, when the distance between local elements increases, it seems that top-down neuro-modulatory mechanisms are necessary to group these elements in a unitary percept.

Our results suggest that the prefrontal cortex might be a crucial component in providing top-down modulation in the process of integrating elementary features into a holistic global percept. Consistent with this suggestion, in the PET study of global perception by Fink et al. (1997) which we discussed earlier, significant activation of the medial prefrontal cortex was detected along with the temporo-parietal activation. It is then natural to ask what the specific role of the prefrontal cortex in global perception might be. It is worth noting that in the present study, as well as in most of those reported earlier (e.g. Windmann et al. 2006; Barcelò et al. 2000; Piccini et al. 2003), participants were informed about the nature of the target to be detected. Under such conditions, the prefrontal cortex is reasonably involved in the activation and the maintenance of a representation of the sought target in working memory (see also Windmann et al. 2006; Barcelò et al. 2000).

Recent research in humans has shown that the activation of a relevant representation in working memory constitutes an important top-down modulator for visual selection (Desimone 1998). Specifically, it has been demonstrated that when an object is maintained in working memory, attention automatically shifts to objects that match the sample (Downing 2000), or share a defining feature with the sample (Soto et al. 2005), or are even only semantically related to the sample (Moores et al. 2003), which ultimately will gain a privileged access to awareness. Such top-down factors might arguably exert a determinant influence over selection of targets that are relatively difficult to discriminate (Duncan and Humphreys 1989), but be not essential for detecting very salient targets, which may induce a bottom-up selection (e.g. Theeuwes 1991). Thus, in our perceptual grouping task, patients with prefrontal lesions might not have detected stimuli with high inter-element distance values because they failed to activate or maintain a relevant representation in working memory. Such deficit, however, had little impact on detection of stimuli with low interelement distance values.

The precise mechanisms by which prefrontal projections influence the activity of targeted visual neurons are poorly understood at present. The prefrontal cortex does not connect directly with the primary visual cortex in the primate brain, but connects to many extra-striate areas, including the inferior temporal cortex (Miller and Cohen 2001). The prefrontal cortex could activate and hold on-line a representation of the relevant target in these areas (Rainer et al. 1998; Tomita et al. 1999; Miller and Cohen 2001) which, in turn, could amplify and focus activity of neurons in lower-order ares, thus highlighting features and contributing to the "pop-out" phenomenon. In line with this interpretation, neuropsychological (Barceló et al. 2000) and neuroimaging research (Corbetta et al. 1993) has shown that the prefrontal cortex can modulate extrastriate processing to enhance sensory representations according to their behavioural relevance. Moreover, electrophysiological studies suggest that the prefrontal cortex may help establish feature binding of relevant object representations by inducing high-frequency firing in the gamma band range (Keil et al. 1999).

Our data, together with those of Piccini and colleagues using the same paradigm, implicate the temporo-parietal junction and the ventromedial prefrontal cortex as two crucial neural underpinnings of perceptual grouping. Interestingly, these two brain regions take part in an attentional system deemed to be crucial for detection of task-relevant stimuli (Corbetta and Shulman 2002). One might speculate then that these two brain regions play complementary roles during global perception, with the temporo-parietal junction mediating conscious awareness of relevant stimuli, and the ventral regions of prefrontal cortex maintaining task relevancy. Evidence from recognition memory tasks is relevant to this idea: unlike other amnesics, patients with ventromedial prefrontal lesions not only tend to falsely recognize (select) items that are semantically related to the studied ones, and thus consistent with a representation of the studied material, but also endorse items that are unrelated to the studied ones, and therefore task-irrelevant (Ciaramelli et al. 2006). Future studies using visual search paradigms (e.g. Moores et al. 2003) might be useful to verify the merit of this proposal more directly.

To conclude, by investigating perceptual grouping using robust psychophysical methods, we have shown that the prefrontal cortex may be instrumental in integrating local elements into a coherent whole under difficult conditions of segregation. In contrast, when segregation is easier (as is probably more usual in real life situations), more local cortical inter-connectivity without the involvement of prefrontal cortex may be sufficient.

Acknowledgements We thank Silvia G. Bonifazi, Michela Coccia, and Luisa Rinaldesi for referring temporal patients to us, Rachele Agostini for assistance with the collection of the control data, and Giuseppe di Pellegrino and Papik Lauro-Grotto for their helpful comments on a draft of the paper.

