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THE EFFECT OF CONTEXT ON CONTOUR INTEGRATION:

EVIDENCE FROM PSYCHOPHYSICAL AND CLINICAL STUDIES

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ITALIAN ABSTRACT

Nell'ultimo decennio, diverse ricerche hanno analizzato come il sistema visivo integri stime di strutture locali di un'immagine in forme globali complesse (ad esempio contorni spazialmente estesi). Altro interessante tema di ricerca, strettamente relato al precedente, riguarda l'effetto del contesto sul processamento visivo. In tale lavoro di tesi si cerca di collegare questi due temi di ricerca, analizzando come l'informazione contestuale influenzi il processamento di contorni (che richiede l'integrazione di elementi locali in una struttura globale). Particolare importanza è data all'origine di tali effetti contestuali, analizzando se meccanismi locali o globali o entrambi siano coinvolti. Data la rilevanza clinica di tale tema di ricerca, analizziamo l'effetto del contesto sull'integrazione di contorni anche nell'invecchiamento e nella schizofrenia.

In particolare nel primo studio analizziamo come il contesto influenzi la localizzazione di contorni e se meccanismi *locali* siano sufficienti per rendere conto di tali effetti. Punto di partenza per tale studio è il lavoro di Dakin e Baruch [2009] che mostra come elementi contestuali *quasi*-perpendicolari (rispetto all'orientamento del contorno) riducano il tempo di esposizione dello stimolo necessario per localizzare il contorno e identificarne la forma (rispetto ad elementi orientati in modo casuale). Elementi contestuali *quasi*-paralleli, invece, causano un aumento di tale durata. A differenza dello studio di Dakin e Baruch [2009], nel presente lavoro utilizziamo un semplice compito di localizzazione di contorni, senza identificazione di forma. Nello specifico, chiediamo ai soggetti di rilevare la posizione di un contorno (paradigma a scelta forzata tra due alternative) in diversi tipi di contesto: casuale, *quasi*-parallelo e *quasi*-perpendicolare (rispetto al contorno). Il contorno-target può essere uno *snake* (i cui elementi sono allineati con l'orientamento locale del contorno) o un *ladder* (i cui elementi sono perpendicolari all'orientamento locale del contorno). Nel primo esperimento testiamo come il contesto nelle immediate vicinanze del contorno-target moduli la *soglia di durata di esposizione* (cioè la durata minima di esposizione allo stimolo che permette di localizzare correttamente il contorno il 75% delle volte). Testiamo poi (Esperimento 2) se gli effetti del contesto generalizzino

ad altre misure di soglia; nello specifico misuriamo una *soglia di orientation-jitter*, che rappresenta una misura di tolleranza alla perturbazione di orientamento degli elementi lungo il contorno. Inoltre, nell'Esperimento 3 verifichiamo che gli osservatori non confondano il contesto quasi-parallelo come contorno-target. Infine, nell'Esperimento 4 studiamo la relazione tra effetti contestuali sulla localizzazione globale di contorni e incertezza riguardo l'orientamento locale degli elementi che costituiscono il contorno. Nello specifico, verifichiamo l'ipotesi che l'incertezza di orientamento locale introdotta dal *crowding visivo* (cioè l'influenza deleteria di elementi visivi "fiancheggianti" sul riconoscimento di oggetti) possa rendere conto degli effetti contestuali sulla localizzazione globale di contorni.

In linea con lo studio di Dakin e Baruch [2009], i risultati dell'Esperimento 1 mostrano una riduzione ed un aumento nella sensibilità a contorni-snake in presenza di contesti rispettivamente quasi-paralleli e quasi perpendicolari (entrambi gli effetti rispetto alla condizione con contesto casuale). La sensibilità a contorni-ladder è invece superiore in presenza di qualsiasi contesto organizzato. Il secondo esperimento indica che il contesto influenza la soglia di orientation-jitter nello stesso modo in cui modula la soglia di durata di esposizione. In particolare i partecipanti tollerano minori perturbazioni di orientamento lungo il contorno se gli elementi contestuali sono quasi-paralleli piuttosto che orientati in modo casuale. La tolleranza invece aumenta quando gli elementi contestuali sono quasi-perpendicolari al contorno. Tali effetti sono consistenti e non possono essere attribuiti al fatto che gli osservatori confondano il contesto quasi-parallelo come contorno-target (Esperimento 3). Nel quarto esperimento, infine, quantifichiamo l'incertezza locale (circa l'orientamento degli elementi che costituiscono i nostri contorni) e mostriamo come ciò contribuisca a – ma non possa spiegare completamente – gli effetti del contesto sulla localizzazione globale di contorni.

Ad una visione d'insieme, i risultati del primo studio indicano che l'effetto del contesto generalizza alla semplice localizzazione di contorni (senza identificazione di forma). Inoltre i risultati mostrano che gli effetti del contesto sono consistenti indipendentemente dal tipo si soglia stimata. Infine, tale primo studio mostra come l'incertezza di orientamento locale introdotta dal crowding visivo contribuisca a – ma non possa spiegare completamente – tali effetti contestuali sulla localizzazione di contorni globali.

Al fine di analizzare cos'altro possa contribuire agli effetti del contesto sulla localizzazione di contorni, nel secondo studio esaminiamo il ruolo di meccanismi globali ed in particolare di interazioni tra strutture globali. Nello specifico, nell'Esperimento 5 manipoliamo il contesto su una scala più ampia, in modo da ottenere stimoli che possano promuovere l'emergere di strutture globali attorno al contorno-target. Come negli esperimenti precedenti, chiediamo ai partecipanti di localizzare il contorno-target.

I risultati (Esperimento 5) confermano il pattern di effetti contestuali per la localizzazione di contorni-snake, cioè interferenza da contesti paralleli e facilitazione da contesti perpendicolari. Infatti, l'accuratezza nella localizzazione di contorni-snake è maggiore con contesti perpendicolari e minore con contesti paralleli (entrambi gli effetti rispetto alla condizione con elementi contestuali orientati in modo casuale). Rispetto al primo studio, emerge un risultato interessante per i contorni-ladder: mentre la localizzazione di ladders è ancora migliore con contesti paralleli piuttosto che casuali (come mostrato nel primo studio), ora non riportiamo più alcun effetto da contesti perpendicolari. Si noti che ciò non può essere attribuito alla differenza negli stimoli utilizzati nel secondo studio rispetto al primo (piccoli contorni "ad arco" vs- contorni "standard"). Infatti, l'Esperimento 6 indica che gli effetti del contesto sulla localizzazione di contorni sono indipendenti dallo stimolo utilizzato. Infine, i risultati dell'Esperimento 7 mostrano che gli opposti effetti del contesto parallelo sulla localizzazione di snakes e ladders (cioè peggiore localizzazione di snakes ma migliore performance con ladders rispetto alla condizione con contesto casuale) non riflettono l'uso di differenti strategie per svolgere il compito.

Complessivamente, i risultati del secondo studio indicano che anche meccanismi globali contribuiscono agli effetti contestuali sulla localizzazione di contorni. Ciò conferma l'ipotesi che il contesto influenzi l'integrazione di contorni sia ad un livello locale di processamento che ad uno globale. Inoltre, i nostri risultati indicano che gli effetti del contesto sono consistenti, indipendenti dallo stimolo utilizzato e generalizzano a diverse misure di performance (soglia di durata di esposizione, soglia di orientation-jitter, accuratezza).

Riassumendo, i due studi psicofisici indicano chiaramente che l'origine degli effetti del contesto sulla localizzazione di contorni è sia *locale* che *globale*. Nella discussione consideriamo come il nostro risultato di un robusto effetto del contesto sulla localizzazione di contorni possa essere utilizzato per confrontare e vincolare ulteriormente i diversi modelli computazionali di integrazione di contorni presenti in letteratura [Elder & Goldberg, 2002; Field, Hayes, & Hess, 1993; Geisler, Perry, Super, & Gallogly, 2001; May & Hess, 2007; Yen & Finkel, 1998]. In particolare, per rendere conto di tutti gli effetti del contesto riportati nei due studi, proponiamo un processo a due stadi, basato sulle connessioni locali ipotizzate nel modello di Yen e Finkel [1998]. In particolare, ipotizziamo un primo stadio in cui gli elementi locali sono integrati per mezzo di connessioni *co-axial* e *trans-axial* (cioè che si estendono rispettivamente in modo parallelo e perpendicolare all'orientamento locale degli elementi) ed un secondo stadio in cui strutture globali simili competono attivamente. Discutiamo poi come tale processo a due stadi posa rendere conto di tutti gli effetti contestuali che riportiamo sia per contorni-snake che per contorni-ladder.

Nel terzo studio studiamo integrazione e segmentazione di contorni nell'invecchiamento. Nello specifico analizziamo come l'età influenzi l'abilità di "escludere" informazione contestuale irrilevante al fine di integrare in modo efficiente elementi locali in contorni spazialmente estesi. La scelta di testare persone anziane è motivata dai risultati di recenti studi di neurofisiologia [Hua, Li, He, Zhou, Wang, & Leventhal, 2006; Schmolesky, Wang, Pu, & Leventhal, 2000], che riportano ridotte connessioni laterali intra-corticali inibitorie in neuroni senescenti della corteccia visiva primaria, verosimilmente conseguenti ad una ridotta inibizione GABA-mediata [Leventhal, Wang, Pu, Zhou, & Ma, 2003]. Se l'invecchiamento è caratterizzato da ridotta inibizione, anche l'abilità di escludere informazione irrilevante dovrebbe essere danneggiata. Inoltre, una ridotta inibizione potrebbe anche rendere conto di un maggiore effetto dello sfondo sull'integrazione di contorni (verosimilmente a causa di una ridotta inibizione dei *false matches* locali tra elementi del contorno e dello sfondo).

Per testare tali ipotesi, analizziamo come l'integrazione di contorni in soggetti giovani ed anziani sia influenzata dalla presenza di informazione di orientamento irrilevante lungo il contorno. Inoltre, studiamo anche l'effetto dello sfondo. In particolare, in un compito a scelta forzata tra due alternative (Esperimento 8), chiediamo ai partecipanti di indicare in quale intervallo lo stimolo presenti una deviazione dalla circolarità (DDC). Testiamo tre condizioni: *tangenziale*, in cui gli elementi del contorno sono allineati con il contorno stesso; *mista*, in cui gli elementi del contorno hanno orientamenti alternativamente tangenziali ed ortogonali (rispetto all'orientamento locale del contorno); *rumore*, in cui il contorno è circondato da uno sfondo di elementi con orientamenti casuali.

A differenza dei giovani, gli anziani mostrano soglie di DDC significativamente più alte (cioè prestazione peggiore) quando vi è perturbazione del co-allineamento lungo il contorno (condizione *mista*) rispetto alla condizione in cui tutti gli elementi sono allineati al contorno (condizione *tangenziale*). Un risultato interessante è che nella condizione *tangenziale* la prestazione degli anziani è paragonabile a quella dei giovani. Gli anziani sono fortemente danneggiati anche dalla presenza di elementi con orientamenti casuali nello sfondo, come mostrato dall'aumento del livello di DDC necessario per raggiungere il criterio di performance (75% di rilevazioni corrette) in presenza rispetto ad assenza dello sfondo.

Complessivamente, i risultati del terzo studio suggeriscono una ridotta capacità di escludere informazione non rilevante lungo un contorno nei soggetti anziani. Inoltre, i nostri risultati mostrano che l'invecchiamento riduce anche la capacità di inibire false matches locali, che possono emergere tra elementi del contorno e dello sfondo. Al contrario, l'abilità dei soggetti anziani di integrare elementi locali in strutture globali è preservata. Tali risultati sono coerenti con l'evidenza di una riduzione nelle connessioni intra-corticali laterali inibitorie nell'invecchiamento [Hua *et al.*, 2006; Schmolesky *et al.*, 2000]. Tale riduzione può potenzialmente spiegare il maggiore effetto dello sfondo che negli anziani. Essa inoltre potrebbe anche rendere conto della ridotta performance di uno specifico meccanismo che integra solo gli elementi il cui orientamento e la cui posizione sono coerenti con un contorno sottostante ed ignora quelli con orientamenti non allineati con il contorno. In particolare, proponiamo che i cambiamenti nella connettività intra-corticale introdotti sopra possano influenzare specificamente un circuito inibitorio/soppressorio e lasciare intatte le operazioni di integrazione.

Nel quarto studio studiamo integrazione di contorni, sensibilità al contesto e processamento di orientamento locale nella schizofrenia. I soggetti affetti da schizofrenia mostrano diversi deficits nel processamento visivo (per una revisione si veda Butler, Silverstein and Dakin [2008]), compresa una detezione di contorni marcatamente ridotta. Sebbene ciò sia stato largamente attribuito ad un deficit di raggruppamento (binding) o integrazione globale – cioè un'inabilità di combinare struttura locale distribuita nello spazio – in tale studio presentiamo evidenza che la ridotta detezione di contorni nella schizofrenia verosimilmente origina da deficitario processamento locale combinato con anormale processamento del contesto visivo.

Misuriamo in primo luogo la tolleranza dei pazienti alla perturbazione di orientamento lungo il contorno, presentato in diversi contesti (random, quasi-parallelo e quasi-perpendicolare rispetto al contorno). Riportiamo una prestazione deficitaria dei pazienti nel rilevare contorni circondati da contesto random (Esperimento 9). In tale condizione, infatti, i pazienti tollerano minore perturbazione di orientamento lungo il contorno rispetto ai controlli sani. È interessante notare che i pazienti sono proporzionalmente meno influenzati negativamente dalla presenza di contesti quasi-paralleli rispetto ai controlli (Esperimento 9). In linea di principio, tali risultati sono coerenti con precedenti evidenze di ridotta *surround suppression* nella schizofrenia [Barch, Carter, Dakin, Gold, Luck, Macdonald, Ragland, Silverstein, & Strauss, 2012; Dakin, Carlin, & Hemsley, 2005; Tadin, Kim, Doop, Gibson, Lappin, Blake, & Park, 2006; Uhlhaas, Phillips, Mitchell, & Silverstein, 2006a; Uhlhaas, Phillips, Schenkel, & Silverstein, 2006b; Yoon, Rokem, Silver, Minzenberg, Ursu, Ragland, & Carter, 2009]. Misuriamo poi l'abilità di soggetti con schizofrenia di discriminare l'orientamento dei componenti locali dei nostri contorni (Esperimento 10). I pazienti mostrano una prestazione deficitaria in tale compito, ma anche una ridotta influenza deleteria di elementi-distrattori (cioè sono meno inclini al crowding visivo).

Complessivamente, i risultati del quarto studio suggeriscono che l'anormale detezione di contorni nella schizofrenia verosimilmente origina da imprecisa discriminazione di orientamento locale e anormale processamento del contesto. Infatti i pazienti mostrano ridotta influenza del contesto nella localizzazione di contorni globali ed anche ridotta suscettibilità al crowding visivo. Nella discussione proponiamo che la ridotta sensibilità all'orientamento locale e al contesto nella schizofrenia possano risultare da un anormale *gain control* (cioè i processi inibitori intra-corticali che permettono ai neuroni di ottimizzare il loro limitato range di operatività), che è implicato sia nella generazione della selettività all'orientamento sia nella *surround suppression* [Crook & Eysel, 1992; Katzner, Busse, & Carandini, 2011; Okamoto, Naito, Sadakane, Osaki, & Sato, 2009; Sillito, 1975; Sillito, Kemp, Milson, & Berardi, 1980]. Infatti, la ridotta discriminazione di orientamento locale nella schizofrenia (Esperimento 10), ma anche il ridotto effetto deleterio di contesti quasi-paralleli sull'abilità dei pazienti di localizzare contorni (Esperimento 9) suggeriscono un deficit in un circuito che dal punto di vista computazionale è *inibitorio*. Considerando ciò, nella discussione analizziamo il ruolo dell'inibizione nell'integrazione di contorni (cruciale per esempio nel modello di Yen e Finkel [1998] ed anche nel processo a due stadi che proponiamo nel nostro secondo studio); inoltre valutiamo se alcune componenti inibitorie possano essere coinvolte anche nel crowding visivo.

Complessivamente, i risultati dei quattro studi mostrano come il contesto giochi un ruolo sostanziale nel processamento visivo di strutture complesse, con il coinvolgimento di meccanismi sia *locali* che *globali*. Oltre a fornire una migliore comprensione di come il nostro sistema visivo trasformi un insieme di inputs locali in percetti globali coerenti e come tale processo sia influenzato dal contesto, tale lavoro di tesi è rilevante anche dal punto di vista clinico. Infatti i nostri risultati, che mostrano come deficits specifici di determinate popolazioni cliniche in realtà riflettano anormale o deficitario processamento del contesto, sono potenzialmente rilevanti per impostare programmi di riabilitazione mirati.

ENGLISH ABSTRACT

Much research over the last decade has examined how the visual system links estimates of local image-structure into global, complex forms (e.g. spatially extended contours). Closely related to this issue is a second outstanding research-topic, namely the effect of context on visual processing. Here we bring together these two themes by addressing how contextual information influences the processing of contours (which requires the integration of local elements into a global structure). A particular importance is given to the source of these contextual effects, by investigating whether *local* or *global* mechanisms or both are involved. Given the adaptive relevance of this issue also from a clinical point of view, we investigate the topic also in ageing and in schizophrenia.

Specifically, in the first study we analyse how context affects contour-localisation and whether *local* mechanisms are sufficient to account for these effects. The starting point for this study is the work by Dakin and Baruch [2009] showing that near-perpendicular surrounding-elements reduce the exposure-duration required to localise and determine the shape of contours (compared to performance with randomly-oriented surrounds) while near-parallel surrounds increase this time. Differently form that study here we use a simple contour-localisation task, which does not require shape-identification. Specifically, we ask observers to detect the position of a contour (two-alternative forced choice – 2AFC – paradigm) embedded in different types of context: random, near-parallel or near-perpendicular relative to the contour-path. The target-contour can be either a *snake* (i.e. a contour whose local elements are aligned to the contour-path) or a *ladder* (i.e. a contour where constituent-elements are orthogonal to the contour-path). Specifically, in Experiment 1 we test how the immediate surround modulates *threshold exposure-duration* (i.e. the minimum stimulus-duration corresponding to 75% correct contour-localisation). We then test the generality of the effects of context (Experiment 2), by measuring *threshold orientation-jitter*, which represents a measure of tolerance to orientation-jitter along the contour-path. Additionally, in Experiment 3 we check for the possibility that observers mistake the near-parallel surround as target-contour. Finally, in Experiment 4 we test the relationship between contextual effects on *global* contour-

localisation and *local* uncertainty (about the orientation of each contour-element). In particular we test the hypothesis that the local orientation uncertainty introduced by visual *crowding* (i.e. the disruptive influence of "visual clutter" on object recognition) can account for the contextual effects on global contour-localisation.

