

Contrast dependence of perceptual grouping in brain-damaged patients with visual extinction

MARINA PAVLOVSKAYA^{1,*}, DOV SAGI² and NACHUM SOROKER¹

¹*Loewenstein Rehabilitation Hospital and Sackler School of Medicine, Tel-Aviv University, Tel Aviv, Israel*

²*Department of Neurobiology/Brain Research, The Weizmann Institute of Science, Rehovot, Israel*

Received 1 January 1999; revised 14 December 1999; accepted 27 April 2000

Abstract—Extinction is manifested in conditions of bilateral simultaneous stimulation, as a failure to detect the stimulus contra-lateral to the side of a cerebral lesion, while the same stimulus is correctly detected there when presented in isolation. The phenomenon is usually interpreted in terms of impaired mobilization of attention from an attended to an unattended object. We have recently shown, using pairs of Gabor patches as stimuli, that pair detection is maximally improved in conditions where the two stimuli presented simultaneously to the two halves of the visual field are co-oriented and co-axial and their location is not too eccentric. Here we add new information by showing that contrast isotropy of the stimulus pair is important in producing this orientation-similarity gain. The further advantage of co-oriented co-linear stimuli over co-oriented parallel (vertical) stimuli was shown exclusively with iso-contrast stimulus pairs, and was significantly enhanced when the contrast level of the stimulus pair was low. Stimulus properties producing reduced extinction seem to correlate with the selectivity pattern and contrast dependence of (a) spatial lateral facilitation observed in psychophysical studies with normal observers, and (b) long-range interactions observed in the primary visual cortex. Thus, two remote visual stimuli seem to be processed as a single object when the corresponding neuronal activities are linked via long-range lateral interactions. The present demonstration of contrast dependency in such processing, strengthens our previous conjecture that even in the presence of significant, extinction producing, parietal damage, the primary visual cortex preserves the capacity to encode, using long-range lateral interactions, an image description in which visual objects are already segregated from background.

Keywords: Spatial-interactions; grouping; neglect; extinction; visual-attention.

INTRODUCTION

Visual extinction is a common, poorly understood consequence of unilateral cerebral damage, where a patient fails to detect one of two simultaneously presented

*To whom correspondence should be addressed. E-mail: marinap@netvision.net.il

stimuli (the one more contra-lateral to the lesion), despite the fact that each stimulus is correctly detected when presented in isolation. The phenomenon points to a competition between visual stimuli, each of which is processed to some extent (as it is detected in isolation), and thus can serve as a tool in studying visual segmentation. A critical question here is the individualization of the visual objects presented, as extinction reflects competition between different display items. A typical case of extinction is when a patient (e.g. with a right hemisphere damage) who is simultaneously presented with two patterns (e.g. letters, Gabor patches), one to the right of the fixation point and one to the left, fails to detect the left pattern, despite a high detection rate of the same left pattern in the absence of the right pattern.

Recent research has shown that extinction can be reduced (i.e. increased detection of the 'extinguished' pattern), when the two patterns can be thought of as a single object (Ward *et al.*, 1994; Mattingley *et al.*, 1997). For example, a horizontal line (—) on the left and an arrowhead (>) on the right, could be associated to produce an arrow. These results point to the existence of some grouping process that marks the two patterns as a single object before entering the competition stage implicated by the extinction phenomenon.

These grouping processes are expected to operate over long retinal separations. Recent anatomical (Malach *et al.*, 1993; Bosking and Fitzpatrick, 1995), physiological (Gilbert, 1993; Polat and Norcia, 1996) and psychophysical (Polat and Sagi, 1993, 1994) evidence point to the existence of a rich network of long-range interactions in the primary visual cortex, having a well defined architecture. These studies support a network in which co-oriented co-axial unites are connected, possibly subserving the detection of long contours and thus bridging the gap between the local feature-detection systems operating on small scales and the requirement for efficient contour integration over longer spatial extents, as shown in some psychophysical tasks (Field *et al.*, 1993; Kovács and Julesz, 1993).