References

Barcelo F, Suwazono S, Knight RT (2000) Prefrontal modulation of visual processing in humans. Nat Neurosci 3:399–403

Cass JR, Spehar B (2005) Dynamics of collinear contrast facilitation are consistent with long-range horizontal striate transmission. Vision Res 45:2728–2739

Chelazzi L, Miller EK, Duncan J, Desimone R (1993) A neural basis for visual search in inferior temporal cortex. Nature 363:345–347

Ciaramelli E, Ghetti S, Frattarelli M, Ladavas E (2006) When true memory availability promotes false memory: evidence from confabulating patients. Neuropsychologia 44:1866–1877

Corbetta M, Miezin FM, Shulman GL, Petersen SE (1993) A PET study of visuospatial attention. J Neurosci 13:1202–1226

Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. Nat Rev Neurosci 3:201–215

Damasio H, Damasio AR (1989) Lesion analysis in neuropsychology. Oxford, New York

Das A, Gilbert CD (1995) Long-range horizontal connections and their role in cortical reorganization revealed by optical recording of cat primary visual cortex. Nature 375:780–784

Desimone R (1998) Visual attention mediated by biased competition in extrastriate visual cortex. Philos Trans R Soc Lond B Biol Sci 353:1245–1255

Desimone R, Duncan J (1995) Neural mechanisms of selective visual attention. Annu Rev Neurosci 18:193–222

Downing PE (2000) Interaction between visual working memory and selective attention. Psychol Sci 11:467–473

Duncan J, Humphreys GW (1989) Visual search and stimulus similarity. Psychol Rev 96:433–458

Field DJ, Hayes A, Hess RF (1993) Contour integration by the human visual system: evidence for a local "association field". Vision Res 33:173–193

Fink GR, Halligan PW, Marshall JC, Frith CD, Frackowiak RSJ, Dolan RJ (1997) Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. Brain 120:1779–1791

Humphreys GW (1987) To see but not to see. A case study of visual agnosia. Lawrence Erlbaum, Hove, UK

Keil A, Muller MM, Ray WJ, Gruber T, Elbert T (1999) Human gamma band activity and perception of a gestalt. J Neurosci 19:7152–7161

Kovacs I, Julesz B (1993) A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation. Proc Natl Acad Sci USA 90:7495–7497

Miller EK, Cohen JD (2001) An integrative theory of prefrontal cortex function. Annu Rev Neurosci 24:167–202

Miller EK, Erickson CA, Desimone R (1996) Neural mechanisms of visual working memory in prefrontal cortex of the macaque. J Neurosci 16:5154–5167

Miyashita Y, Hayashi T (2000) Neural representation of visual objects: encoding and top-down activation. Curr Opin Neurobiol 10:187–194

Moores E, Laiti L, Chelazzi L (2003) Associative knowledge controls deployment of visual selective attention. Nat Neurosci 6:182–189

Palmer SE (1999) Vision science. Photons to phenomenology. MIT, Cambridge

Piccini C, Lauro-Grotto R, Del Viva M, Burr D (2003) Agnosia for global patterns: when the cross-talk between grouping and visual selective attention fails. Cogn Neuropsychol 20:3–25

Polat U, Sagi D (1993) Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. Vision Res 33:993–999

Rainer G, Asaad WF, Miller EK (1998) Selective representation of relevant information by neurons in the primate prefrontal cortex. Nature 393:577–579

Robertson L, Lamb M (1991) Neuropsychological contributions to theories of part/whole organization. Cogn Neuropsychol 23:299–330

Soto D, Heinke D, Humphreys GW, Blanco MJ (2005) Early, involuntary top-down guidance of attention from working memory. J Exp Psychol HPP 31:248–261

Spinnler H, Tognoni, G (1987) Standardizzazione e Taratura Italiana di Test Neuropsicologici. Ital J Neurol Sci 6(Suppl 8)

Theeuwes J (1991) Cross-dimensional perceptual selectivity. Percept and Psychophys 50:184–193

Tomita H, Ohbayashi M, Nakahara K, Hasegawa I, Miyashita Y (1999) Top-down signal from prefrontal cortex in executive control of memory retrieval. Nature 401:699–703

Watson AB, Pelli DG (1983) QUEST: a Bayesian adaptive psychometric method. Percept Psychophys 33:113–120

Windmann S, Wehrmann M, Calabrese P, Gunturkun O (2006) Role of the prefrontal cortex in attentional control over bistable vision. J Cogn Neurosci 18:456–471

Yamaguchi S, Yamagata S, Kobayashi S (2000) Cerebral asymmetry od the top-down allocation of attention to global and local features. J Neurosci 20:RC72