Consistent with Dakin and Baruch's [2009] study, our results of Experiment 1 show a reduction and a substantial increase in snake-sensitivity in the presence of near-parallel and near-perpendicular surrounds, respectively. Ladder-sensitivity, instead, is increased in the presence of any organized surrounds (i.e. near-parallel or near-perpendicular). Experiment 2 indicates that context influences threshold orientation-jitter (which represents the tolerance to orientation-jitter) in the same way it affects threshold exposure-duration. In particular, observers tolerate less orientation-jitter along the contour when surrounding-elements are near-parallel compared to randomly oriented. Their tolerance increases when contextual-elements in the immediate surround are near-perpendicular compared to randomly oriented. These contextual effects are genuine and cannot be attributed to e.g. observers mistaking the near-parallel surround as target-contour (Experiment 3). In Experiment 4 we quantify observers' local uncertainty (about the orientation of the elements that comprised our contours) and show that this contributes to, but cannot completely explain, the effects of context on global contour-localisation.

Taken together, results of the first study indicate that the effect of context generalises to simple contour-localisation (without contour-shape identification). Additionally, our results show that the effects of context generalise across different threshold-based performance-measures. Finally, we report that while the local orientation uncertainty introduced by visual crowding may contribute to contextual influences on global contour processing it cannot, in isolation, entirely explain the effects of context on our contour-localisation task.

To test what else can account for the effects of context on contour-localisation, in a second study we directly examine the role of *global* mechanisms and in particular the role of interactions between global structures. Specifically, in Experiment 5 we extend

the manipulation of context (random, parallel, perpendicular) to a larger scale (not just in the immediate surround of the target-contour) to obtain stimuli that promote the emergence of global structures in the surround of the target-contour. Again observers are requested to localise the contour (2AFC paradigm).

Results (Experiment 5) confirm the pattern of contextual effects for snake-localisation, namely interference from parallel surrounds and facilitation from perpendicular surrounds. Indeed, accuracy in snake-localisation is higher with perpendicular surrounds and lower with parallel surrounds (both compared to the random surround condition). Compared to the first study, an interesting result emerges for ladder: whereas ladder-localisation is still better with parallel than random surrounds (as showed in the first study), now we do not report any difference in performance with perpendicular and random surrounds. Note that this cannot be attributed to the slightly different stimuli we used in the second compared to the first study (small "arc"-contour vs. "standard" contour). Indeed, Experiment 6 indicates that the effects of context on contour-localisation are stimulus-independent. Finally, results of Experiment 7 indicate that the different effects of parallel surrounds on snake- and ladder-localisation (i.e. worse snake-localisation but better ladder-localisation with parallel compared to random surrounds) are genuine and do not reflect the use of different strategies to perform the task.

Taken together, results of the second study indicate that also global mechanisms contribute to the contextual effects on contour-localisation, supporting the idea that context influences contour integration at both local and global stages of processing. Additionally, results also confirm that the effects of context are substantial and genuine, stimulus-independent and generalise across performance-measures (threshold exposure-duration, threshold orientation-jitter, accuracy).

To sum up, the two psychophysical studies clearly indicate that the source of the effects of context on contour-localisation is both *local* and *global*. In the general discussion we consider how our finding of a robust effect of context on contour-localisation might be used to compare and further constrain the several computational models of contour integration present in the literature [Elder & Goldberg, 2002; Field, Hayes, & Hess, 1993;

Geisler, Perry, Super, & Gallogly, 2001; May & Hess, 2007; Yen & Finkel, 1998]. In particular, to account for all the effects of context we report, we propose a two-stage process, which is based on the local connections postulated in the Yen & Finkel's [1998] model. Specifically, we hypothesise a first stage where local elements are linked through co-axial and trans-axial connections (i.e. running parallel and perpendicular to the local orientation of the elements, respectively) and a second stage where similar global structures actively compete. We then discuss how this two-stage process could account for all the contextual effects we report for both snakes and ladders.

In the third study we test contour integration and segmentation in ageing. Specifically, we investigate how ageing affects the ability to discard irrelevant contextual information in order to efficiently integrate local elements into spatially extended contours. The choice of testing older observers is motivated by the findings of recent neurophysiological studies [Hua, Li, He, Zhou, Wang, & Leventhal, 2006; Schmolesky, Wang, Pu, & Leventhal, 2000], which report reduced inhibitory intra-cortical lateral connections in senescent neurons of the primary visual cortex, possibly as a consequence of reduced GABA-mediated inhibition [Leventhal, Wang, Pu, Zhou, & Ma, 2003]. If aging is characterized by reduced inhibition, also the ability to discard irrelevant information should be impaired in older observers. Additionally, reduced inhibition may also account for an increased effect of background-noise on contour integration (possibly due to reduced inhibition of local *false matches* between contour- and background-elements).

To test these hypotheses we analyse how contour integration in younger and older observers is affected by the presence of irrelevant orientation information along the contour. Additionally we also investigate the effect of adding background-noise. Specifically, we use a 2AFC detection task (Experiment 8) and ask observers to indicate in which intervals there is a deviation from circularity (DFC). We test three conditions: *tangential*, where all contour-elements are aligned with the underlying circular contour-path; *mixed*, where contour-elements have alternating tangential and orthogonal orientations (relative to the contour-path); *noise*, in which background-noise surrounds the contour.

Differently from the younger observers, older participants show significantly higher DFC-thresholds (i.e. worse performance) when co-alignment along the path is perturbed (*mixed* condition) compared to the baseline condition where all contour-elements are tangential to the path. Interestingly, in the *tangential* condition older observers are as accurate as younger observers in detecting the DFC. Older observers are strongly affected also by the presence of background-noise, as revealed by the increase in the DFC-level necessary to attain the performance criterion (75% correct detection) in the presence compared to absence of background-distractors.

Taken together, results of the third study suggest that older observers are poor at discarding irrelevant orientation information along the contour. Additionally, our findings suggest that ageing also affects the ability to suppress local false matches, which may arise between contour- and background-elements. The ability of older observers to integrate local elements into a global structure is instead preserved. These results are consistent with reduced inhibitory intra-cortical lateral connections in ageing [Hua *et al.*, 2006; Schmolesky *et al.*, 2000], which can account for the increased effect of background-noise. Those same changes can account also for the reduced performance of a specific mechanism that integrates only elements whose orientations and position are consistent with the underlying path while discarding those with orientations non-co-aligned to the path. In particular, we speculate that those changes in intra-cortical connectivity could specifically affect an inhibitory/suppressive circuitry while leaving integrative operations unperturbed.

In the fourth study we investigate contour integration, sensitivity to context and local orientation processing in schizophrenia. People with schizophrenia exhibit deficits in visual processing (for a review see Butler, Silverstein and Dakin [2008]), including markedly poor detection of extended contours. Although this has been attributed to a deficit in binding or global integration – i.e. an inability to pool local structure across space – here we present evidence that it likely originates from poor local processing combined with abnormal processing of visual context.

We first measure schizophrenia patients' tolerance to orientation-jitter along the

contour-path in different surrounds (random, near-parallel and near-perpendicular). We report that patients are poor at detecting contours embedded in random noise (Experiment 9). Indeed, in the baseline condition (random surround) patients tolerate less orientation-jitter along the contour-path than healthy observers. Interestingly, patients are proportionally less disrupted by the presence of near-parallel surrounds than healthy observers (Experiment 9). Conceptually, these results are consistent with earlier reports of reduced surround suppression in schizophrenia [Barch, Carter, Dakin, Gold, Luck, Macdonald, Ragland, Silverstein, & Strauss, 2012; Dakin, Carlin, & Hemsley, 2005; Tadin, Kim, Doop, Gibson, Lappin, Blake, & Park, 2006; Uhlhaas, Phillips, Mitchell, & Silverstein, 2006a; Uhlhaas, Phillips, Schenkel, & Silverstein, 2006b; Yoon, Rokem, Silver, Minzenberg, Ursu, Ragland, & Carter, 2009]. We then measure schizophrenia people's ability to discriminate the orientation of the local components of our contours (Experiment 10) and show that patients are poor at this task but also less affected by the disruptive influence of distractor-elements (i.e. they are less prone to visual crowding).

Taken together, these results suggest that abnormal contour detection in schizophrenia likely originates from imprecise discrimination of local orientation combined with abnormal processing of visual context. Patients indeed, show a reduced disruptive influence of context on contour-localisation paired with a reduced susceptibility to crowding. We suggest that reduced sensitivity to local orientation and to orientation-context in schizophrenia could result from abnormal *gain control* (i.e. the inhibitory cortical processes that allow neurons to optimise their limited operating range), which is implicated both in the generation of orientation-tuning in visual cortex and in surround suppression [Crook & Eysel, 1992; Katzner, Busse, & Carandini, 2011; Okamoto, Naito, Sadakane, Osaki, & Sato, 2009; Sillito, 1975; Sillito, Kemp, Milson, & Berardi, 1980]. Indeed, the reduced local orientation discrimination in schizophrenia people (Experiment 10), but also the reduced effect of near-parallel surrounds on patients' ability to localise contours (Experiment 9) suggest a deficit in a circuitry that, from a computational point of view, is *inhibitory*. With that in mind, in the discussion we consider the role of inhibition in contour integration (which is crucial e.g. in the Yen & Finkel's [1998] model and also in the two-stage process we propose in Study 2) and also whether some inhibitory components may be involved in visual crowding.

Overall, the results of the four studies show that context plays a substantial role in the visual processing of complex structures with both *local* and *global* mechanisms involved. Besides providing a better understanding of how the visual system turns a patchwork of local inputs into coherent global percepts and how this process is influenced by context, this work is also clinically relevant. Indeed, our findings that deficits specifically shown by some clinical populations actually reflect abnormal or deficient processing of context are potentially relevant to set up focused rehabilitation programs.

PSYCHOPHYSICAL STUDIES

INTRODUCTION

FROM LOCAL TO GLOBAL

There is a long-standing interest in how the visual system links estimates of local image-structure into global, complex forms (e.g. spatially extended contours). An outstanding question, which much of the research in the last decade has focussed on, is how the visual system can link the elements of a contour – while avoiding linkage with background/irrelevant structure – to produce a salient contour that *pops-out* from the background. If we consider that contours contain much of the important information within complex natural visual scenes, we immediately understand why this linking process has always intrigued researchers. Indeed, the integration of individual contour-elements and the segregation of contours from the background represent two critical steps towards shape-identification and object-recognition, supporting much of our visually guided behaviour.

The interest in this local-to-global process dates back to the beginning of the last century, when early studies in the Gestalt psychology attempted to identify the rules, which govern such perceptual association or grouping [Koffka, 1935; Wertheimer, 1923]. These studies represent a pioneer work in this field, in that they anticipated the importance of some geometric relationships between elements for the local-to-global process. In particular, two Gestalt rules – the *law of good continuation* and the *law of proximity* – are relevant to describe how local elements are grouped into extended contours. Indeed, later studies that used more sophisticated and controlled psychophysical paradigms [Field *et al.*, 1993] confirmed the importance of contour continuity [Bex, Simmers, & Dakin, 2001; Field *et al.*, 1993; Hess, Ledgeway, & Dakin, 2000; Ledgeway, Hess, & Geisler, 2005] and inter-element distance [Kovacs & Julesz, 1993]. The research on *contour integration* – concerned with grouping or binding of local features into spatially elongated contours – has extensively contributed to further understand how our visual system solves this local-to-global problem.

Before analysing in details the studies on contour integration, it is important to spend a few words on how local image-structure is analysed by our visual system. Such local analysis represents indeed the first step towards perception and recognition of complex forms. At the early stages of visual processing (primary visual cortex, V1) the image is represented by a patchwork of neurons, each of which is primarily responsive to locally oriented image-structure falling within a limited area of visual space known as *classical receptive field* (CRF) [Hubel & Wiesel, 1962]. The CRF of a visual cell is traditionally defined as the region of space where stimuli evoke action-potential responses. The properties of the CRF define the stimulus attributes, which each cell is tuned to. In Figure 1 the circular windows cut out from the light blue oval illustrate the view of several V1 neurons. A range of studies has shown that different cells in V1 are tuned to different stimulus attributes such as orientation, direction of motion, disparity, size, contrast, and colour [De Valois, Albrecht, & Thorell, 1982; De Valois, Yund, & Hepler, 1982; Hubel & Wiesel, 1968, 1977; Livingstone & Hubel, 1988; Poggio, 1995; Schiller, Finlay, & Volman, 1976]. To express this property, V1 neurons have often been referred to as *feature detectors* or *local filters*.

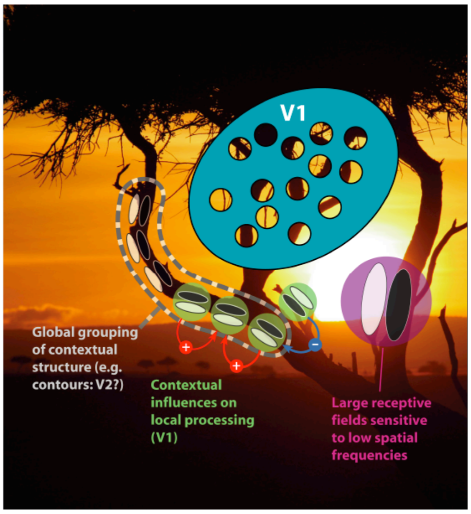

Figure 1. V1 neurons respond to locally oriented image-structure falling within a limited area of visual space known as *classical receptive field (CRF)*. The circular windows cut out from the light blue oval represent the

view of several V1 neurons. Among the stimulus features, which V1 neurons are selectively responsive to, is size, with small CRF (shaded in green) and large CRF (shaded in purple) conveying sensitivity to high and low spatial frequencies, respectively. Such neurons do not work in strict isolation, but contextual information can influence local processing (through facilitatory, "+", or inhibitory, "−" connections) as well as contributing to the grouping of local structure into more complex global structures (such as spatially extended contours, dotted grey shape). *Reproduced from Dakin and Frith [2005].*

In recent years, increased evidence has demonstrated that cells are not independent computational entities. Indeed, it has been extensively reported that surrounding structures outside a V1 neuron's CRF can massively influence its response (Figure 1). In particular, structure falling well outside a neuron's CRF can modulate the action-potential response evoked in that cell by an appropriate stimulus falling within its CRF. This is referred to as *contextual modulation*. [Allman, Miezin, & McGuinness, 1985; Gilbert & Wiesel, 1990; Kapadia, Ito, Gilbert, & Westheimer, 1995; Knierim & van Essen, 1992; Nelson & Frost, 1978; Nothdurft, Gallant, & Van Essen, 1999; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995; Zipser, Lamme, & Schiller, 1996]. An important feature of this phenomenon is that the modulating surrounding stimuli do not evoke a response in that cell when presented alone. This is because they are outside the CRF of that cell, in what is called the *non-classical receptive field (nCRF)*. Although 90% of neurons in V1 are inhibited by the activation of their neighbours [Jones, Grieve, Wang, & Sillito, 2001] – a phenomenon termed *surround inhibition*, which is thought to enhance salient visual structures – contextual modulations are not exclusively inhibitory but can also be facilitatory. For example, the response of a V1 neuron to a target-line falling in its CRF is suppressed when embedded in identical, iso-oriented lines [Knierim & van Essen, 1992], but is facilitated if the surrounding lines outside the CRF are orthogonal to the target [Knierim & van Essen, 1992; Nothdurft *et al.*, 1999]. Several studies suggest a fundamental role of the nCRF in figure-ground segmentation [Knierim & van Essen, 1992], extended contour representation [Fitzpatrick, 2000; Gilbert & Wiesel, 1990], corners [Sillito *et al.*, 1995] and local curvature coding [Krieger & Zetzsche, 1996; Wilson & Richards, 1992] and contrast gain control modulation [Heeger, 1992; Wilson & Humanski, 1993].

CONTOUR INTEGRATION

The path paradigm

In the first studies that specifically addressed the issue of contour segregation [Barlow & Reeves, 1979; Beck, Rosenfeld, & Ivry, 1989; Moulden, 1994; Smits, Vos, & van Oeffelen, 1985; Uttal, 1983] observers were required to detect straight contours composed of dots or short line-segments embedded in a field of similar elements with random position and orientation. The main criticism, which this approach is subject to, is that the stimuli used (wide spatial and orientation-spectra elements) did not necessarily require the integration of the outputs of different cells, but could be detected simply by a single, large receptive field cell (the simple filter model, [Hess & Dakin, 1997]).

To solve this problem, Field, Hayes and Hess [1993] developed what they called the "path paradigm". Unlike previous approaches, stimuli (see Figure 2 for an example) were made of Gabor patches (i.e. sinusoids multiplied by 2-D Gaussian profiles), which, mirroring the receptive field structure of cells in V1, rule out any single-cell explanation [Field *et al.*, 1993]. Another advantage of this approach is that it bases the measurement of contour integration on a more solid psychophysical procedure (e.g. criterion-free measures of contour detectability, density cue control). In contour integration studies using the "path paradigm", observers' psychophysical task is to detect the presence of a smoothly curved contour (path), composed of spatially separated oriented Gabor patches, embedded in an array of similar but randomly oriented background-elements.

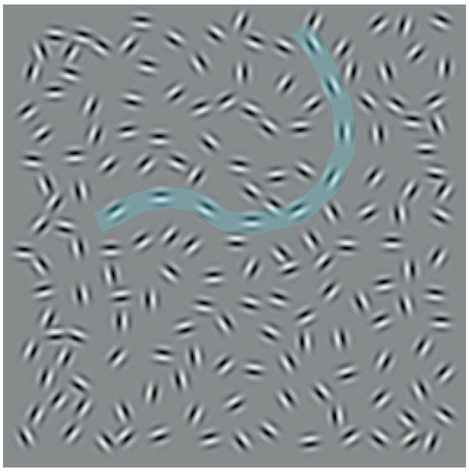

Figure 2. An example of the stimuli generally used in path paradigms. Observers are requested to detect a smoothly curved contour in a field of randomly oriented background-elements. In this example the contour-elements have orientation tangential to the underlying path. Here the contour is shaded for illustrative purposes.