It is common for a stroke patient showing extinction to have a unilateral extensive cortical lesion in the territory of the middle cerebral artery (MCA), including the posterior parietal region. The primary visual cortex, supplied by the posterior cerebral artery (PCA), is usually intact in such patients. The improvement in contra-lesional extinction that is shown when stimulus properties are manipulated in a manner corresponding with activation of a primary cortex network subserving grouping operations, can provide us with important information concerning the functionality of primary visual cortex. We have recently shown (Pavlovskaya *et al.*, 1997), using pairs of Gabor patches as stimuli, that in patients with extinction, pair detection is improved when the two stimuli are co-oriented and co-axial and their location is not too eccentric. Reduction of extinction was shown to depend on the basic stimulus properties known to reflect connectivity constraints at the primary visual cortex (Gilbert, 1993; Malach *et al.*, 1993; Bosking and Fitzpatrick, 1995; Polat and Norcia, 1996; Suguta, 1999). To explain these findings, we have proposed that two remote visual stimuli are processed as a

single object when the corresponding primary cortical activities are linked by long-range lateral interactions. We also suggested that intact parietal lobes are not necessary for correct linkage of spatially separated parts of an object (though other experimental data suggests that the parietal lobes may have a role in linking color with shape (Friedman-Hill *et al.*, 1995)). The low-level grouping process suggested here may improve detection of the grouped items but not necessarily recognition of the individual items. Previous investigations of grouping effects in extinction have found both increased (Baylis *et al.*, 1993) and decreased (Ward *et al.*, 1994; Mattingley *et al.*, 1997) extinction, depending on stimuli and task. Recognition of individual targets may require individualization and thus may not benefit from grouping, though detection of simple features may (Adini and Sagi, 1992).

In the present study we examine contrast effects on pair detection in brain damaged patients suffering from extinction. Several studies point to contrast dependence of long-range cortical interactions. Single cell recordings from cat visual cortex (area 17) show that long-range interactions change with neuronal activity level, being excitatory at low activity levels and inhibitory with high activity levels (Polat *et al.*, 1998). Recent psychophysical studies, using arrays of Gabor signals, have shown stimulus saliency dependence on contrast (Bonneh and Sagi, 1999). In these studies, two different Gabor textures were presented to the different eyes of normal observers, producing binocular rivalry. With low contrast stimuli, uniform textures were found to dominate non-uniform textures presented to the other eye, while with high contrast stimuli, non-uniform textures dominated uniform textures (Bonneh and Sagi, 1999). The authors proposed that grouping processes operating on uniform textures, that follow Gestalt principles such as similarity and proximity, are better expressed with low contrast stimuli, while segmentation processes, operating on locations where textures change, are better expressed with high contrast stimuli. This transition between grouping and segmentation, or between facilitatory and inhibitory effects, results probably from the dynamics of lateral cortical interactions, as shown by recent modeling work (Stemmler *et al.*, 1995; Somers *et al.*, 1998).

Eight right hemisphere-damaged patients with contra-lateral extinction participated in the study. Patients were presented with one or two Gabor signals, of either the same orientation (vertical or horizontal) or different orientation, having to report the number of detected signals. Contrast (high and low) was manipulated using iso- or aniso-contrast pairs. We predicted that severity of extinction would be affected by the relative saliency of both stimuli (being most severe when contrast of ipsilesional signal exceeds that of the contra-lesional one). In accordance with known characteristics of long-range cortical interactions, grouping (manifesting as reduced extinction) was expected to operate best in conditions of contrast isotropy of the stimulus pair, especially with low contrast signals.

METHODS

Patients

Eight first-episode stroke patients participated in the study (see Table 1 for a detailed description). There were six females and two males at an age range of 49–74 years (65.2 ± 8.7). All had infarctions (ischemic in five, hemorrhagic in three) confined to the territory of the right middle cerebral artery. Portions of the frontal, parietal and temporal cortical areas were involved in 4, 5 and 4 patients, respectively. The intra-hemispheric white matter was involved in all patients, of whom two had other brain regions intact. The capsular-putaminal region was involved in five patients. All the eight patients had left hemiplegia or hemiparesis. None of them had a visual field defect, but contra-lesional extinction upon bilateral simultaneous visual stimulation was present in all. Soon after the onset of stroke, six of the patients manifested left-sided neglect in the standardized “Behavioral Inattention Test” (Wilson *et al.*, 1987; cut-off for normality: 130; patients’ scores ranging between 36 and 129), while two patients scored within the normal range. At the time of testing (5–16 weeks after the onset of stroke) neglect manifestations in activities of daily living were much more infrequent and attenuated.

Procedure

The patients fixated on a central (aligned with the midsagittal plane of the body) point displayed on a high resolution (1280×1024) computer monitor, and were

Table 1.

Patients’ demographic and clinical data

Patient	Age/ sex	Hand.	Educ.	Motor imp.	Sensory imp.	VFD	Ext.	BIT	TAO (w)	Pathology
SN	74/F	R	11	++	+	–	e	136	5	I: Rt. P, F, CSO
SS	53/M	L	18	++	++	–	e	129	16	H: Rt. T, P, C-P, CSO
DH	67/M	R	8	++	+	–	e	141	8	H: Rt. C-P, CSO
LH	49/F	R	10	±	+	–	e	79; 123	8	I: Rt. CSO diffuse
RR	65/F	R	0	++	++	–	e	68	8	I: Rt. F, T, P, C-P, CSO
SD	73/F	R	6	++	++	–	e	36	10	H: Rt. F, T, P, C-P, CSO
EA	69/F	R	12	++	+	–	e	89; 118	12	I: Rt. F, T, P, C-P, CSO
SL	72/F	R	7	±	+	–	e	44; 117	8	I: Rt. CSO diffuse

Hand. = Handedness (R = right, L = left); Educ. = Education (years of formal schooling); Imp. = Impairment (– = none, ± = mild, + = moderate, ++ = severe); VFD = Visual field defect (– = none); Ext. = Extinction upon bilateral simultaneous stimulation (e); TAO = Time (weeks) after the onset of stroke; I = Ischemic infarction; H = Parenchymal hemorrhage; Rt. = right hemisphere; P = Parietal; F = Frontal; T = Temporal; CSO = Centrum semi-ovale; C-P = Capsular-Putaminal region; BIT = Behavioral Inattention Test (cut off score for normality: 130, maximal score: 146). The scores presented here were obtained upon admission to rehabilitation. A second test score performed about a month later was available for 3 patients. The patients were admitted to the study at a later stage, when frank neglect behaviour was no longer evident, but extinction still persisted at this stage).

briefly presented (40–160 ms) with one (right or left) or two (bilateral, at same eccentricity), horizontal or vertical Gabor signals which served as stimuli. Pairs of signals ($\lambda = \sigma = 0.225^\circ$ for all patients, except L.H. [0.112°]) were presented on half of the trials, while on the other half only one signal was presented. In conditions of bilateral simultaneous stimulation, the Gabor patches were either 1) of the same orientation: (i) horizontal, iso-oriented and co-axial; (ii) vertical, iso-oriented; or 2) of different orientations (one horizontal and one vertical).

Stimulus duration, eccentricity and contrast varied among the patients, in accordance with the individual level of task performance (duration: 40–160 ms; eccentricity: 1.4° – 6.1° [during bilateral stimulation, inter-target separation is twice the eccentricity]; contrast level: 17–55% [Gabor signal amplitude relative to mean display luminance — 50 cd/m^2]). There were 4 inter-stimulus contrast arrangements in bilateral stimulation: left (contra-lesional) stimulus contrast higher than right (ipsi-lesional) stimulus contrast (Cc); left lower than right (cC); low iso-contrast