Crucial parameters for contour integration

Several parameters (Figure 3) have been shown to play a critical role in this task including: contour curvature (or path angle, i.e. the change in orientation between adjacent elements), inter-element distance and the orientation of the Gabor elements with respect to the local orientation of the contour they form. Observers can reliably detect contours with path angles up to 60° [Field *et al.*, 1993] and inter-element distance up to 4-6 times the Gabor wavelength [Kovacs & Julesz, 1993]. Contour detection performance is best if elements match the local orientation of the contour ("snakes"), but relatively poor if elements are oriented perpendicular to the contour ("ladders") [Bex *et al.*, 2001; Field *et al.*, 1993; Hess *et al.*, 2000; Ledgeway *et al.*, 2005]. The poorest performance, however, is obtained with elements oriented at 45° relative to the contour [Ledgeway *et al.*, 2005]. The effect of contour-element rotation is critical since (statistically) contour patterns contain equal amounts of redundancy (i.e. they are essentially a spatially contiguous patch of near iso-oriented structure) irrespective of element-rotation. That observers find the location of ladder-contours so difficult supports the notion that this paradigm probes the processes underlying human contour detection. Also the density of elements plays an important role in contour integration, at least for moderately and highly curved contours [Li & Gilbert, 2002; Pennefather, Chandna, Kovacs, Polat, & Norcia, 1999]. Moreover, sensitivity to contours increases with exposure-duration [Roelfsema, Scholte, & Spekreijse, 1999], similarity in phase [Dakin & Hess, 1999; Hess & Dakin, 1999; Keeble & Hess, 1999] or spatial frequency of the contour-elements [Dakin & Hess, 1998, 1999]. Contours can also be integrated within and across depth with similar constraints on stimulus parameters [Hess & Field, 1995; Hess, Hayes, & Kingdom, 1997].

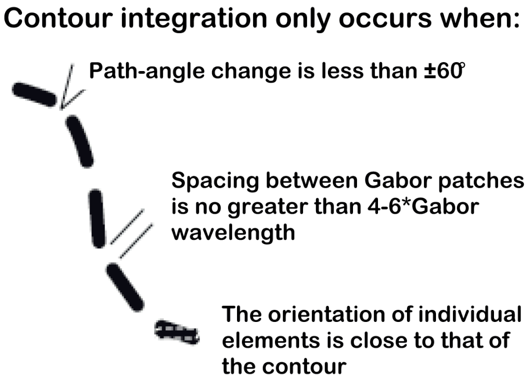

Figure 3. Summary of the necessary conditions for contour integration (adapted from Hess and Field [1999]). Other parameters that affect contour integration are: elements' density, exposure-duration, similarity in phase or spatial frequency of the contour-elements and number of elements that comprise the contour.

The association field model

Field *et al.* [1993] introduced the term "association field" to interpret their original findings and predict human performance on contour integration tasks. The model (Figure 4) defines the necessary geometric relationships required for linking adjacent local filters. Specifically, the responses of local filters to individual elements are combined only if conjoint constraints on position and orientation are satisfied. Facilitatory connections between filters occur only if they have locations and orientation mutually consistent with the presence of a contour. On the opposite, those filters with locations and orientations inconsistent with the presence of a path tend to inhibit each other. This implies that the amount of nearby aligned and correctly oriented contour-structure is crucial to determine the association output. Colinearity increases the strength of the association whereas an increase in distance, curvature or misalignment from co-circularity leads to weaker association. Note that the association field model does not make any predictions about the contribution of the orientation structure in the immediate surround (grey dotted lines in Figure 4).

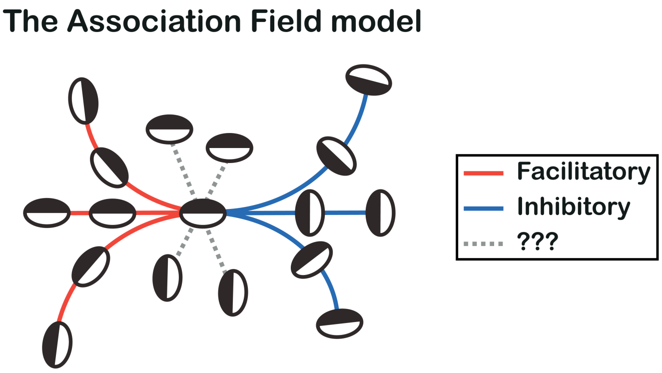

Figure 4. The association field model [Field *et al.*, 1993]. Facilitatory connections (red lines) between filters only occur if they have orientations and positions consistent with the presence of a contour. Filters with orientations and positions inconsistent with an underlying contour inhibit each other (blue lines). This model does not make any predictions about the contribution of oriented elements in the immediate surround (grey dotted lines).

To summarize, according to Field *et al.* [1993], the integration of individual elements into extended contours requires cooperative interactions between feature detectors distributed across space with different orientation preferences. Therefore, prime candidates for the neural substrate of the association field model are neurons of the primary visual cortex (V1). Indeed, several studies [Blakemore & Campbell, 1969; Campbell, Cooper, Robson, & Sachs, 1969; Hubel & Wiesel, 1959, 1962] have shown that these cells are primarily responsive and tuned to locally oriented image-structure falling within their classical receptive field (CRF). However, this is not enough. Indeed, the association field model postulates the presence of connections between filters that may result into combination of their outputs.

Long-range horizontal connections between cells in V1 [Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Gilbert & Wiesel, 1989; Hirsch & Gilbert, 1991; Kapadia, Westheimer, & Gilbert, 2000; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Stettler, Das, Bennett, & Gilbert, 2002; Ts'o, Gilbert, & Wiesel, 1986; Weliky, Kandler, Fitzpatrick, & Katz, 1995] represent a plausible neural substrate for this linking process. Three reasons make these connections good candidates. First of all, long-range horizontal connections allow neurons to exert influence well beyond their CRF. Second of all, consistent with the conjoint constraints on position and orientation [Field *et al.*, 1993], these connections are strongest between cells selective for like orientations, with spatially offset receptive fields [Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Malach, Amir, Harel, & Grinvald, 1993]. Finally, long-range horizontal connections extend further along the axis of the neuron’s preferred orientation [Bosking *et al.*, 1997]. This supports the suggestion by Field *et al.* [1993] that strong associations occur not only along the axis of the cell’s preferred orientation but also when neurons have positions and orientations mutually consistent with the presence of a contour.

Based on these characteristics, long-range connections seem to be a plausible neural mechanism for linking local elements into extended structures. However, recent findings of combined anatomical and physiological studies [Angelucci, Levitt, Walton, Hupe, Bullier, & Lund, 2002] have shown that the scale of horizontal connections in V1 is not sufficient to account for the spatial range of local-to-global integration as observed, e.g. in contour integration. Angelucci *et al.* [2002] concluded that extra-striate feedback circuits [Gilbert & Wiesel, 1989; Girard, Hupe, & Bullier, 2001] could be involved in the local-to-global integration of visual signals. In addition, several studies have demonstrated the involvement of higher visual areas – such as the lateral occipital complex (LOC), V2, V3a, VP, V4v [Altmann, Bulthoff, & Kourtzi, 2003; Kourtzi & Kanwisher, 2001; Schira, Fahle, Donner, Kraft, & Brandt, 2004] – in contour processing. Nevertheless, higher visual areas seem to respond to the contour per se, independently of how it is defined, that is independently of the simple image features [Kourtzi & Kanwisher, 2001].

The Yen and Finkel's [1998] model

Inspired by the approach of Field *et al.* [1993], Yen and Finkel [1998] developed a more detailed model of contour integration and perceived contour salience in complex images (Figure 6). In this model, a co-circularity constraint (Figure 5) is used to determine the pattern of connectivity between units, which are akin to oriented V1 cells. In other words, similarly to Field *et al.*'s [1993] model, the relative orientation and position of the two interconnected cells jointly determine the strength and sign of the neural interactions.

Yen and Finkel [1998] incorporated in their model three sets of long-range horizontal connections that modify the response of the basic processing units: (i) *co-axial*, (ii) *trans-axial* and (iii) *inhibitory* connections.

The facilitatory co-axial connections (i.e. running "parallel" to the local contour direction) are very similar to the connections hypothesized in the association field model [Field *et al.*, 1993], with linkages spreading out in circular arcs form the orientation axis of the cell. The association strength of these connections decreases rapidly as distance between cells, curvature or deviation of the local orientation from the relevant circular arc increases. In particular, regarding the last factor the Yen and Finkel's [1998] model proposes that the connection strength between two cells at locations A and B decreases as their orientations deviate from the tangents to the unique circle passing through both A and B (Figure 5).

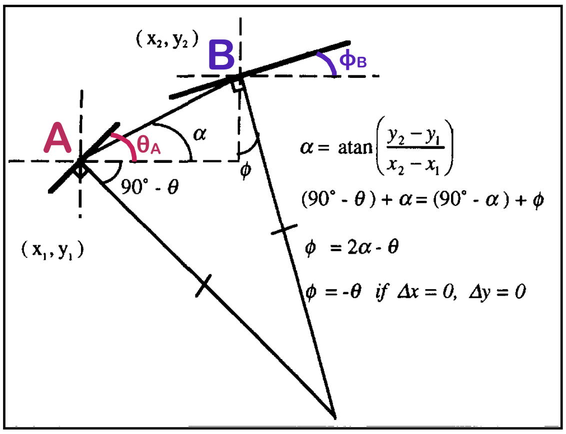

Figure 5. Computation of the "preferred" orientation based on the co-circularity constraint. According to the Yen and Finkel's [1998] model, a cell at location A and whose orientation is θ_A will be strongly facilitated if the cell at location B has an orientation equal to ϕ_B. Note that θ_A and ϕ_B are the tangents to the circle passing through A and B. *Adapted from Yen and Finkel [1998].*

The second set of facilitatory connections (trans-axial connections, i.e. running "perpendicular" to the local orientation of the units) allows interactions between cells with parallel receptive fields. Also for these connections the strength of interactions falls off rapidly with distance and deviation from "preferred" orientation. In this model, co-axial and trans-axial connections compete (Figure 6), so that only one set can be active in a given unit at a given time.

The third set of connections operates at a second stage of processing, after co-axial and trans-axial patterns of activity around a given point in space have been compared. These inhibitory connections switch off the responses of all those units whose facilitation from other active cells falls below a given threshold. This inhibitory activity helps distinguishing signal from noise based on the degree of facilitation. This is obtained by minimizing the response of the cells that are facilitated by accidental alignment of unrelated elements. In this way inhibition suppresses the response of "distractor" elements in the background (i.e. elements optimally oriented to be facilitated by elements on a contour) and prevent them from being attached to the "target" contour.

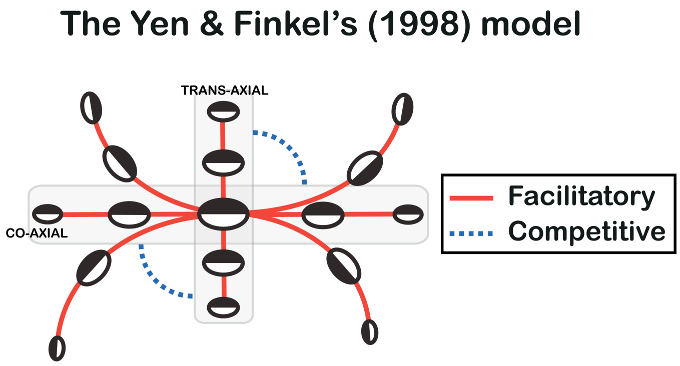

Figure 6. The Yen and Finkel's [1998] model. Both co-axial connections (i.e. between detectors consistent with snake-contours) and trans-axial connections (i.e. between detectors consistent with ladder-contours) are facilitatory. In a second stage these two configurations actively compete.

In this cortical-based model, contour integration reflects the level of synchronization of activity of units responding to interrelated contour-segments, which strongly depends on the balance of facilitatory and inhibitory inputs from contour- versus background-elements. In particular, the authors assume that cells that are strongly facilitated enter a "bursting" mode, which allows them to synchronize with other similarly bursting cell. Units that enter the bursting mode are modelled as homogeneous coupled neural oscillators with a common fundamental frequency but different phases. Only oscillators that have strong, reciprocal facilitated connections are coupled together; a set of coupled oscillators together represent a contour. The authors propose that contour integration depends on the synchronization of activity of units responding to interrelated contour-segments and the perceptual salience of a contour equals the sum of the activity of all synchronized units. This implies that long contours will become more salient than short contours (they activate more units).

To summarize, in the Yen and Finkel's [1998] model the most important factor in the estimation of the salience of a contour is temporal synchronization. Other crucial factors are the spatial structure of the anatomical connections and the balance of facilitatory and inhibitory inputs from contour- vs. background-elements.

In both Field *et al.*'s [1993] model and Yen and Finkel's [1998] model interactions between units depend conjointly on their position and orientation. Is this conjoint constraint really necessary to bind local elements into extended contours? Recently, Watt, Ledgeway and Dakin [2008] have tested and compared an implementation of the association field of Field *et al.* [1993] – which is selective for both where elements are with respect to each other and what form their combination makes (e.g. a part of a circle) – with two other families of models selective only for where elements are with respect to each other. All models exhibited similar performance to human observers, although they were qualitatively different from each other. This findings weaken the assumption of Field *et al.* [1993] that contour-elements have to fulfil the criteria of position and orientation in order to be linked together. However, it has to be noted that the principles of contour integration as expressed by the association field model are in line with the statistical properties of contours in natural scenes. Indeed, pairs of local orientation estimates are more likely to arise from the same contour if they are tangent to a common circle (i.e. if they are co-circular [Geisler *et al.*, 2001]).

EFFECT OF CONTEXT ON LOCAL AND GLOBAL IMAGE-STRUCTURE

Local image-structure and context

Some contexts increase an item's conspicuity more than others. For example, a red circle clearly stands out amongst blue lines, but it is more difficult to notice amongst red ovals. Outside the field of contour integration, several psychophysical studies have investigated how context affects our sensitivity to local image-structure. For example, Sagi [1990] showed that the detection of an oriented target in a field of identical elements depends on the distance from distracters to the target and also non-monotonically on distracter-density. Similarly, other studies have reported that the number of contextual-elements simultaneously presented with the target determines whether the target will pop-out from the background. Specifically, it has been shown [Bacon & Egeth, 1991; Bravo & Nakayama, 1992; Meinecke & Donk, 2002; Nothdurft, 2000; Sagi & Julesz, 1987; Schubö, Schroger, & Meinecke, 2004] that target search efficiency benefits from an increase in the number of contextual-elements (which likely reflects the use of a processing-mode based on the global aspects of the stimulus array, established e.g. by grouping processes). Another parameter, which determines whether context will affect local processing, is the similarity between target and contextual-elements. The more distinct target and contextual-elements are, the better the target will be detected [Wolfe & Horowitz, 2004]. Also the similarity among contextual-elements has been shown to affect local processing. In particular, several studies have reported better target detection (i.e. reduced reaction times) in homogeneous compared to heterogeneous displays [Campana & Casco, 2003; Casco, Campana, & Gidiuli, 2001; Meinecke & Donk, 2002; Schubö, Akyurek, Lin, & Vallines, 2011; Schubö, Wykowska, & Muller, 2007]. The homogeneity of the contextual-elements is likely to fast similarity grouping and to signal out the element that does not belong to the uniform structure [Schubö *et al.*, 2011].

Our sensitivity to local-image structure also strongly depends on whether target and contextual-elements are consistent with the presence of a contour. Polat and Sagi [1993, 1994], for example, showed that the detection of a Gabor-element is facilitated when it is flanked by two similar patches so that their overall configuration is consistent with the presence of a contour ("colinear facilitation"). Although this is a very interesting finding because it suggests the possibility of a close link between colinear facilitation and contour integration, any inference about a common mechanism should be made very carefully. Indeed, the two phenomena present some important perceptual differences. First of all, colinear facilitation is a threshold phenomenon, whereas contour integration operates at supra-threshold levels. Additionally, contour integration seems to be more robust to orientation and phase perturbation than colinear facilitation ([Field *et al.*, 1993; Hess & Dakin, 1997; Polat & Sagi, 1993], although see [Wehrhahn & Dresp, 1998; Yu & Levi, 1997; Zenger & Sagi, 1996]), which is instead more dependent on eccentricity [Hess, Dakin, & Field, 1998; Williams & Hess, 1998]. With this differences in mind, it is however interesting to consider the proposal that the building blocks for contour integration might be the same neural mechanisms that underlie colinear facilitation [Dresp, 1993; Kapadia *et al.*, 1995; Polat & Sagi, 1993, 1994].

Global-image structure and context

In terms of global processing (of groups of elements), several studies have investigated the impact of context (local contour-structure and/or surrounding contextual-elements) on contour integration. As anticipated in the previous section, contextual information provided by the local contour-structure exerts a crucial impact on contour integration. Indeed, contour-elements orientation drastically affects our ability to detect contours. Several studies [Bex *et al.*, 2001; Field *et al.*, 1993; Hess *et al.*, 2000; Ledgeway *et al.*, 2005] have shown that contour detection performance is poor if contour-elements are perpendicular to the local orientation of the contour (ladders). Rotating contour-elements by 90° – so that they match the local orientation of the contour (snakes) – considerably improves detection. The poorest detection performance, however, is obtained when contour-elements are oriented at 45° relative to the contour [Ledgeway *et al.*, 2005].

More recently, some authors have investigated the impact of contextual information – other than local contour-structure – on contour processing. In particular, three studies [Dakin & Baruch, 2009; Kingdom & Prins, 2009; Schumacher, Quinn, & Olman, 2011] have investigated the effect of surround-orientation (relative to the contour-path) and reported a suppressive effect and a substantial facilitation in the presence of parallel and perpendicular surrounds, respectively.

Kingdom and Prins [2009] investigated the effect of texture-surround on contour-shape coding. To this end they measured the "shape-frequency after-effect (SFAE)" using three types of adaptor: "contour-only" (no surround-texture flanking the adapting contour), "parallel-surround" (central adapting contour flanked by an array of similar contours), "orthogonal-surround" (Gabors in the flanking contours rotated by 90°). The strength of adaptation in the parallel-surround condition was halved compared to the contour-only condition. However, rotating elements in the flanking contours by 90° mostly restored the after-effect. The authors explained these results by suggesting that contour-shape mechanisms are inhibited by nearby parallel but not orthogonal texture orientations. They also suggested that the processing of contour-shapes involves those neurons in the visual cortex that are inhibited by similar orientations outside their classical receptive fields.

Dakin and Baruch [2009] looked at the interaction of contextual effects between contour and background, and within the contour itself by examining how contour integration is influenced by the orientation structure of the context immediately surrounding the contour. They used "S"-shaped contours (Figure 7) and measured observers' ability to perform a combined contour-localisation and shape-identification task. Specifically, observers were presented a test stimulus (see an example in Figure 7a) – for a variable exposure-duration – containing a single contour (either snake or ladder) embedded in background-noise. This display was immediately followed by a second screen (Figure 7b) where two isolated (i.e. not embedded in background-noise) contours were presented. The observers' task was then to indicate which of the two contours matched the shape of the contour they had seen in the previous display. Note that this task has two components, namely *contour-localisation* – which in turns requires the integration of local isolated elements into spatially extended structures – and *contour-shape identification.* In particular, to perform the task it is necessary to first localise the contour amongst background-elements in the first display and then compare each contour in the second screen with the pattern localised in the first display.

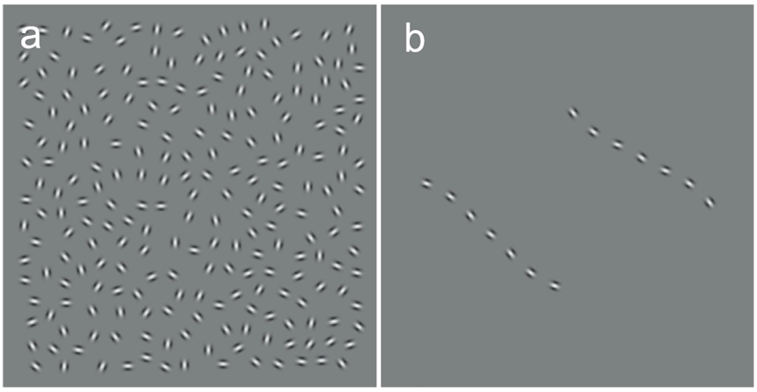

Figure 7. In Dakin and Baruch's [2009] study observers were first presented a test-stimulus (a) containing a single contour (either snake or ladder) embedded in background-noise. In a second screen (b) two isolated contours (i.e. non-embedded) were shown and observers were required to identify the contour they had just seen in the previous display. Note that this task involves both *contour-localisation* and *contour-shape identification*. *Reproduced from Dakin and Baruch [2009].*

To test the effect of the immediate surround on their combined contour-localisation and shape-identification task, the authors manipulated the relative orientation of background distracter-elements compared to their nearest contour-element (weighted by contour-distracter distance) to generate surround conditions ranging from near-parallel to near-perpendicular (see examples of near-parallel and near-perpendicular surround conditions with a snake-contour in Figure 8).

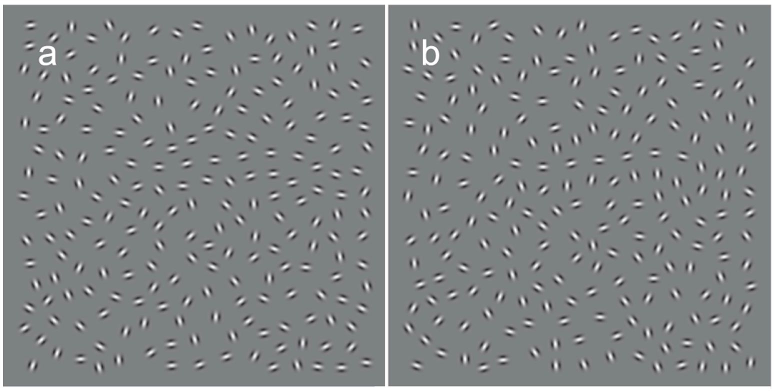

Figure 8. Two examples of the stimuli used by Dakin and Baruch [2009]: (a) a snake-contour embedded in near-parallel surround; (b) a snake-contour surrounded by elements near-perpendicular to the contour-path. Note that the contour is easier to spot in (b) than in (a). *Reproduced from Dakin and Baruch [2009].*

The authors showed robust psychophysical effects that were consistent with facilitation and suppression of contour-structure in the presence of near-perpendicular and near-parallel surrounds, respectively. Specifically, they reported that near-perpendicular surrounding-elements reduced the exposure-duration observers required to localise the snake-contour and identify its shape, while near-parallel surrounds increased this time (both compared to performance with randomly oriented surrounds). This pattern of results is expressed as sensitivity modulation in Figure 9: as can be seen, snake-sensitivity (white circles) is lower with near-parallel (0° surround orientation offset) than random surrounds and higher with near-perpendicular (90° surround orientation offset) compared to random surrounds. Performance with ladder-contours (grey squares) is instead better with any organized compared to random surrounds (Figure 9). More recently, the same pattern of results has also been shown for the detection of straight vertical contours [Schumacher *et al.*, 2011], with parallel surrounding-elements reducing performance and perpendicular surrounds increasing contour detection (both compared to the random surround condition).

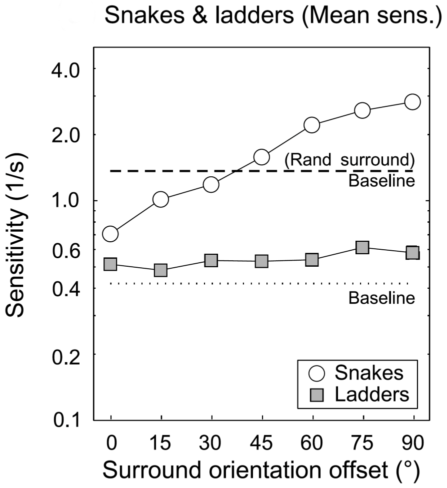

Figure 9. Results obtained by Dakin and Baruch [2009] in their combined contour-localisation and shape-identification task. Sensitivity for snakes (with circles) is higher with near-perpendicular (90° surround orientation offset) than random surrounds, and lower with near-parallel (0° surround orientation offset) compared to random surrounds. Sensitivity for ladders (grey squares), instead, is higher with any organized surrounds (compared to the baseline, i.e. random surround). *Reproduced from Dakin and Baruch [2009].*

Dakin and Baruch [2009] proposed that a two-stage filtering model of contour integration (incorporating an orientation-opponent stage after a first-stage filtering) could account for such effects of context. However, given that their task had two components (contour-localisation and contour-shape identification) it is possible that the effects of context they showed are actually more related to one component than the other. Moreover, as a consequence of the display size used in this study many of the contours would have been presented quite distant from the fovea (mean eccentricity ~3.5 deg.) and it is possible that this contributed to the effects. Indeed, Hess and Dakin [1997, 1999] showed that contour integration in the peripheral visual field is limited in a manner that suggests it could be relying on the output of large receptive fields. Recently, May and Hess [2007] reported a selective loss of sensitivity for "ladders" in the periphery, and suggested that this result arises from a phenomenon known as *visual crowding*.

CROWDING AND CONTOUR INTEGRATION

Visual crowding: a definition and the parameter that determine its strength

Visual crowding refers to the disruptive effect of "clutter" (task-irrelevant flanking features) on our ability to recognise (not detect) objects (for reviews see Levi [2008] and Whitney and Levi [2011]). Crowding is ubiquitous, impacts virtually all everyday tasks (Figure 10) and its effects are particularly evident when objects are presented in the peripheral visual field [Levi, 2008].

Figure 10. An example of visual crowding, a phenomenon that affects virtually all everyday tasks *(reproduced from Whitney and Levi [2011])*. When fixating the bull's eye in the centre of the image, it is relatively easy to recognise the boy on the right, but it is almost impossible to recognise the boy on the left, because of the presence of nearby construction signs.

Several principles determine the strength of crowding (Figure 11). First of all, target-flankers similarity (Figure 11a), with objects similar to the target crowding more than dissimilar ones. This has been shown for many low-level stimulus dimensions such as orientation, spatial frequency, contrast polarity, colour, direction and speed [Bex & Dakin, 2005; Chung, Levi, & Legge, 2001; Kooi, Toet, Tripathy, & Levi, 1994; van den Berg, Roerdink, & Cornelissen, 2007; Wilkinson *et al.*, 1997]. Another major determinant of crowding is the location of target and flankers, both in relation to one another and in the visual field. Crowding only occurs if target and flankers fall within the *interference zone* (shaded in grey in Figure 11b), a roughly elliptical zone, whose principal axis falls on a line extending from the zone centre to the fovea [Bouma, 1970; Toet & Levi, 1992]. Along this axis can be observed what has been called the "in-out" anisotropy [Bex, Dakin, & Simmers, 2003; Chastain, 1982; Petrov & Popple, 2007; Toet & Levi, 1992], whereby flankers that are nearer to fixation can get closer to the target without interfering than more eccentric flankers. The interference zone grows with target's eccentricity [Bouma, 1970; Toet & Levi, 1992] but is independent of target's size [Bouma, 1970; Pelli, 2008; Toet & Levi, 1992; Tripathy & Cavanagh, 2002]. The strength of crowding also depends on the configuration of target and flankers (Figure 11c), with weaker crowding when flankers group together (as in example #3 of Figure 11c), e.g. into contours that exclude the target [Livne & Sagi, 2007].

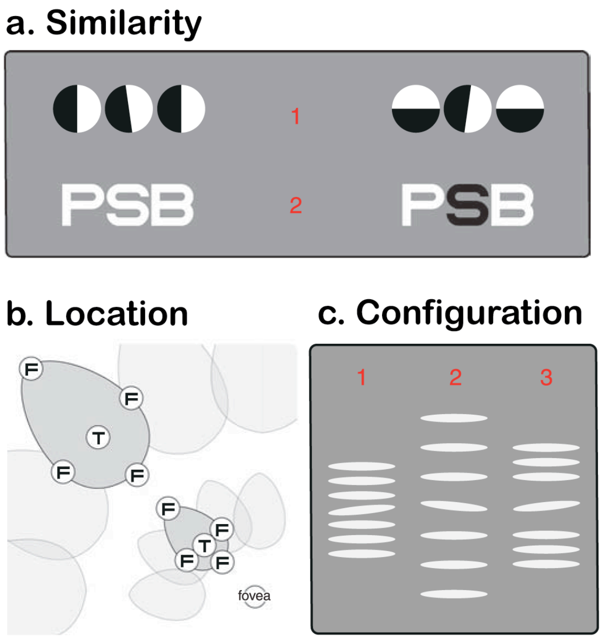

Figure 11. Determinants of crowding (adapted from Dakin *et al.* [2010]). (a) Similarity: the more flankers are similar to the target, the more they crowd. If one fixates the red numbers in turn, it is more difficult to recognize the central element of the triplets in the left configurations than in the right ones. (b) Location: crowding occurs only if target (T) and flakers (F) fall within the "interference zone" (shaded in grey). (c) Configuration: crowding is weaker if flankers group together excluding the target. Note how fixating at "1"

the identity of the central element is lost. Increasing elements' separation helps a little (fixate "2"). When flankers group together (as in the rightmost example), the identity of the central element is clear.

Crowding as spatial averaging

Current accounts of crowding involve some form of averaging of the attributes (e.g. orientation [Parkes, Lund, Angelucci, Solomon, & Morgan, 2001] or position [Dakin *et al.*, 2010; Greenwood, Bex, & Dakin, 2009]) of features falling within the flanking and target regions. In the paradigm of Parkes *et al.* [2001], for example, observers' ability to judge the orientation of a near-vertical Gabor element presented in the periphery is compromised when the target is crowded by vertical Gabor flanking-elements, but is actually improved when a small (sub-threshold) orientation cue is added to flankers. This is strong evidence that the orientation cue arising from flankers is incorporated into the crowded percept of the target through a process which is – or at least looks like - *averaging*. In terms of crowding of orientation, similarity between flankers and target influences the magnitude of crowding (more similar flankers crowd more, see Figure 11a), and the effect of similarly oriented flankers is to induce observers to make target reports that are consistent with the target-orientation having been averaged with the orientation of the flankers [Parkes *et al.*, 2001]. Note that, as pointed out by Freeman and Simoncelli [2011], there is a curious paradox in all of this: why would the visual system compute detailed local information only to discard it by spatially extensive averaging? Why would such a substantial amount of information be discarded? An alternative view could be that what is actually available is not a representation of the average but a crude representation of the stimulus (resembling an average).

Crowding as excessive/inappropriate feature integration

Crowding has also been linked to processes involved in object recognition [Levi, 2008; Pelli, Palomares, & Majaj, 2004; Pelli & Tillman, 2008]. Specifically, as pointed out in a recent review [Levi, 2008], there is a growing consensus that crowding arises during the second stage of a two-stage process of object recognition. According to this model, simple features are first detected – probably by V1 neurons (first stage) – and then integrated to form the perception of an object (second stage). In this framework, crowding would be the consequence of *excessive* feature integration – whereby detected features would be combined over an *inappropriately* large area, which includes the target as well as the flankers. In particular, crowding would take place when the features of target and flankers fall within the same "integration field" [Levi, 2008; Pelli *et al.*, 2004; Pelli & Tillman, 2008]. As stated by Levi [2008], this integration field, which operates over an increasingly larger area as one moves further into visual periphery, is akin to a second-stage receptive field that combines the simple features detected in a previous stage into an object. The consequence of this integration fields' size limitation is that in crowded displays the integration process would incorporate information also from flankers' signals. Note that, according to this explanation of crowding, the features of target and flankers would be detected independently and, when both fall within the same integration field, they would be merged into a percept that is often described as *jumbled* or *indistinct*. This jumbled percept looks like inappropriate combining rather than a failure to detect [Pelli & Tillman, 2008].

A variation of this explanation is that crowding is contour grouping "gone awry" [Dakin *et al.*, 2010; Livne & Sagi, 2007, 2010; May & Hess, 2007]. According to this proposal, which is based on the finding that crowding of orientation is more pronounced within contours [Livne & Sagi, 2007], a failure in feature binding would result in the experience of illusory conjunctions of physically disjunct features.

Crowding and contour integration: the same underlying mechanisms?

Several studies have reported crowding in tasks involving fine discrimination of contrast, spatial frequency and orientation [Andriessen & Bouma, 1976; Parkes *et al.*, 2001; Wilkinson *et al.*, 1997]. Little or no effect of crowding has been found for detection tasks

[Andriessen & Bouma, 1976; Parkes *et al.*, 2001; Wilkinson *et al.*, 1997]. However, May and Hess [2007] have suggested that the failure to detect peripheral ladders could be a form of crowding, caused by inappropriate feature integration by large integration fields in the periphery [Pelli *et al.*, 2004]. In particular, they showed that a "crowding-based" model could account for the poor detection of ladders in periphery. More recently, Chakravarthi and Pelli [2011] directly tested the proposal by May and Hess [2007] that the "association field" in contour integration and the "combining field" (i.e. the critical spacing area) in crowding might be one and the same. They asked observers to perform a contour integration task and a crowding task on the same stimulus and found that observers were equally sensitive to alignment (i.e. the Gestalt goodness of continuation) in both tasks. In particular, better alignment increased binding (grouping), which led to improved performance for contour integration but worse performance under crowding. The authors conclude that the same binding mechanisms underlie contour integration and crowding. This suggestion is consistent with a growing consensus [Dakin *et al.*, 2010; Livne & Sagi, 2007; May & Hess, 2007] that contour integration and crowding are related. Greenwood *et al.* [2010], for example, emphasized the remarkable similarity between the averaging processes that characterize crowding, and the processes of contour integration, which group local elements into spatially extended edges [Field *et al.*, 1993]. This work fits with a proposal from Livne and Sagi [2007] that contour integration can explain configural effects – created by the global arrangement of flankers – on crowding.

STUDY 1: CONTEXT INFLUENCES CONTOUR-LOCALISATION – A *LOCAL* EFFECT?[*]

In the first study we sought to analyse how contextual information affects global contour-localisation. Specifically, using different threshold-based performance measures (threshold exposure-duration, threshold orientation-jitter) we tested how contour-localisation – which involves the integration of local elements into an extended global structure – is affected by the manipulation of the immediate context surrounding the path. In particular we sought to clarify and extend several aspects of the earlier Dakin and Baruch's [2009] study.

First of all, we wished to determine whether context affects simple contour-localisation without shape-identification (which instead was necessary to perform the task used by Dakin and Baruch [2009]; for more details about their task see the Introduction). This is important in order to better understand the level at which contextual effects exert their influence. In particular we wished to determine if the effects reported by Dakin and Baruch [2009] were an inevitable consequence of that study having had observers make an explicit contour-shape identification. To this end we used a 2AFC localisation task where observers had to indicate which side of an image contained a contour (either snake or ladder). We note that, since our task requires only contour-localisation (without shape-identification) it is also less cognitively demanding [Pennefather *et al.*, 1999] and thus can be useful to test contour integration in clinical population. We essentially used a "standard" contour integration task where the global shape of the contour (which was not known in advance and changed from trial to trial) was not informative in itself. Note that we are not saying that this is a *pure* localisation task. Indeed contour integration clearly requires at least a partial representation of both location and shape. While we do not rule out any role for contour-shape processing, our underlying assumption is that

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[*] Based on **Robol, V.**, Casco, C., Dakin, S.C. (Under Review) The role of crowding in contextual influences on contour integration. *Journal of Vision*.

explicit shape-identification is not possible without some forms of shape-localisation.

The second aspect we investigated is the generality of the effect of context by measuring its influence on different threshold measurements (threshold exposure-duration in Experiment 1 and threshold orientation-jitter in Experiment 2).

It is important to have a threshold orientation-jitter measure to allow comparison of our results to the final experiment (Experiment 4) where we attempted to determine what role visual crowding of local contour-elements might play in our task. We did this by measuring orientation-discrimination of a single tilted target flanked by two similar elements (at eccentricity and element-spacing comparable to Experiments 1 and 2) to estimate orientation uncertainty of our contour-elements in different surrounds. We then compared contextual effects on threshold estimates from Experiment 2 and Experiment 4.

The core assumption of our approach is that contour integration involves an explicit progression from local to global structure. Specifically, in order to segment a contour made of individual elements from background-noise, the visual system must first extract local information and then integrate local inputs into coherent global structures, such as spatially extended contours [Field *et al.*, 1993]. In this framework, the effects of context at a local level (e.g. crowding of local elements) can influence downstream global processes in the cortical processing of visual form (such as global contour-localisation).

Experiment 1

Effect of context on the minimum exposure-duration required for contour-localisation

In Experiment 1 we wished to determine if the effects of context on a combined contour-localisation and shape-identification task (reported by Dakin and Baruch [2009]) extend to a simpler contour-localisation task. The motivation for the choice of a simple contour-localisation task was to provide a closer link to existing studies [Field *et al.*, 1993] and, at the same time, use a less cognitively demanding task [Pennefather *et al.*, 1999].