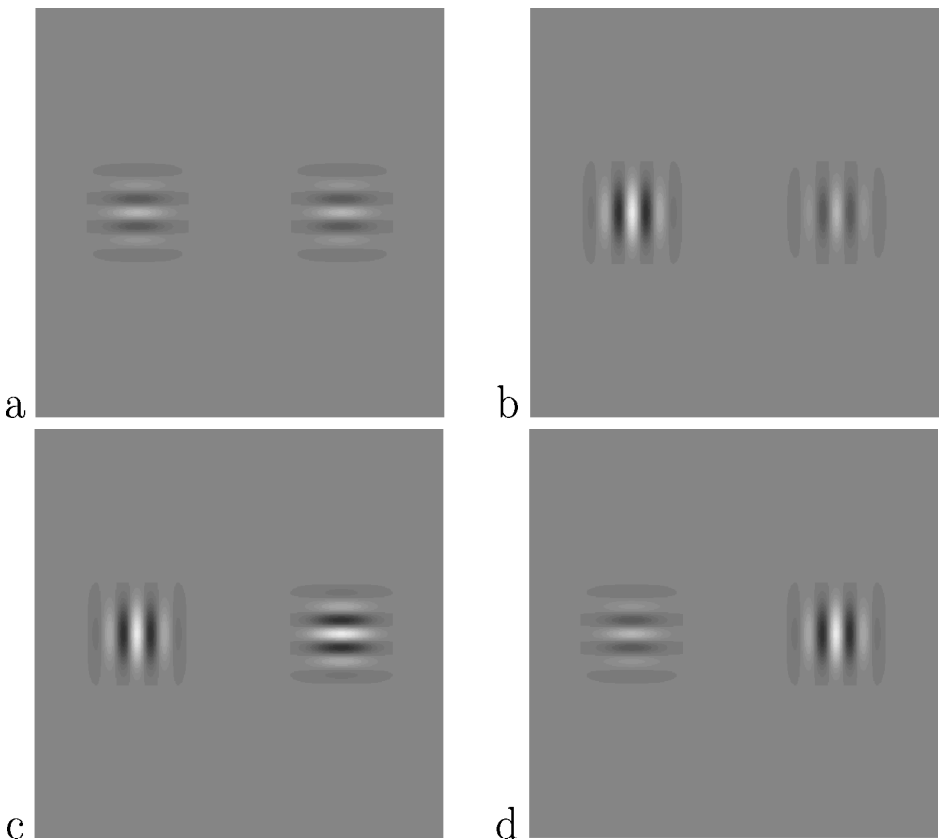


Figure 1. Stimulus contrast arrangements. Examples of orientation/contrast arrangements in bilateral stimulation conditions: (a) cc-HH, (b) Cc-VV, (c) CC-VH, (d) cC-HV. c = low contrast, C = high contrast, H = horizontal, V = vertical. Cc = high contrast on the left and low contrast on the right, VH = vertical patch on the left and horizontal patch on the right.

pairs (cc); high iso-contrast pairs (CC) (Fig. 1). Stimuli were presented in blocks of 50 trials. All trials in a block shared the same eccentricity and contrast–location assignment. Within each block, trials employing unilateral (left and right) and bilateral, horizontal and vertical Gabor signals were interleaved in pseudo-random order. The patients had to verbally respond with the perceived number of targets (0, 1, 2) and indicate target location (left, right, both). As detection rate at the non-neglected field was close to perfect (rate of correct detection of unilateral right-sided stimuli was 95% or more, see Fig. 2), the present patients could always correctly detect at least one target in the bilateral presentation. This experimental paradigm was in essence as in Pavlovskaya *et al.* (1997). Modifications were made in the present research in order to enable manipulation of stimulus contrast and inter-stimulus contrast differences.

RESULTS

Contrast effect on stimulus detectability is shown in Fig. 2, separately for unilateral (left/right) and bilateral (iso-oriented/differently oriented) stimuli. Contrast manipulation created 4 types of blocks (conditions: CC, Cc, cc, cC), defined here in accordance with contrast arrangement during the bilateral stimulation trials in the block, as explained before. Data represent the averaged performance of 8 patients.

As can be seen in Fig. 2, detection of unilateral stimuli on the left hemifield was inferior to that on the right hemifield, in all conditions (χ^2 test: $p < 0.001$), consistent with the presence of contra-lateral visual neglect. Detectability of

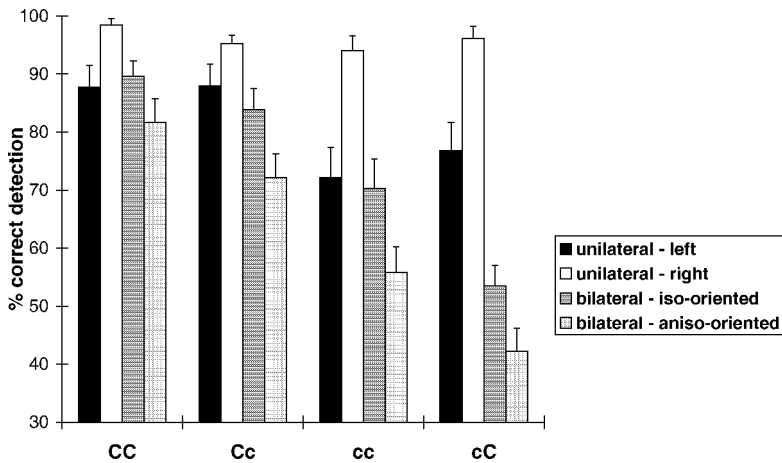


Figure 2. Unilateral and bilateral target detection in different contrast arrangements. Performance scores (% correct detection) are shown for unilaterally presented targets (left/right) and simultaneous bilateral targets (iso-oriented/aniso-oriented), using an average number of 332 trials per datum column. Data, averaged from 8 patients, is shown separately for contrast isotropy (high contrast on both sides [CC]/low contrast on both sides [cc]) and anisotropy (high on left, low on right [Cc]/low on left, high on right [cC]). Vertical bars indicate 1 standard error of the mean.