Methods

Observers

Six observers (VR, SCD, MST, EA, EI, ALF) – of which four naïve to the purposes of the study (MST, EA, EI, ALF) – participated in Experiment 1. All had normal or corrected-to-normal vision. Four of them (VR, SCD, MST, EA) were experienced psychophysical observers.

Apparatus

The experiment was run on an Apple MacBook computer under the Matlab programming environment (MathWorks, Natick, MA) and incorporated elements of the Psychophysics Toolbox extensions [Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997]. Stimuli were presented on a CRT monitor (LaCie [Paris, France] Electron Blue 22”).

The monitor was calibrated with a Minolta photometer and linearized in software, giving a mean and maximum luminance of 50 and 100 cd/m^2, respectively. The display resolution was 1024 x 768 pixels and the refresh rate was 75 Hz.

Stimuli

Test stimuli (Figure 12) consisted of *snake*- and *ladder*-contours composed of seven spatial-frequency band-pass Gabor micro-patterns, embedded in a field of distracter-Gabors [Field *et al.*, 1993]. In snake-contours Gabors were co-aligned with an underlying contour-spine, whereas in ladder-contours they were oriented at 90° relative to the contour-spine. The separation of contour-elements was 56 arcmin (i.e. 3.5λ) and the whole-stimuli subtended 12.8 deg. square containing on average 220 elements (σ = 3.9 elements). All elements were in cosine phase, had a peak spatial frequency of 3.75 c/deg with an envelope σ of 5.7 arcmin, and were presented at 95% contrast.

We adapted the methodology previously used by Dakin and Baruch [2009] to generate the contour. Rather than constraining contours to be "S"-shaped (required in Dakin and Baruch [2009] for the 2AFC shape-identification task) we used standard contours with a 15° path angle where the sign of the orientation difference between subsequent elements was randomised. To ensure elements were clearly located in either the left or the right half of the image we forced the middle/fourth element of our seven-elements paths to (a) pass through a region within ±0.53 deg. of the centre of a given image-half and (b) to have an orientation within ±45° of vertical. In addition contours were generated such that no one element of the contour passed within 0.9 deg. of the edge of the image and such that the contour did not cross itself.

We made our stimuli by first inserting two contours – one in the left and one in the right half of the image – and then dropping distracter-elements in the background maintaining a minimum inter-element separation of 40 arcmin (so matching the mean-distance of any element – within contour or background – to its nearest neighbour). Unlike standard contour detection paradigms – but like Dakin and Baruch [2009] – we manipulated the orientation of distracter-elements depending on their proximity to their nearest contour. Specifically, we had three surround conditions each with a different mean orientation of surrounding-elements relative to contour-elements: random, near-parallel, near-perpendicular (Figure 12). We refer to the random surround condition – where the orientation of distracter-elements was not modified depending on contour distance – as the "baseline" condition. The near-parallel and near-perpendicular conditions were generated as in Dakin and Baruch [2009], but in brief, we first computed the distance of all background-elements to their nearest contour-element. Then we used the inverse of the Gaussian function ($\sigma = 1.0$ deg.) of the distance between distracters and contour-elements to set the orientation of distracter-elements, offset by 0° (near-parallel) or 90° (near-perpendicular).

At this point in the stimulus generation procedure we have an image containing two contours (e.g. two snakes), on either side of fixation, where the distracter-elements surrounding each have been subject to the same contextual constraints (w.r.t. the contour on each side). We made our "random contour" by simply randomising the orientation of the elements of one of these contours. The observers' task was then to report the side of the image containing the structured contour (either snake or ladder). Figure 12a shows an example (with the contrast of surround reduced for the purpose of illustration). Stimulus presentation was immediately followed by a mask composed of a field of randomly oriented elements (with on average the same number and separation of Gabors as the test stimulus). This display persisted until observers had made a response (Figure 12b).

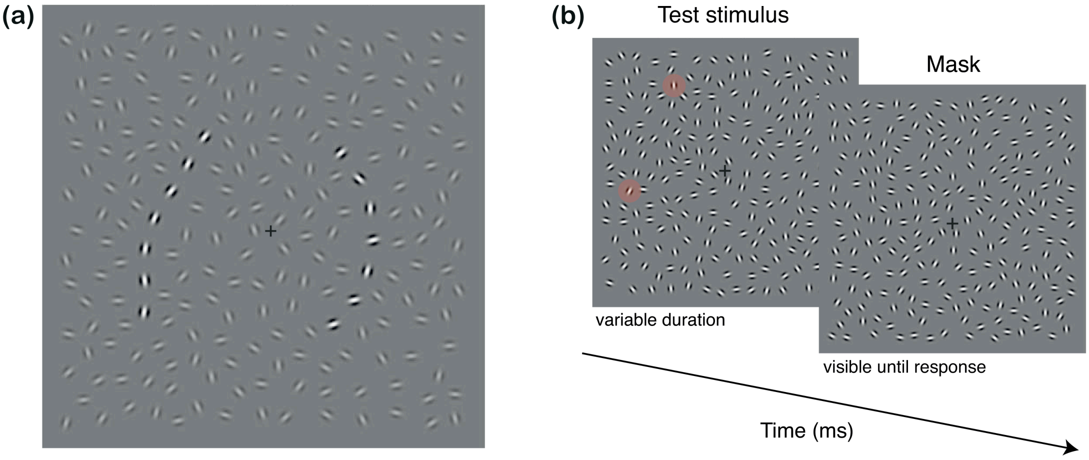

Figure 12. (a) An example of the stimuli from Experiment 1 (with the contrast of distracters reduced for illustrative purposes). Observers had to report which side of the image contained a structured contour (either snake or ladder). In this case the contour is surrounded by near-perpendicular elements, which generally enhance detectability. Note that the random-path on the right was generated in essentially the same way as the structured contour, except that the orientation of path-elements was randomised prior to presentation. Because of this the orientation of distracters surrounding the random-path is comparable to the context of the structured contour in that elements are near-perpendicular to the contour-spine used to generate the random-path. (b) A typical trial of Experiment 1: the test stimulus, which contained a structured contour either on the left or on the right (here the first and the last elements of the path are shaded to assist the reader in finding the contour) was immediately followed by a mask with randomly oriented elements. This display persisted until observers had made a response.

Design

We used a within-subjects design. The independent variable was the orientation offset of the contour's immediate context, defined as the mean orientation of the surrounding-elements relative to the contour-elements. We tested three levels of orientation offset: 0° (surrounding-elements near-parallel to the contour-elements), 90° (surrounding-elements near-perpendicular to the contour-elements), and random (surrounding-elements randomly oriented). The dependent variable was the minimum exposure-duration of the test stimulus that led to 75% correct contour-localisation (*threshold exposure-duration*, see *Procedure*). Note that this is a slightly lower performance criterion than used previously [Dakin & Baruch, 2009], which will lead to generally slightly lower thresholds.

Procedure

Stimuli were viewed binocularly at a distance of 129 cm from the display. Observers fixated a centrally presented marker during presentation of test and masking stimuli. We monitored eye position during the experiment; observers were able to maintain good fixation even at longer exposure-durations. Participants were presented a test stimulus (for a variable exposure-duration) containing a structured and a random contour embedded within distracter-elements and located right and left of the fixation marker. This screen was immediately followed by a mask, which contained randomly oriented Gabors and remained on the screen until observers made a response (using the computer keyboard) to the question "Which side of the stimulus contained the structured contour?". Visual feedback (the contrast-polarity of the fixation marker) indicated a correct or incorrect response. The exposure-duration of the test stimulus was controlled by an adaptive staircase procedure (QUEST [Watson & Pelli, 1983]) with correct and incorrect responses causing respectively reduction and increase in exposure-duration. The procedure converged on the exposure-duration that led to 75% correct contour-localisation. We refer to this measure as the *threshold exposure-duration*. Snakes and ladders were tested in separate runs, each of which comprised all three orientation offset levels of the elements surrounding the contour.

For each type of structured contour (snake and ladder) observers completed three runs of 135 trials each (45 trials per surround condition). Thus, for each observer, we obtained the mean threshold exposure-duration for each type of structured contour embedded in a particular kind of surround over 135 trials. Before data collection every observer completed a practice session of at least 135 trials for each type of contour (in separate runs). All observers started with a run of "snake" stimuli. Order of the other runs has been counterbalanced between observers.

Statistical analysis

To test the effect of contour-elements' orientation and the effect of the immediate surround, we carried out a two-way repeated-measures ANOVA – with factors *type of contour* (two levels: snakes vs. ladders) and *immediate surround* (three levels: random, near-parallel and near-perpendicular) – on the log-transformed threshold-values. Bonferroni correction has been used to adjust p-values for multiple comparisons. Alpha-value was set to 0.05 for all statistical tests.

Results and discussion

Figure 13a presents results (averaged across six observers) from various conditions tested in the first experiment. Graphed data are mean threshold exposure-durations (the minimum presentation time supporting 75% correct contour-localisation). Sensitivity-values (the inverse of mean thresholds) and normalized sensitivity (ratio of sensitivities for organized – i.e. near-parallel or near-perpendicular – versus random surrounds) across observers are plotted in Figures 13b and 13c, where also data from Dakin and Baruch [2009] are presented[†]. Note that for threshold exposure-duration, the smaller the number the less time observers need to attain the criterion level of performance (75% correct contour-localisation). The inverse is true for sensitivity (the smaller the number the lower the sensitivity to the contour).

The ANOVA on log-transformed threshold-values show a significant effect of the factors *type of contour* ($F_{1,5} = 308.3$, $p < 0.001$) and *immediate surround* ($F_{2,10} = 10.40$, $p = 0.004$) as well as a significant interaction ($F_{2,10} = 6.78$, $p = 0.014$). The significant effect of the factor *type of contour* indicates substantially poorer performance with ladders than snakes, consistent with previous findings [Bex *et al.*, 2001; Dakin & Baruch, 2009; Field *et al.*, 1993; Ledgeway *et al.*, 2005]. Specifically, in the baseline condition (random surrounds), ladder-threshold is about five times higher than snake-threshold (mean threshold (ms) ± SE = 1790 ± 366.32 vs. 354.78 ± 144.67). The significant effect of the factor *immediate surround* clearly indicates a substantial influence of context on contour-localisation. However, the

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[†] To better compare our data to Dakin and Baruch's [2009] results, sensitivity and normalized sensitivity have been calculated on the mean threshold-values across observers (as done in Dakin and Baruch [2009]).

significant *type of contour x immediate surround* interaction suggests a different effect of context on localisation of snakes and ladders. Specifically, as indicated by Figure 13a and *post-hoc* comparisons, there is substantial reduction ($t_5 = -3.82$, $p = 0.025$) and modest elevation ($t_5 = 3.11$, $p = 0.05$) in snake-threshold in the presence of near-perpendicular and near-parallel surrounds, respectively. For ladders, instead, there is a tendency for threshold to be lower in the presence of any of the two organized surrounds (near-parallel and near-perpendicular). These results indicate that observers need *less time* to correctly localise snakes in the presence of near-perpendicular compared to random surrounds. By contrast, they need *more time* for snake-localisation in the near-parallel surround condition than in the baseline condition (random surrounds). In contrast, ladder-localisation is facilitated by the presence of organized surrounds.

Figure 13c presents the ratio of sensitivities for organized (i.e. near-parallel or near-perpendicular) versus random surrounds with snakes and ladders (i.e. sensitivities for snakes and ladders in organized surrounds normalized to the corresponding performance with random backgrounds). The ratio of these two relative sensitivities (black symbols) compares the effect of surround on snakes and ladders and indicates that for snake-localisation (without shape-identification) there is an extra sensitivity gain in the presence of near-perpendicular surrounds (Snakes/Ladders ratio = 1.25) and an extra sensitivity loss with near-parallel surrounds (Snakes/Ladders ratio = 0.30).

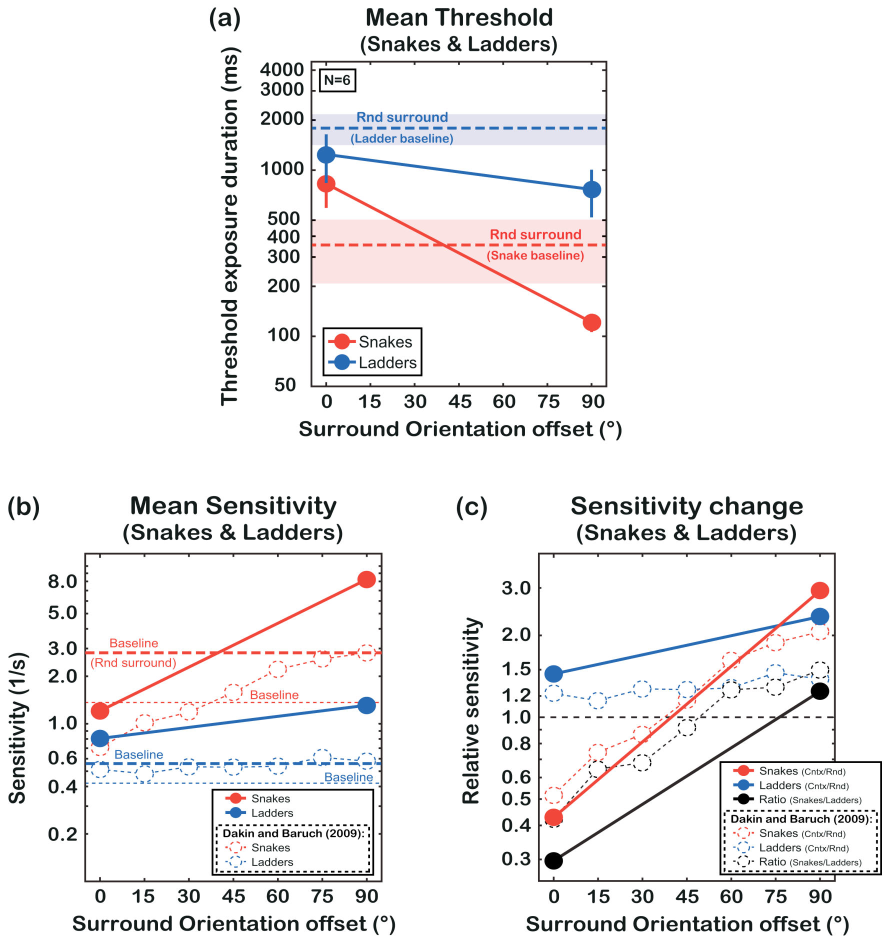

Figure 13. Results from Experiment 1 averaged across six observers. Red and blue symbols denote performance with snakes and ladders, respectively, measured with random surrounds (dashed lines), and as a function of surround orientation (filled circles). Little dashed symbols indicate data from Dakin and Baruch [2009]. Error bars represent standard errors. (a) Threshold exposure-duration (the minimum exposure-duration supporting 75% correct contour-localisation). Thresholds for snakes are reduced in the presence of near-perpendicular surrounds (90° orientation offset) and increased when the surround is near-parallel (0° orientation offset). Thresholds for ladders are decreased in presence of any of the two organized surrounds. (b) Sensitivity (the inverse of mean threshold). There is a reduction and elevation in snake-sensitivity with near-parallel and near-perpendicular surrounds, respectively. Ladder-sensitivity is increased in the presence of any of the two organized surrounds. (c) Ratio of sensitivities for organized (*Cntx*, i.e. near-parallel or near-perpendicular) versus random surrounds (*Rnd*) with snakes and ladders. The ratio of these two relative sensitivities (black symbols) compares the effect of surround on snakes and ladders and indicates that for snake-localisation there is an extra sensitivity gain with near-perpendicular surrounds and an extra sensitivity loss with near-parallel surrounds.

Taken together, these results suggest that the immediate context a contour arises in has a direct influence on simple contour-localisation (without shape-identification). These effects of context are broadly consistent with those found by Dakin and Baruch [2009] in their combined contour-localisation and shape-identification task (represented with little dashed symbols in Figures 13b and 13c). The authors found that snake-sensitivity was reduced of a factor of ~0.5 when the surround was near-parallel compared to random and increased of a factor of ~2 in the presence of near-perpendicular surrounds. For ladders, instead, they reported a relative sensitivity of ~1.2 with near-parallel surrounds and ~1.3 with near-perpendicular surrounds (Figure 13c). We also find that performance with snakes is consistent with facilitation in the presence of near-perpendicular surrounds (relative sensitivity equal to 2.92) and suppression in the presence of near-parallel surrounds (relative sensitivity equal to 0.43), and that performance with ladders reflects a facilitation in the presence of any surrounds (relative sensitivity equal to 1.44 and 2.35 with near-parallel and near-perpendicular surrounds, respectively). The comparison between our results and Dakin and Baruch's [2009] findings indicate a substantial and consistent effect of context on contour integration (if one accepts that integration is effectively probed by the localisation task, which was common to this and the earlier study).

Experiment 2 examines if the effect of context generalises to another threshold-based measure of performance (i.e. threshold orientation-jitter, which reflects the tolerance to orientation-jitter along the contour-path).

Experiment 2

Effect of context on tolerance to orientation-jitter in snake-localisation

Both Experiment 1 and the earlier study by Dakin and Baruch [2009] used threshold exposure-duration measure as a practical psychophysical procedure for measuring performance. Threshold-based paradigms have advantages over standard “path paradigms” that use per cent correct measure, which are limited in that e.g. they do not allow calculation of performance-ratios across conditions. In order to be able to quantify the contribution to contextual effects from the influence e.g. of crowding (Experiment 4) it would be desirable for our performance measure to be expressed in units not of time but of tolerable orientation uncertainty. Furthermore, a similar effect of context on other threshold measures would argue for generality of the findings from Experiment 1. Finally a fixed-exposure-duration paradigm has the potential to lead to faster threshold measurement that would be useful in the clinical field (reducing “test-stress” and the probability of eye movements).

Methods

Observers

The same six observers of Experiment 1 (VR, SCD, MST, EA, EI, ALF) served as participants in Experiment 2.

Apparatus

We used the same apparatus and display parameters as in Experiment 1.

Stimuli

In Experiment 2 we used only *snakes* as structured contours because in pilot trials we found that even modest levels of orientation-jitter reduced ladder-localisation to chance but with large inter-trial differences (rendering staircases unusable). Increasing the fixed exposure-duration helped but greatly extended test-time (precluding e.g. possible clinical translation). For this reason here we measure performance only for localisation of snakes. The parameters of the Gabors and the methodology to create contours and manipulate the immediate surround (random, near-parallel, near-perpendicular) of contours were the same as in Experiment 1. As before stimuli contained a structured contour and a random contour embedded within distracter-elements and located right and left of the fixation mark.