unilateral right-sided stimuli showed a ceiling effect (detection rate: 93–99%). In contradistinction, detection of unilateral left-sided stimuli was significantly lower with low-contrast stimuli (conditions: cc, cC) as compared to high-contrast stimuli (conditions: CC, Cc). As a consequence, contra-lateral neglect, as revealed by the difference between detectability of unilateral right- and left-sided stimuli, sharing the same contrast level and presented in same conditions, was more prominent when using low-contrast (cc) than high-contrast (CC) stimuli.

In all four contrast combinations of bilateral stimulation trials, correct detection (i.e. observer's report about the two perceived stimuli) was significantly higher when the two signals were of the same orientation (both horizontal, or both vertical), as compared to trials using differently oriented signals (χ^2 test: $p < 0.001$). These results point to the existence of orientation selective spatial interactions in extinction, thus corroborating our previous findings (Pavlovskaya *et al.*, 1997). Incorrect detection in bilateral stimulation conditions reflected almost exclusively missed perception of the stimulus presented on the left (patient SN was exceptional in showing a reversed pattern, of ipsi-lesional extinction, as observed sometimes in neglect patients during the convalescence period. Her data was reversed accordingly). Therefore, the difference between detection rate of unilateral left-sided stimuli, and pair detection in bilateral stimulation trials can serve as a rough measure of extinction severity. As can be seen in Fig. 2, the advantage of single left target detection over pair detection was most prominent when using differently oriented pairs of signals. In all four-contrast combinations, unilateral left-sided targets were better detected than pairs having different orientations (χ^2 test: $p < 0.001$).

When pairs sharing the same orientation were presented, extinction was significantly reduced, and practically disappeared or was even reversed when the signals were iso-oriented and iso-contrast. In the cc and CC conditions, the difference in performance between single left and iso-oriented pair detection did not reach significance at the 0.05 level. However, with aniso-contrast stimuli (Cc, and especially cC), extinction (i.e. inferiority of pair detection as compared to single left-sided target detection) is revealed also for iso-oriented pairs (χ^2 test: $p < 0.001$), although its severity is less than that shown with differently oriented pairs.

In order to examine more closely the effect of orientation similarity on pair detection, in its relation to inter-stimulus contrast differences, we separated performance scores on trials using iso-oriented co-axial targets (HH [both signals horizontal], Fig. 1a), from trials using co-oriented vertical targets (VV, Fig. 1b), and trials employing differently oriented targets (VH and HV, Fig. 1c, d). Figure 3 shows the deviation of actual pair detection from the expected pair-detection level (calculated on the basis of unilateral [right and left] actual detections, assuming statistical independence of the two single detection processes). This deviation, separately presented for each of the four contrast combinations, is used here as a quantitative measure of extinction severity (ES).