Prior to stimulus presentation we jittered the orientation of the elements within the structured contour. We did this by generating Gaussian random offsets with a standard deviation in the range 0-90° (note that this is the generating standard deviation – the true/wrapped standard deviation will be lower). A generating Gaussian standard deviation of 90° will produce a near-isotropic distribution of orientations. The level of orientation-jitter was under control of an adaptive staircase procedure (QUEST [Watson & Pelli, 1983]), as described in the *Procedure*. The orientation of distracter-elements was not modified further based on the new (noisy) contour orientation structure. Thus in the near-parallel condition, for example, the immediate surround was near-parallel to the contour-spine even if the orientation of each contour-element had been drastically altered. As in Experiment 1 the mask was composed of a field of randomly oriented elements (with on average the same number and separation of Gabors as the test stimulus).

Design

The experiment had a within-subjects design. The independent variable was the *surround orientation offset*: the mean orientation of the surrounding-elements relative to the contour-spine (three levels: random, near-parallel, near-perpendicular). The dependent variable was the maximum orientation-jitter along the contour-path supporting 75% correct contour-localisation (*threshold orientation-jitter*, see *Procedure*).

Procedure

The procedure was similar to Experiment 1, except for (a) the duration of the test stimulus, which was fixed (1000 ms), and (b) the variable controlled by the adaptive staircase procedure [Watson & Pelli, 1983], which was orientation variability along the contour-path (rather than exposure-duration, as before). We selected a relatively long fixed exposure-duration of 1000 ms because pilot experiments revealed that the minimum exposure-duration for all observers to perform snake-localisation at 75% correct with a high level of orientation-jitter (~15°) was around this value. Note that by using this duration our experiments can be more closely related to existing studies on contour integration [Field *et al.*, 1993], where this same duration has been used. We monitored eye position during the experiment; observers were able to maintain good fixation even if exposure-duration was relatively long.

Correct and incorrect responses led to an increase or a decrease in orientation-jitter, respectively. The procedure converged on the orientation-jitter that led to 75% correct contour-localisation. We refer to this measure as the *threshold orientation-jitter*. Each run comprised all three surround-orientation conditions (random, near-parallel, near-perpendicular). Observers completed at least three runs of 135 trials each (45 trials per surround condition). In this way, for each observer we obtained the mean threshold orientation-jitter in each surround condition over at least 135 trials.

Statistical analysis

To test the effect of the immediate surround, we carried out a one-way repeated-measures ANOVA – with factor *immediate surround* (three levels: random, near-parallel and near-perpendicular) – on the log-transformed threshold-values. P-values have been adjusted for multiple comparisons using the Bonferroni correction. Alpha-value was set to 0.05 for all statistical tests.

Results and discussion

Figure 14a presents results from Experiment 2 averaged across six observers. Graphed data are thresholds orientation-jitter, which are a measure of tolerance to orientation-jitter along the contour-path. Thus the smaller the number, the less orientation-jitter observers tolerate, and the poorer (more noise-sensitive) their performance. We first note that observers tolerate a higher degree of orientation-jitter along the contour in the presence of near-perpendicular than random surrounds (mean threshold ± SE = 22.58° ± 1.06° vs. 11.39° ± 0.67°). By contrast, they tolerate less orientation-jitter with near-parallel than random surrounds (mean threshold ± SE = 6.42° ± 0.88° vs. 11.39° ± 0.67°). The ANOVA on the log-transformed thresholds confirms that the factor *immediate surround* has a significant effect on snake-localisation ($F_{2,10} = 60.08$, $p < 0.001$). *Post-hoc* comparisons indicate lower tolerance to orientation-jitter in the presence of near-parallel than random surrounds ($t_5 = -5.39$, $p = 0.006$) and higher tolerance with near-perpendicular than random surrounds ($t_5 = 8.22$, $p < 0.001$).

Figure 14b compares results from Experiments 1 and 2. Graphed data are individual performance in near-parallel (white symbols) and near-perpendicular surrounds (grey symbols) relative to performance with random surround (i.e. divided by performance in the random surround condition). Specifically, we plot duration sensitivity (1/sec.) for Experiment 1 and threshold orientation-jitter for Experiment 2 since in both cases higher values mean better performance. Note that as ratios in Experiment 1 increase ratios in Experiment 2 also become larger ($r_4 = 0.89$, $p < 0.001$). This means that as duration sensitivity (1/sec.) to the contour increases – and thus observers need less time for localisation (lower threshold exposure-duration reflected in higher Cntx/Rnd ratios on the x-axis) – then the tolerance to orientation-jitter along the contour increases (i.e.

higher Cntx/Rnd ratios on the y-axis).

Taken together, the results of Experiments 1 and 2 indicate similar effects of context on threshold exposure-duration and threshold orientation-jitter for snake-localisation, arguing for the general finding that near-perpendicular surrounds promote contour-localisation while near-parallel surrounds also affect contour-localisation (and not just shape-identification).

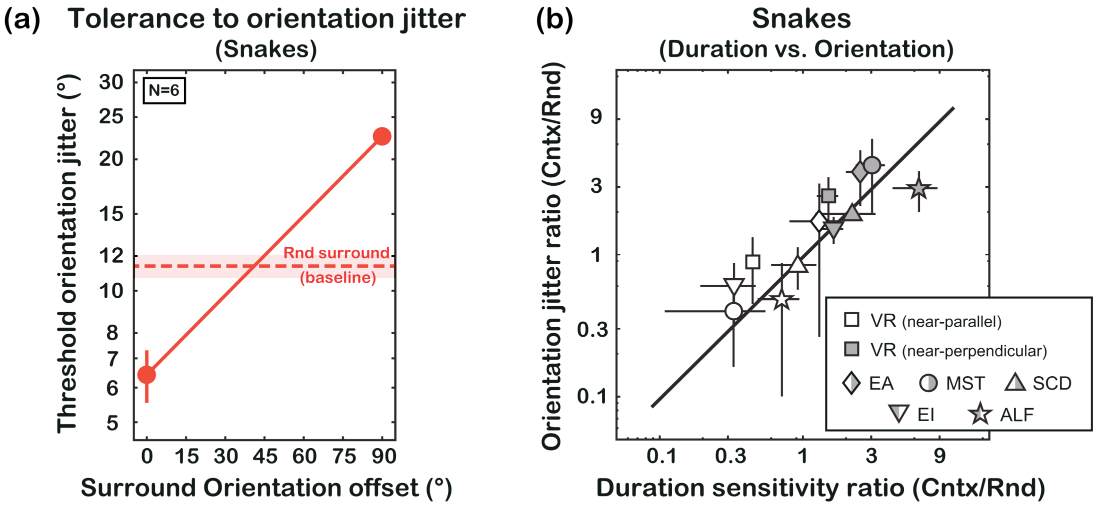

Figure 14. (a) Threshold orientation-jitter (the maximum orientation-jitter supporting 75% correct contour-localisation) from Experiment 2, averaged across six observers. Plotting conventions are as Figure 13; error bars represent standard errors. Note similarity to Figure 13b. Observers tolerate a higher degree of orientation-jitter along the contour-path with near-perpendicular than random surrounds. Near-parallel surrounds, instead, decrease tolerance compared to the baseline. (b) Comparison of results from Experiments 1 and 2. Graphed data are individual duration sensitivity ratios and threshold orientation-jitter ratios in near-parallel (white symbols) and near-perpendicular surrounds (grey symbols), representing performance with organized surrounds (Cntx, i.e. near-parallel or near-perpendicular) relative to random surrounds (Rnd). Error bars represent standard errors. The black line is the 1:1 line. Note that as duration sensitivity ratios increase also threshold orientation-jitter ratios increase.

Previously, several studies have demonstrated that contour detection decreases as a function of the increase in orientation-jitter of local contour-elements [Field *et al.*, 1993; Geisler *et al.*, 2001; Hess & Dakin, 1999; Hess & Field, 1995]. These studies, however, did not explicitly measure threshold orientation-jitter, but rather per cent correct contour detection (accuracy), which do not allow calculation of performance ratios across different conditions. Two recent studies [Kuai & Yu, 2006; Schumacher *et al.*, 2011] directly measured tolerance to orientation-jitter in contour detection tasks. Kuai and Yu [2006] measured threshold orientation-jitter with closed circular contours and showed that observers tolerated on average 12° of orientation-jitter, both at 4° and at 20° of eccentricity. More recently, Schumacher *et al.* [2011] used a threshold orientation-jitter measure to quantify the spatial scale of the orientation-dependent surround effects on contour detection. They also confirmed the contextual effect found by Dakin and Baruch [2009], however their observers tolerated a higher degree of orientation-jitter (~27° with randomly oriented distracters) than ours (~11° in the random surround condition). The higher detection performance they showed could be due to the fact that they used straight contours falling on fixed positions.

Experiment 3

The near-parallel effect: context mistaken as target-contour?

A plausible strategy that observers could have used in Experiment 2 is to first localise candidate snake-contours on each side of the pattern and then decide which is more "snake-like". This second operation could be very difficult when the target-snake is not smooth (as frequently occurs in Experiment 2, in which we varied the amount of orientation-jitter along the contour-path). Therefore, the lower tolerance to orientation-jitter with near-parallel surrounds (Experiment 2) might be, at least in part, a consequence of observers mistaking the context surrounding the random-path as target-snake. To rule out this possibility, we modified the stimuli of Experiment 2 such that Gabors on the opposite side of the target-snake were all randomly oriented. If observers really mistake the near-parallel surround along the random-path as target-contour, we predict no "near-parallel effect" with these modified stimuli.

Methods

Observers

One expert observer (VR) and three naïve observers (EI, ALF) participated in Experiment 3.

Apparatus

We used the same apparatus and display parameters as in Experiments 1 and 2.

Stimuli

We modified the stimuli of Experiment 2 by randomizing the orientation of the immediate context surrounding the random-path (the target-contour was still surrounded by organized context). By doing so, Gabors on the opposite side of the target-contour were all randomly oriented. We did so to avoid that observers mistake the near-parallel surround along the random-path as target-snake.

Design and procedure

The experimental design and the procedure were as in Experiment 2. Observers – who again were asked to localise the structured contour – completed at least two runs of 135 trials each (45 trials per surround condition).

Results and discussion

Results again indicate a halving in tolerance to orientation-jitter with near-parallel compared to random surrounds (mean threshold ± SE = 6.08° ± 1.25° vs. 12.41° ± 0.55°), as observed for the same three participants in Experiment 2 (mean threshold ± SE = 5.97° ± 0.63° vs. 11.95° ± 0.57°). These findings rule out the possibility that the near-parallel disadvantage we reported in the previous experiments could be due to observers mistaking the near-parallel surround along the random-path as target-contour.

Experiment 4

The role of crowding of local contour-elements in the effect of context on contour-localisation

In the course of these and earlier experiments (Dakin and Baruch [2009]) contours would frequently fall in the parafovea (typically 3-4 deg. eccentricity). At these eccentricities, and with the inter-element spacing used in our contour-stimuli we would expect that *visual crowding* would interfere with our localisation task (which involves the integration of local elements into an extended global structure). Since several groups have linked contour integration and crowding [Chakravarthi & Pelli, 2011; Dakin *et al.*, 2010; Livne & Sagi, 2007; May & Hess, 2007], we next sought to directly investigate the contribution of *crowding* of local contour-elements to the effect of context on global contour-localisation.

To this end we had first to estimate the observers' local uncertainty as to the orientation of the elements that comprise the contours. We did this by measuring orientation-discrimination (2AFC, clockwise vs. anticlockwise) with Gabors of similar size/spatial frequency, mutual-separation, and eccentricity as contour-elements in Experiments 1, 2 and 3. The target was either an isolated Gabor or a Gabor presented with two flankers (Figure 15). Flankers could be randomly oriented, near-parallel or near-perpendicular relative to vertical orientation.

Based on the local connections postulated by Yen and Finkel [1998] and on the proposal that crowding might be the consequence of excessive feature integration [Pelli *et al.*, 2004; Pelli & Tillman, 2008], we expect different levels of orientation uncertainty in the different conditions. In particular, we expect more crowding (i.e. higher orientation uncertainty) when flankers are near-parallel (compared to randomly oriented) because of a higher probability of integration through *trans-axial* local connections (i.e. running "perpendicular" to the local orientation of the elements [Yen & Finkel, 1998]). Conversely, we predict less crowding in the near-perpendicular (compared to random) flanker-pair condition, where the probability of integration would be close to zero. Additionally, if the effects of context on global contour-localisation we reported in the previous experiments are entirely based on the level of local integration (and thus the probability of *false matches*) between contour- and surrounding-elements, we expect that the modulation of crowding on local elements in the different flanker-pair conditions would fully account for the contextual effects on global contour-localisation.

Methods

Observers

The same observers of Experiments 1 and 2 (VR, SCD, MST, EA, EI, ALF) participated in Experiment 4.

Apparatus

We used the same apparatus and display parameters as in Experiments 1, 2 and 3.

Stimuli

In Experiment 4 we used Gabors with the same parameters as those used in the contour experiments above (cosine phase, peak spatial frequency = 3.75 c/deg, envelope $\sigma = 5.7$ arcmin, 95% contrast). The target for the orientation judgement (clockwise or anticlockwise of vertical) was either an isolated Gabor (*isolated-target condition*) or a Gabor presented with two flakers (see following paragraphs and Figure 15). In all conditions the target fell in the parafovea (upper side of the screen, 3.2 deg. eccentricity).

We repeatedly tested the same location in the visual field because we aimed at determining the role of *local orientation uncertainty* in the effects of context on contour-localisation, without additional uncertainty, e.g. arising from element-localisation. Additionally, we picked the upper visual field – where crowding is maximized – in order to make a liberal estimate of the contribution of crowding. Note that we did not include conditions that involved contour-like targets since within-contour flankers (inevitably) are cues to the identity of the target. Here we focus on conditions where flankers are non-informative in order to quantify local orientation uncertainty about individual elements *in the absence of global (multi-element) cues*.

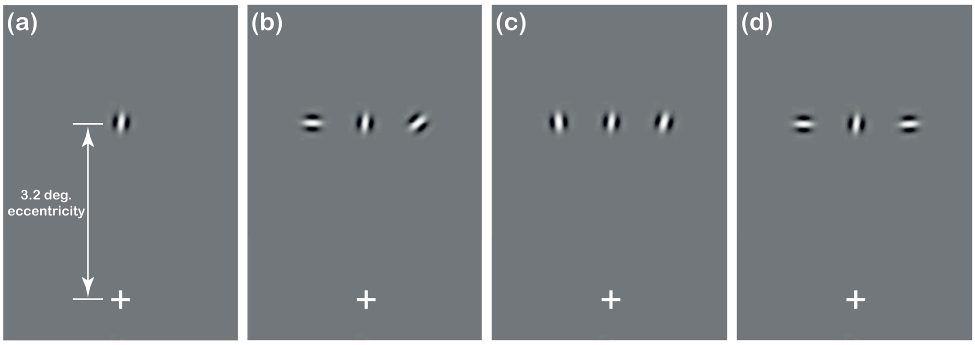

Figure 15. Examples of stimuli from Experiment 4; observers judged the orientation of the central Gabor (in these examples 6°-clockwise-tilted). The central Gabor was presented either in isolation (a) or with two flankers, whose orientation could be random (b), near-parallel (c) or near-perpendicular (d) relative to vertical. When flankers are near-parallel, the orientation-discrimination task becomes very difficult if one fixates the marker. This is typical of the near-parallel condition that induces very high levels of crowding compared to the isolated-target condition.

In the *flanker-pair conditions* target and flankers fell on the same horizontal axis and element separation was 40 arcmin (so matching the minimum inter-element separation used in the contour-localisation experiments). Flanker orientation could be random, near-parallel or near-perpendicular relative to vertical (the orientation around which target orientation-discriminations were made). We obtained near-parallel and near-perpendicular flankers by adding orientation noise (Gaussian-distributed, $\sigma = 22°$) to perfectly parallel and perpendicular flankers. The value $\sigma = 22°$ corresponds to the average standard deviation of the orientation difference between a given contour-element and its nearest surrounding background-element (computed using stimuli from the near-parallel condition of the contour-localisation experiments). This matched the orientation statistics of our crowding stimuli and contour-localisation stimuli (so that, for example, the orientation offset of a near-parallel flanker relative to vertical in Experiment 4 was on average the same as the orientation offset of the nearest near-parallel background-element relative to the contour-spine in Experiments 1, 2 and 3).

We manipulated the target tilt (clockwise or anticlockwise of vertical), pre-selecting seven tilts (-6°, -4°, -2°, 0°, +2°, +4°, +6° in the isolated-target condition; -9°, -6°, -3°, 0°, +3°, +6°, +9° in the random, near-parallel and near-perpendicular flanker-pair conditions) to fit psychometric functions. These values were selected based on pilot data that indicated they bracketed the psychometric function for the observers tested under these conditions of crowding. Note that the orientation of flanking-elements was not modified further based on the target tilt manipulation.

Design

We used a within-subjects design and tested four conditions: (i) isolated-target, (ii) target plus randomly-oriented flanker-pair, (iii) target plus near-parallel flanker-pair, (iv) target plus near-perpendicular flanker-pair. In each condition the independent variable was the degree of tilt of the target and had seven levels: -6°, -4°, -2°, 0°, +2°, +4°, +6° (in the isolated-target condition), -9°, -6°, -3°, 0°, +3°, +6°, +9° (in the random, near-parallel and near-perpendicular flanker-pair conditions). The dependent variable was the probability to report that the target was tilted clockwise of vertical.

Procedure

Stimuli were viewed monocularly (with observers' dominant/sighting eye) at a distance of 129 cm from the display. Observers fixated a centrally presented marker during presentation of the test stimulus, which appeared peripherally in the upper portion of the screen (3.2 deg. eccentricity) and lasted 100 ms. This relatively short duration was selected because ~100 ms is the shortest time at which we showed an effect of context on contour-localisation (see Figure 13a). We monitored eye position during the experiment; participants were able to maintain good fixation.

Observers indicated (using the computer keyboard) whether the target was tilted clockwise or anticlockwise of vertical. Visual feedback (the contrast-polarity of the fixation marker) indicated a correct or incorrect response. We used the method of constant stimuli to present different levels of target tilt. The four conditions (each testing seven target tilt-levels) were presented in the same run and observers completed at least two runs of 448 trials each (16 trials per tilt-level in each condition). Raw data were fit with cumulative Gaussian functions, to give an estimate of bias (the μ parameter) and threshold orientation-discrimination (the σ parameter).

Because threshold can be re-expressed as a response-variance (σ^2), we can exploit additivity of variance under convolution [Morgan & Ward, 1985; Watt & Hess, 1987] to compare different flanker-conditions [Barlow, 1956; Dakin, 2001; Pelli & Farell, 1999]. Specifically, we can calculate the amount of *extra* orientation uncertainty added by a particular configuration of flankers. For example, let us suppose that observers show a greater response-variance with randomly oriented flanker-pair (i.e., their orientation-discrimination is poorer) than when no flankers are present. This greater response-variance ($\sigma^2_{\text{rand\_obs}}$) can be re-expressed as observers' response-variance in the isolated-target condition ($\sigma^2_{\text{local\_obs}}$) plus some extra orientation variance arising from the presence of random flankers ($\sigma^2_{\text{rand\_int}}$):

$$\sigma^2_{\mathrm{rand\_obs}} = \sigma^2_{\mathrm{local\_obs}} + \sigma^2_{\mathrm{rand\_int}} \,.$$

From this equation we can quantify the effective amount of *extra* orientation uncertainty ($\sigma_{\text{rand\_int}}$) added by the presence of random flankers:

$$\sigma_{\text{rand\_int}} = \sqrt{\sigma^2_{\text{rand\_obs}} - \sigma^2_{\text{local\_obs}}}\,.$$

The *extra* orientation uncertainty $\sigma_{\text{rand\_int}}$ represents the standard deviation of the orientation-jitter that must be added to observers' internal (Gaussian-random) representation of the element orientation in order to equate performance with random flankers. A similar approach can be employed to examine the extra uncertainty introduced by near-parallel compared to random surrounds.

Statistical analysis

To test the effect of flankers, we carried out a one-way repeated-measures ANOVA – with factor *flanker-condition* (four levels: no-flankers, random flankers, near-parallel flankers and near-perpendicular flankers) – on the log-transformed threshold-values. The presence of a statistically significant bias was assessed with one-sample t-tests on the μ parameters of the best fitting psychometric functions. Paired-samples t-tests have been used to compare the results of Experiments 2 and 4. P-values have been adjusted for multiple comparisons using the Bonferroni correction. Alpha-value was set to 0.05 for all statistical tests.

Results and discussion

Figure 16b presents mean thresholds orientation-discrimination across six observers for each condition tested in Experiment 4. Thresholds are the standard deviation parameter (σ) of the best fitting psychometric functions. The one-way repeated-measures ANOVA on the log-transformed thresholds indicates a significant effect of the factor *flanker-condition* ($F_{3,15} = 45.49$, $p < 0.001$). *Post-hoc* comparisons show that the presence of randomly oriented flankers doubles threshold compared to the isolated-target condition ($t_5 = 10.70$, $p < 0.001$). Near-parallel and near-perpendicular pairs of flankers, instead, cause on average a 3X ($t_5 = 12.71$, $p < 0.001$) and a 1.5X ($t_5 = 3.82$, $p = 0.037$) threshold-elevation, respectively. On average, observers' orientation-judgements are unbiased in all conditions ($p > 0.05$), which means their reports are symmetrically distributed around the stimulus midpoint. These trends are reflected in Figure 16a, which plots example psychometric function from observer SCD in the four conditions tested.

The extra orientation uncertainty (calculated as described in the *Procedure*) added by the three flanker-pair conditions (compared to the isolated-target condition) is on average 4.43° (random), 6.49° (near-parallel) and 2.93° (near-perpendicular). Note that our finding that near-perpendicular flankers crowd less than random flankers is inconsistent with a model of crowding based strictly on orientation averaging (under which theory one would always predict that the larger the orientation difference between target and flanker the larger the amount of crowding). Instead it would be consistent with a lower probability of integration between target and flankers compared to the random flanker-pair condition. Indeed, *trans-axial* connections [Yen & Finkel, 1998] are more likely to occur in the random than in the near-perpendicular flanker-pair condition. Our results also indicate that the near-parallel condition adds *an additional* 4.74° of uncertainty compared to the random condition. This result is consistent with the proposal that crowding might reflect excessive feature integration [Pelli *et al.*, 2004; Pelli & Tillman, 2008], in our case through local *trans-axial* connections [Yen & Finkel, 1998]. Note that the fixed position of the stimulus (above the fixation cross) has no role in explaining lower thresholds with near-perpendicular than random and near-parallel flanker-pairs. Indeed, a control experiment (run on observer VR) with the stimulus randomly presented above or below fixation produced an identical pattern of results.

Figure 16c compares results from Experiments 2 and 4. Specifically, for both experiments we plotted Context/Random ratios (i.e. Parallel/Random and Perpendicular/Random). To calculate these ratios we used *thresholds orientation-discrimination* for the crowding experiment (Experiment 4) and *1/thresholds orientation-jitter* for the contour-localisation experiment (Experiment 2). In this way in both cases we have a measure of uncertainty: *local orientation uncertainty* for Experiment 4 and *global contour-localisation uncertainty* for Experiment 2. The data suggest that the *local* orientation uncertainty (on individual elements) introduced by crowding from different types of flankers (possibly through excessive feature integration) may contribute, at least in part, to the effects of context on global contour-localisation we showed in Experiment 2, even if it is insufficient, in isolation, to explain those effects. Indeed, for the near-parallel conditions the global contour-localisation uncertainty is higher than the local orientation uncertainty ($t_5 = 3.09$, $p = 0.027$). Similarly, for the near-perpendicular conditions the global contour-localisation uncertainty is lower than the local orientation uncertainty ($t_5 = -3.24$, $p = 0.023$).

Taken together, the results of Experiments 2 and 4 indicate that the modulation of crowding of local contour-elements contributes to (but cannot fully account for) both contextual effects on contour-localisation. Within a framework that assumes an explicit progression from local to global processing, this supports the idea that context influences contour-localisation at both local and global stages of processing and, more generally, is consistent with the notion that the local effects of crowding eventually influence downstream stages involved in the cortical processing of global visual form.

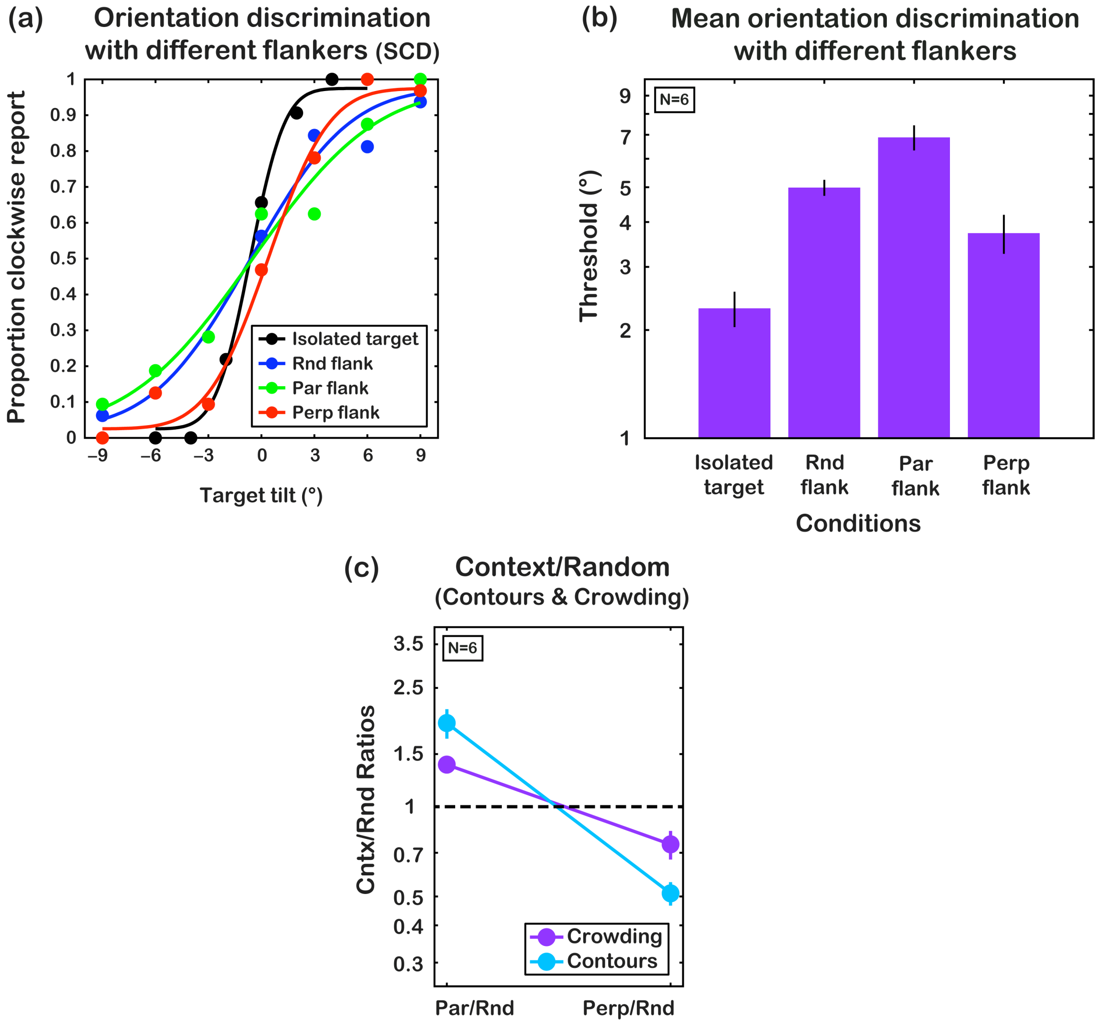

Figure 16. (a) Psychometric function from one observer (SCD) in each condition tested in Experiment 4 (black = isolated target; blue = random flankers; green = near-parallel flankers; red = near-perpendicular flankers). The graph presents the proportion of “clockwise” responses as a function of the target tilt. (b) Mean thresholds orientation-discrimination for each condition tested in Experiment 4. Error bars depict standard errors. The presence of any flanker-pair (random, near-parallel, near-perpendicular) greatly increased thresholds. (c) Comparison between Experiments 2 and 4: plotted data are Context/Random ratios (i.e. Parallel/Random and Perpendicular/Random), which represent a measure of *global contour-localisation uncertainty* (light blue lines and circles) and a measure of *local orientation uncertainty* (violet lines and circles). Note that the local orientation uncertainty introduced by crowding contributes to (but cannot fully account for) both contextual effects on global contour-localisation.

GENERAL DISCUSSION

We measured observers' ability to perform a contour-localisation task (that did not require detailed contour-shape identification). We report a reduction and substantial increase in snake-sensitivity in the presence of near-parallel and near-perpendicular surrounds, respectively, whereas ladder-sensitivity is increased in the presence of any of the two surrounds (Experiment 1). We also find that context has a similar effect on the exposure-duration required to localise the contour (Experiment 1) and on our tolerance to orientation-jitter (Experiment 2). Finally, while the local orientation uncertainty (on individual elements) introduced by crowding (Experiment 4) may contribute to contextual influences on contour processing it cannot, in isolation, entirely explain the effects of context on our contour-localisation task.

Disruption of contour processing by near-parallel surrounds

It is known that near-parallel surrounds disrupt shape processing in the absence of location-uncertainty as is evident by the reduction in contour-shape adaptation that one observes in the presence of near-parallel surrounds [Kingdom & Prins, 2009]. The authors suggested that the most likely underlying mechanism for the parallel effect is based on the operation of neurons in V1 – which show iso-orientation surround suppression – feeding their responses directly into shape-coding neurons in higher visual areas. Our data suggest that near-parallel surrounds affect contour-localisation. Indeed, performance on our contour-localisation task is vulnerable to a disruptive effect of near-parallel surrounds consistent with the measurements made by Dakin and Baruch [2009]. Additionally, we report similar effects of near-parallel surrounds on both threshold exposure-duration and on threshold orientation-jitter. It is interesting to speculate what might account for this effect in the two cases. Reducing exposure-duration may cause the observer to spatially under-sample the image (leading to a consistent reduction in performance across context-conditions). In isolation this however cannot account for the selective disruption of contour-localisation by near-parallel surrounds. We speculate that a high probability of incorrect linkages between contour- and surrounding-elements – possibly through *trans-axial* local connections [Yen & Finkel, 1998] – contributes to performance in the near-parallel condition. Increasing orientation-jitter may drive up the probability of incorrect linkages arising between contour-elements and surrounding-elements, which would selectively penalise the near-parallel condition (where candidate "false matches" are more likely to arise).

Modelling the effects of context on contour-localisation

Several computational models of contour integration have been proposed [Elder & Goldberg, 2002; Field *et al.*, 1993; Geisler *et al.*, 2001; May & Hess, 2007; Yen & Finkel, 1998] whose performance is consistent with human observers' ability to localise contours within noise [Field *et al.*, 1993]. We now briefly consider how our finding of a robust effect of context on contour-localisation might be used to compare and further constrain these models.

The "association field" model [Field *et al.*, 1993] defines the necessary geometric relationships required for linking adjacent local filters. According to Field *et al.* [1993], the responses of local filters to individual elements are combined only if conjoint constraints on position and orientation are satisfied. Facilitatory connections between filters occur only if they have locations and orientations mutually consistent with the presence of a contour. On the opposite, those filters with locations and orientations inconsistent with the presence of a path tend to inhibit each other. This implies that the amount of nearby aligned and correctly oriented contour-structure is crucial to determine the association output. Colinearity increases the strength of the association whereas an increase in distance, curvature or misalignment from co-circularity leads to weaker association. This model cannot account for ladder-localisation and does not directly take into account contextual effects on contour-localisation.

Inspired by this approach, Yen and Finkel [1998] developed a model of contour integration and perceived contour salience in complex images. In this model, a co-circularity constraint determines the pattern of connectivity between units (akin to oriented V1 receptive fields). Similarly to Field *et al.*'s (1993) model, the relative orientation and position of interconnected cells determine the strength and the sign of their interactions. Yen and Finkel [1998] use (i) *co-axial*, (ii) *trans-axial* and (iii) *inhibitory* long-range horizontal connections to modify the response of local units. The facilitatory co-axial connections (i.e. running "parallel" to the local contour direction) are very similar to the connections hypothesized in the association field model [Field *et al.*, 1993], with linkages spreading out in circular arcs along the orientation axis of the cell. The second set of facilitatory connections (trans-axial connections, i.e. running "perpendicular" to the local orientation of the units) allows interactions between cells with parallel receptive fields. The third set of connections operates at a second stage of processing, after co-axial and trans-axial patterns of activity around a given point in space have been compared. These inhibitory connections switch off the responses of all those units whose facilitation from other active cells falls below a given threshold. In this way, locally parallel and perpendicular configurations can compete. The activity of strongly facilitated units begins oscillating over time, which allows them to synchronize with other similarly oscillating cells. According to Yen and Finkel [1998], contour integration depends on the synchronization of activity of units responding to interrelated contour segments and the perceptual salience of a contour equals the sum of the activity of all synchronized units.

This model can explain the disruptive effect of near-parallel surrounds on snake-localisation. Indeed, in this case there is a high probability that units not belonging to the contour will be facilitated. This will lead to the formation of trans-axial/incorrect configurations, thus increasing the interference from the near-parallel surround. This model can also explain the facilitation from near-perpendicular surrounds, in which case the interference from the surround (in terms of the probability of false matching of contour-elements with background-elements) will be reduced. In contrast to Field *et al.*'s (1993) model, Yen and Finkel's [1998] model supports also ladder-localisation through facilitatory trans-axial connections, which run perpendicular to the local contour direction. However, as it is, this model cannot account for the better localisation of ladders in near-parallel than random surrounds.

May and Hess (2007) developed a contour integration model based on an association field algorithm in which snake- and ladder-associations compete directly for ownership of the elements. In their model ladder-associations are half as strong as snake-associations, implying great impairment for ladder particularly in the periphery where the association field is larger than in fovea. This architecture can account for the near-parallel surround-effect we obtained for snakes. In this case, indeed, there will be additional quite strong snake-associations (between surrounding-elements or between contour-elements and surrounding-elements) that would possibly interfere, thus disrupting contour detection performance. When the snake is surrounded by near-perpendicular elements, instead, the strong snake-association corresponding to the target-contour would “win” over the weaker ladder-associations from the surround. This model can also account for the result that snakes with near-perpendicular surrounds are easier to spot than when they are within random-surrounds. Indeed, there will be fewer links between contour-elements and surrounding-elements when the surround is near-perpendicular to the contour-spine than when it is random. Specifically, there will be more surrounding-elements to align with contour-elements when the surround is random compared to near-perpendicular. For ladder surrounded by near-parallel elements, snake-associations perpendicular to the direction of the path would be stronger than ladder-associations running parallel to the path. Therefore the facilitation from near-parallel surrounds in ladder-localisation might reflect a sort of texture-segmentation. If snake-associations are stronger than ladder-associations one could argue that in the case of ladder surrounded by near-perpendicular elements observers actually detect nearly-snake paths in the surrounds rather than the ladder-target. If this were the case no facilitation would have been observed since the same type of surround was present on both sides of the display.

Geisler, Perry, Super and Gallogly [2001] modelled contour detection performance using a local grouping rule derived from the co-occurrence statistics of the local orientation structure of edges within natural scenes, in combination with a simple integration rule based on transitivity that links local groupings of contour-elements into longer contours. This work was the first to establish that the principles of contour integration (as expressed by the association field model) agree with the statistical properties of contours within natural scenes. For example, pairs of local orientation estimates are more likely to arise from the same contour if they are tangent to a common circle (i.e. if they are co-circular) [Geisler *et al.*, 2001]. Elder and Goldberg [2002] used a similar statistical characterisation of the orientation structure of natural scenes to derive a comprehensive set of grouping rules. Such approaches use orientation structure that is derived from edge structure of natural scenes (derived using either automated edge-detection or manual segmentation) and as such are focused on conjoint orientation/position statistics *within contours*. Our results suggest that – inasmuch as psychophysical paradigms can constrain the likely mechanisms of contour integration – such approaches will fail to predict contour salience with different surrounds. That said the approach is sufficiently general that there is no reason that statistical properties of structure surrounding contours might not be incorporated into grouping rules.

Context effects generalise across different threshold-based performance measures

Taken together, results from Experiments 1 and 2 indicate that the effect of context generalises across threshold measurements. In particular we showed that context affects threshold orientation-jitter and threshold exposure-duration in a similar way. Note that the disruptive effect of near-parallel surrounds cannot be attributed to observers mistaking the near-parallel surround along the random-path as target-snake (a more likely possibility when measuring threshold orientation-jitter since the target-snake is not perfectly smooth). Indeed, Experiment 3 – where an organized surround was present only in the vicinity of the target-snake and not the random-path – showed the same amount of “interference” from near-parallel surrounds. As previously speculated, increasing orientation-jitter may lead to a higher probability of incorrect linkages arising between contour-elements and surrounding-elements, which would selectively penalise the near-parallel condition.