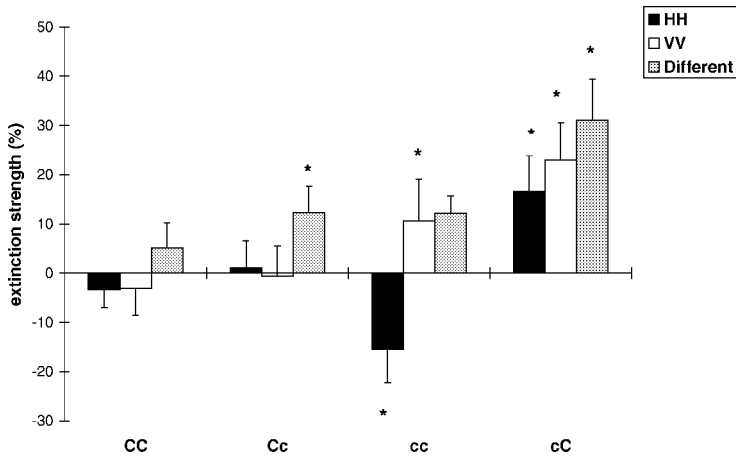


Figure 3. Extinction severity in different contrast arrangements. Deviation of actual pair detection from the expected pair-detection level (calculated on the basis of unilateral [right and left] actual detections, assuming statistical independence of the two single detection processes), is shown for co-oriented co-axial targets (HH, both signals horizontal), co-oriented vertical targets (VV), and differently oriented targets (HV plus VH). This deviation, separately presented for each of the four contrast combinations (CC, Cc, cc and cC, as in Fig. 2), is used here as a quantitative measure of extinction severity (ES). $ES = 100(P_c(\theta_l) \cdot P_c(\theta_r) - P_c(\theta_l\theta_r))$, where P_c , $0 \leq P_c \leq 1$, is the probability of correct detection, θ_{side} being either horizontal (H) or vertical (V) and *side* is left or right. Each P_c value is based on 160–400 trials. The asterisk denotes significance of deviation (t -test: $p < 0.05$). Vertical bars indicate 1 standard error of the mean.

As can be seen, in all four-contrast combinations, the magnitude of extinction is greatest when using differently oriented stimuli. The most dramatic reduction of extinction, with practically its complete elimination, was observed with iso-oriented co-axial (HH) pairs, when both stimuli were also low iso-contrast (cc). Here, pair detection rate is higher than expected from the individual detection rates (assuming statistically independent detection processes), suggesting some cooperative process.

The effect of contrast isotropy of the stimulus pair on orientation-similarity gain is shown more clearly in Fig. 4a, b. Here, the advantage of iso-oriented, relative to aniso-oriented pair detection, which is revealed in HH *vs.* HV comparison, is contrasted to the advantage of VV *vs.* VH, separately for contrast isotropy (CC and cc) and anisotropy (Cc and cC) stimulation conditions (HH = iso-oriented, co-axial pair; VV = iso-oriented, parallel pair).

The further advantage of collinearity of the iso-oriented pair, first demonstrated in our previous study (Pavlovskaya *et al.*, 1997), is shown only in conditions of contrast isotropy. Moreover, contrast isotropy effect on facilitation related to collinearity of the stimulus pair, is enhanced significantly (as shown also in Fig. 3) when the two stimuli are of low contrast. In conditions of contrast anisotropy,

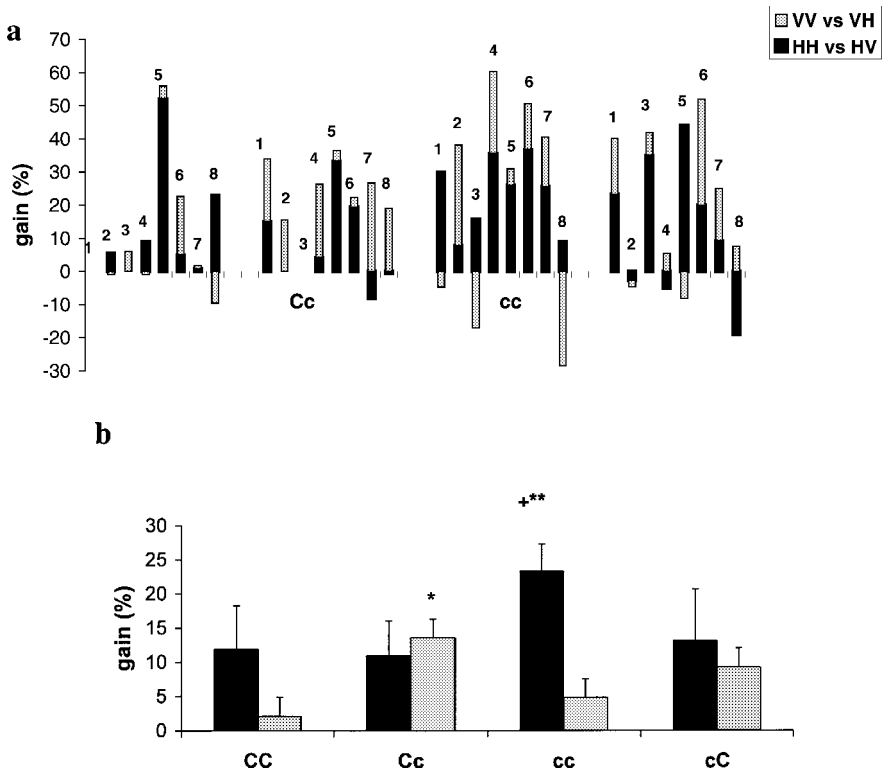


Figure 4. Orientation-similarity gain in conditions of contrast isotropy and anisotropy. The advantage of iso-oriented co-axial (HH) pair detection relative to aniso-oriented (HV) pair detection, is compared to that of iso-oriented vertical (VV) pair detection relative aniso-oriented (VH) pair detection (in both cases orientation-similarity gain is calculated for conditions sharing the same left-sided stimulus), separately for contrast isotropy (CC, cc) and anisotropy (Cc, cC). Gain is defined as negative extinction strength (ES), with similarity gain defined as the gain difference between pairs sharing the same orientation on the left side, namely: similarity gain = $(-ES(HH)) - (-ES(HV))$ or $(-ES(VV)) - (-ES(VH))$. (a) The results are presented separately for eight patients in the same order as in Table 1, i.e. SN on the leftmost column and SL on the rightmost column. Each stacked column compares the contribution of each value (HH vs. HV or VV vs. VH) to the total for a given patient. Note the smallest variability of the results for the cc-condition, when 7 patients among 8 demonstrate the advantage of collinearity (HH vs. HV). (b) Data are averaged from all patients. The further advantage of collinearity of the iso-oriented pair is revealed only in conditions of contrast isotropy, and reach significance (plus sign) only when the two stimuli are of low contrast ($t(16) = 2.24, p < 0.05$). Asterisks denote significance of orientation-similarity gain: *in -Cc VV - VH ($t(8) = 3.80, p < 0.01$); **in -cc HH - HV ($t(8) = 5.84, p < 0.001$). Vertical bars indicate 1 standard error of the mean.

orientation-similarity gain is about the same for collinear and parallel (vertical) pairs, and in the Cc condition the relative gain of parallel pairs is somewhat higher than that of collinear pairs.

DISCUSSION

We have recently shown, using Gabor signals for bilateral simultaneous stimulation, that contra-lesional extinction of brain-damaged patients improves significantly when the two signals co-oriented, and especially when they were also co-axial (Pavlovskaya *et al.*, 1997). In the present study, we add new information by showing that contrast isotropy of the stimulus pair is important in producing this orientation-similarity gain. The further advantage of iso-oriented co-axial (horizontal) stimuli over iso-oriented parallel (vertical) stimuli was demonstrated exclusively in conditions of contrast isotropy, and especially when contrast level of the stimulus pair was low.

The previous (Pavlovskaya *et al.*, 1997) and present findings suggest that stimulus properties producing reduced extinction in brain damaged patients, correlate with the selectivity pattern of spatial lateral interactions observed in normal vision (Polat and Sagi, 1993, 1994), and with the characteristics of long-range interactions observed in the primary visual cortex (Gilbert, 1993; Malach *et al.*, 1993; Bosking and Fitzpatrick, 1995; Polat and Norcia, 1996). The present findings show correlations at the level of network activity, showing improved grouping with low contrast stimuli by the extinction patients. Long range excitatory interactions at the primary visual cortex were also shown to efficiently operate at low contrast levels (Polat *et al.*, 1998).

The findings support a theory of recognition according to which visual objects compete for attention allocation. Extinction seems to reflect failure of shifting attention from the attended (winning) object to the unattended one, and does not necessarily reflect competition over spatial locations (Duncan and Humphreys, 1989; Humphreys *et al.*, 1994). Perceptual grouping of the stimulus pair in early stages of visual processing (on the basis of collinearity, isotropy, and possibly some other basic physical properties), can take place in the undamaged primary visual cortices, prior to attention allocation, and thus obviate attentional shift.

While in previous demonstrations of grouping effects on extinction (Baylis *et al.*, 1993; Ward *et al.*, 1994; Mattingley *et al.*, 1997), perceptual grouping was only subjectively defined, we have shown here that rules underlying cortical neuronal connectivity can predict complete elimination of extinction. This correspondence between reduction of extinction and primary cortex architecture indicates that the primary visual cortex functions properly in patients with extensive parietal damage leading to extinction. Moreover, this result suggests that the primary visual cortex has a major role in defining visual objects for higher level processing. It seems that lateral interactions do not only provide the cortex with activity modulation, but also underlie perceptual grouping essential for elementary figure-ground segregation.

On the basis of the present and our previous (Pavlovskaya *et al.*, 1997) findings we suggest that neuronal activity in early stages of cortical visual processing encodes, using long-range lateral interactions, an image description in which visual objects are already segmented and marked. Lesion mapping of the participating subjects enables us to propose that the segmentation process (i.e. the process of

figure-ground segregation, when elements of the figure are spatially separated) may function properly even in the presence of huge destruction of the parietal cortex.

Acknowledgement

This research was supported by the Israel Center for Psychobiology — The Charles E. Smith Family Foundation.

REFERENCES

- Adini, Y. and Sagi, D. (1992). Parallel processes within the “spot-light” of attention, *Spatial Vision* **6**, 61–77.
- Baylis, G. C., Driver, J. and Rafal, R. D. (1993). Visual extinction and stimulus repetition, *Cognitive Neuroscience* **5**, 453–466.
- Bonneh, Y. and Sagi, D. (1999). Configuration saliency revealed in short duration binocular rivalry, *Vision Research* **39**, 271–281.
- Bosking, W. H. and Fitzpatrick, D. (1995). Physiological correlates of anisotropy in horizontal connections length summation properties in layers 2 and 3 of tree shrew striate cortex, *Soc. Neurosci. Abstr.* **21**, 1751.
- Duncan, J. and Humphreys, G. W. (1989). Visual search and stimulus similarity, *Psychol. Rev.* **96**, 433–458.
- Field, D. J., Hayes, A. and Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local association field, *Vision Research* **33**, 173–193.
- Friedman-Hill, S. R., Robertson, L. C. and Treisman, A. (1995). Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions, *Science* **269**, 853–855.
- Gilbert, C. D. (1993). Circuitry, architecture and functional dynamics of visual cortex, *Cerebral Cortex* **3**, 373–386.
- Humphreys, G. W., Romani, C., Olson, A., Riddoch, M. J. and Duncan, J. (1994). Non-spatial extinction following lesions of the parietal lobe in humans, *Nature* **372**, 357–359.
- Kovács, I. and Julesz, B. (1993). A closed curve is much more than an incomplete one: Effect of closure in figure-ground segmentation, *Proc. Nat. Acad. Sci. USA* **90**, 7495–7497.
- Malach, R., Amir, Y., Bartfeld, E. and Grinvald, A. (1993). Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate visual cortex, *Proc. Nat. Acad. Sci. USA* **90**, 10469–10473.
- Mattingley, J. B., Davis, G. and Driver, J. (1997). Pre-attentive filling-in of visual surfaces in parietal extinction, *Science* **275**, 671–674.
- Pavlovskaya, M., Sagi, D., Soroker, N. and Ring, H. (1997). Visual extinction and cortical connectivity in human vision, *Cognitive Brain Research* **6**, 159–162.
- Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T. and Norcia, A. M. (1998). Collinear stimuli regulate visual responses depending on cell's contrast threshold, *Nature* **391**, 580–584.
- Polat, U. and Norcia, A. M. (1996). Neurophysiological evidence for contrast dependent long range facilitation and suppression in the human visual cortex, *Vision Research* **36**, 2099–2109.
- Polat, U. and Sagi, D. (1993). Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments, *Vision Research* **33**, 993–999.
- Polat, U. and Sagi, D. (1994). The architecture of perceptual spatial interactions, *Vision Research* **34**, 73–78.
- Somers, D. C., Todorov, E. V., Siapas, A. G., Toth, L. J., Kim, D. S. and Sur, M. (1998). A local circuit approach to understanding integration of long-range inputs in primary visual cortex, *Cerebral Cortex* **8**, 204–217.

- Stemmler, M., Usher, M. and Niebur, E. (1995). Lateral interactions in primary visual cortex: A model bridging physiology and psychophysics, *Science* **269**, 1877–1880.
- Sugata, Y. (1999). Grouping of image fragments in primary visual cortex, *Nature* **401**, 269–272.
- Ward, R. S., Goodrich, S. and Driver, J. (1994). Grouping reduces visual extinction: Neuropsychological evidence for weight-linkage in visual selection, *Visual Cognition* **1**, 101–129.
- Wilson, B., Cockburn, J. and Halligan, P. (1987). Development of a behavioral test of visual-spatial neglect, *Archives of Physical Medicine and Rehabilitation* **68**, 98–102.