Clinical implications

If crowding influences contour-localisation then this has interesting implications for the specific mechanism underlying poor contour detection in some clinical populations. For example, several studies have shown that people with schizophrenia are poor at contour integration [Silverstein, Kovacs, Corry, & Valone, 2000; Uhlhaas, Silverstein, Phillips, & Lovell, 2004] as well as being less prone to contextual influences in phenomena such as the "contrast-contrast" illusion [Dakin *et al.*, 2005]. Recently, we have reported evidence that abnormal contour detection in schizophrenia likely originates from imprecise discrimination of *local* orientation together with *abnormal* processing of visual context (i.e. patients show a reduced influence of context on contour-localisation paired with a reduced susceptibility to crowding – see Study 4 and Robol *et al.* [In Prep]).

Crowding affects multiple levels in the cortical processing of visual form

In general, it is a signature of visual crowding that it exerts its influences on identification and not detection tasks (for a review see Levi, 2008). Our finding that crowding influences contour-localisation – a task closely akin to detection – might therefore appear paradoxical until one considers the nature of our stimuli. Contour-localisation tasks always employ stimuli containing high levels of noise and it has been shown recently that it is the spatiotemporal distribution of noise (and not the task *per se*) that determines if crowding will exert an influence on performance. Specifically, Allard and Cavanagh [2011] showed that the spatiotemporal distribution of external luminance noise added to a sine wave grating target determined whether flanking Gabors would interfere with observers' detection performance: spatially and temporally extended noise did not crowd, spatially and/or temporally localised noise did. We believe that the high intrinsic levels of (spatially extended and temporally localised) noise in our stimuli make the contour-localisation process vulnerable to crowding. Allard and Cavanagh [2011] speculate that the reason why their detection task became crowdable is that observers adopted a strategy based on *shape-recognition* to help overcome the noise. Our data flesh out this proposition: our contour-localisation task cannot be performed using a strategy based on *global* shape recognition but instead requires contour integration (i.e. a component of shape processing). We suggest that engagement of these low-level processes – without explicit recognition – is still sufficient to make observers prone to crowding.

As previously discussed, and under the assumption of an explicit progression from local to global in contour integration, the comparison between our results from Experiments 2 and 4 supports the suggestion that the local effects of crowding eventually influence downstream, more global, stages in the cortical processing of visual form. This is consistent with an increasing number of studies reporting that crowding affects a variety of tasks and stimulus attributes, from simple features up to complex forms. Several studies have shown that orientation-discrimination is strongly affected by visual crowding [Andriessen & Bouma, 1976; Parkes *et al.*, 2001; Westheimer, Shimamura, & McKee, 1976; Wilkinson *et al.*, 1997]. Parkes *et al.* [2001], for example, showed compromised orientation-discrimination of a near-vertical Gabor element presented in the periphery when it was flanked by other vertical Gabor elements. However, discrimination improved when a small (sub-threshold) orientation cue was added to the flankers. Also judgements of relative position in Vernier tasks are affected by crowding, with thresholds increasing drastically in the presence of additional flankers [Levi, Klein, & Aitsebaomo, 1985; Westheimer & Hauske, 1975]. Crowding occurs not only between low-level elementary features (e.g. edges or gratings) but also for more complex configurations (e.g. moving stimuli, [Bex & Dakin, 2005; Bex *et al.*, 2003]) as well as between higher-level representations such as faces [Farzin, Rivera, & Whitney, 2009; Louie, Bressler, & Whitney, 2007; Martelli, Majaj, & Pelli, 2005]. Louie *et al.* [2007], for example, reported selective crowding of upright faces by surrounding upright faces, but not by inverted faces or non-face objects.

The notion that crowding affects multiple stages in the cortical processing of visual form is supported by a recent fMRI study [Anderson, Dakin, Schwarzkopf, Rees, & Greenwood, 2011], which shows increasing involvement of visual areas (as one moves through the hierarchy) in determining the crowded percept. Consistent with later visual areas (V2 and beyond) being central in crowding are also findings by Freeman and Simoncelli [2011] showing that a model for mid-ventral processing can account for visual crowding.

CONCLUSION

Context affects contour-localisation, with near-parallel and near-perpendicular surrounds decreasing and increasing performance with snakes, respectively. Ladder-localisation is instead facilitated in the presence of any of the two organized surrounds. These effects generalise across threshold measurements, which may have clinical implications. Finally, the *local* orientation uncertainty introduced by crowding contributes, but cannot entirely explain, the contextual effects on *global* contour-localisation. These findings are consistent with the suggestion that context influences contour processing at both local and global stages and also with the notion that the local effects of crowding may influence global cortical processing of visual form.

STUDY 2: CONTEXT INFLUENCES CONTOUR-LOCALISATION – A *GLOBAL* EFFECT?

In the first study we demonstrated that the *local* uncertainty (about the orientation of each contour-element) introduced by visual crowding contributes to, but cannot fully account for, the effects of context on our contour-localisation task. In the second study we sought to further analyse the source of these contextual effects. First of all we wished to determine whether also *global* structures – which may arise in the surround of the target-contour – might play a role in these contextual effects (Experiment 5). Note that in order to better understand the level at which contextual effects exert their influence it is important to consider both local and global mechanisms, especially in the case of complex stimuli (such as disconnected contours, which comprise several oriented, spatially separated local elements). To this end we used a 2AFC localisation task and tested stimulus-conditions, which could promote the emergence of global structures in the surround of the target-contour.

The second aspect we sought to analyse more thoroughly is the opposite effect of parallel surrounds on snake- and ladder-localisation (i.e. worse snake-localisation but better ladder-localisation, both compared to the random surround condition – see Experiment 1). In particular we were interested in understanding *why* this happens and *what* can account for it. In the general discussion of Study 2 we will propose a two-stage process, which can account for these opposite effects of parallel surrounds on snakes and ladders. As described in details later, our proposal is based on the *local* connections postulated in the Yen and Finkel's [1998] model but with a crucial extension, namely the hypothesis of inhibitory interactions between similar *global* structures. Before making this proposal we will also check whether the effects of context on contour-localisation are stimulus-independent (Experiment 6) and whether the opposite effects of parallel surrounds on snakes and ladders reflect the use of different strategies (Experiment 7).

Experiment 5

The role of global structures in the contextual effects on contour-localisation

In Experiment 5 we wished to determine whether global structures – which may arise in the surround of the target-contour – play a role in the effects of context on contour-localisation. An analysis of the effects of context at a global level follows straightforwardly from the result that local uncertainty (about the orientation of each contour-element) cannot completely explain these effects (see Study 1). To this end we used stimuli where the emergence of global structures along the target-contour was promoted (see the paragraph *Stimuli*).

Methods

Observers

Six observers (VR, CC, RV, RB, ALF, MM) – of which four naïve to the purposes of the study (RV, RB, ALF, MM) – participated in Experiment 5. All had normal or corrected-to-normal vision. Four of them (VR, CC, RB, MM) were experienced psychophysical observers.

Apparatus

Experiments were run on a Pentium 4 computer (Intel, Santa Clara, CA) under the Matlab programming environment (MathWorks, Natick, MA) and incorporated elements of the Psychophysics Toolbox extensions [Brainard, 1997; Kleiner *et al.*, 2007; Pelli, 1997]. Stimuli were presented on a CRT monitor (CTX [City of Industry, CA] PR960F 19"). The display resolution was 1024 x 768 pixels and the refresh rate was 100 Hz.

Stimuli

Test stimuli (Figure 17) consisted of snake- and ladder-contours composed of four spatial-frequency band-pass Gabor micro-patterns, embedded in a field of distracter-Gabors. In snake-contours Gabors were co-aligned with an underlying contour-spine, whereas in ladder-contours they were oriented at 90° relative to the local contour-direction. All elements were in cosine phase, had a peak spatial frequency of 2.27 c/deg with an envelope σ of 0.22 deg., and were presented at maximum contrast. The separation of contour-elements was 1.38 deg. and the whole-stimuli subtended 35.51 x 27.12 deg. rectangle containing ~423 elements. Stimuli were presented on a grey background with mean luminance equal to 28 cd/m^2.

We made our stimuli by first inserting two contours (e.g. two snakes) – one in the left and one in the right half of the image – and then dropping distracter-elements (with random orientations) in the background. The two contours fell on symmetric positions (left and right) along a circle with radius subtending 3.96 deg. Background-elements fell on the remaining positions along this circle and along other 15 concentric circles (with radii subtending 0, 1.32, 2.64, 5.27, 6.59, 7.90, 9.22, 10.52, 11.83, 13.14, 14.44, 15.73, 17.02, 18.31, 19.60 deg). The separation of elements along each circle was 1.38 deg. We then manipulated the orientation of the immediate surround (i.e. 3 Gabors on the 2.64 deg. circle and 5 Gabors on the 5.27 deg. circle) to obtain three surround conditions: *parallel* (elements in the immediate surrounds parallel to the contour-elements), *perpendicular* (elements in the immediate surrounds perpendicular to the contour-elements) and *random* (elements in the immediate surrounds randomly oriented). We refer to the random condition as the "baseline" condition. For each surround condition we then extended the manipulation of local orientations to all the other elements on the 2.64 deg. circle and the 5.27 deg. circle. In this way, the target-contour was surrounded by circular *global* structures (Figure 17).

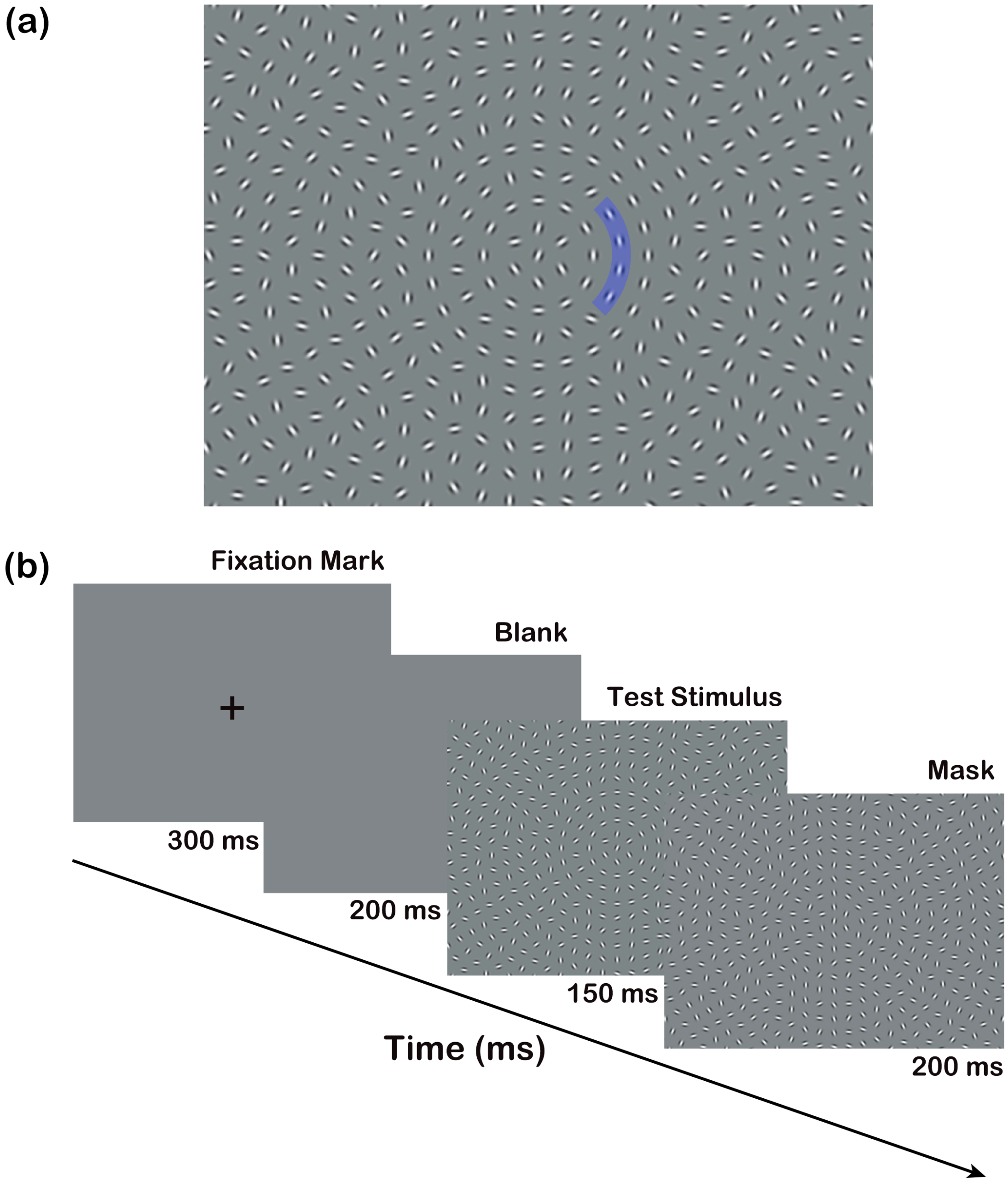

Figure 17. (a) An example of the stimuli from Experiment 5 (with contour-elements shaded in blue to assist the reader in finding the contour). Observers were required to report which side of the screen contained the structured contour (either snake or ladder). This example presents a snake (on the right side of the display) in *parallel* surround. Note the presence of very salient circular *global* structures surrounding the target-contour. (b) A typical trial of Experiment 5: following a fixation mark (300 ms) and a blank screen (200 ms), the test stimulus was presented for 150 ms. Stimulus presentation was immediately followed by a mask (200 ms) composed of a field of randomly oriented elements.

At this point in the stimulus generation procedure we have an image containing two contours (e.g. two snakes), on either side of the display, and global structures in the surround (e.g. with elements tangential to one another, see Figure 17). We made our "random contour" by simply randomising the orientation of the elements of one of these contours. The observers' task was then to report the side of the image containing the structured contour (either snake or ladder). Figure 17a shows an example (with the contour-elements shaded for the purpose of illustration). A mask composed of a field of randomly oriented elements (with on average the same number and separation of Gabors as the test stimulus) immediately followed stimulus presentation. The masking display lasted 200 ms (Figure 17b).

Design

We used a within-subjects design. The independent variable was the orientation of the contour's surrounding elements relative to the circle where they fell. We tested three surround conditions: 0°, 90°, random. The dependent variable was the probability to localise the structured contour (either snake or ladder).

Procedure

Stimuli were viewed binocularly at a distance of 57 cm from the display. Observers fixated a centrally presented marker for 300 ms (Figure 17b). After 200 ms observers were presented a test stimulus (for a duration of 150 ms) containing a structured contour and a random contour embedded within distracter-elements and located right and left of the centre of the screen. This screen was immediately followed by a mask, which contained randomly oriented Gabors and remained on the screen for 200 ms. Observers were asked to give a response (using the computer keyboard) to the question "Which side of the display contained the structured contour?". Snakes and ladders were tested in separate runs, each of which comprised the three surround conditions.

For each type of structured contour (snake and ladder) observers completed one run of 120 trials each (40 trials per surround condition). Before data collection every observer completed a practice session of 60 trials for each type of contour (in separate runs). Order of runs has been counterbalanced between observers.

Statistical analysis

To test the effect of context on snake- and ladder-localisation we carried out a 2x3 repeated-measures ANOVA – with factors *contour* (snakes vs. ladders) and *surround* (random, parallel, perpendicular) – on the probability-values. Bonferroni correction has been used to adjust p-values for multiple comparisons. Alpha-value was set to 0.05.

Results and discussion

Figure 18 shows results obtained in Experiment 5 for snakes (*left*) and ladders (*right*) in the three surround conditions (random: light blue; parallel: violet; perpendicular: blue). We immediately note that the pattern of results for snakes confirms the presence of interference from parallel surrounds and facilitation from perpendicular surrounds, consistent with the results reported in the first study. Note that these findings also further confirm the generality of the effect of context on contour-localisation (at least for snakes): threshold exposure-duration, tolerance to orientation-jitter and detection-probability are affected in the same way by context. For ladders, instead, the pattern of contextual effects is only partially confirmed. Indeed, as can be noted in Figure 18, only parallel surrounds increase detection-probability.

These trends are reflected in the ANOVA results, which show a significant main effect of the factor *contour* ($F_{1,5} = 6.71$, $p = 0.049$) and a significant *contour x surround* interaction ($F_{2,10} = 59.29$, $p < 0.001$). For snakes, *post-hoc* t-tests indicate lower detection-probability with parallel compared to random surrounds (mean probability ± SE are 0.57 ± 0.05 and

0.77 ± 0.04, $t_5 = -4.03$, $p = 0.040$) and higher accuracy in the presence of perpendicular surround than in the baseline condition (mean probability ± SE are 0.86 ± 0.03 and 0.77 ± 0.04, $t_5 = 4.60$, $p = 0.023$). Ladder-localisation, instead, is facilitated in the presence of parallel compared to random surrounds (mean probability ± SE are 0.76 ± 0.04 and 0.57 ± 0.03, $t_5 = 6.80$, $p = 0.004$), but no effect at all can be observed when the surround is perpendicular (mean probability ± SE are 0.57 ± 0.04 vs. 0.57 ± 0.03, $t_5 = -0.12$, $p > 0.05$).

Note that both the interference from parallel surrounds on snake-localisation (violet vs. light blue bars on the *left* of Figure 18) and the lack of any effect from perpendicular surrounds on ladder-localisation (blue vs. light blue bars on the *right* of Figure 18) can be due to the presence of very salient *global* structures in the surround. In both cases, indeed, the target-contour is surrounded by global structures whose elements are aligned to the circle they fell on and also to one another.

To conclude, results of Experiment 5, together with those of Experiment 4, support the idea that both *local* and *global* mechanisms likely contribute to the effects of context on contour-localisation. Indeed by using stimuli that promote the emergence of global structures in the surround of the target-contour (Experiment 5) we report a pattern of results consistent with that of the first study. These results suggest that also interactions between global structures (and not only local orientation uncertainty introduced by crowding) likely play a role in the effects of context on contour-localisation. The only exception seems to be the perpendicular effect on ladder-localisation: the lack of any effect when very salient global structures surround the ladder-contour points to the direction that the higher ladder-localisation in near-perpendicular (compared to random) surrounds we showed in Study 1 should be mostly driven by local factors (such as reduced probability of local false matches between contour- and background-elements compared to the random surround condition).

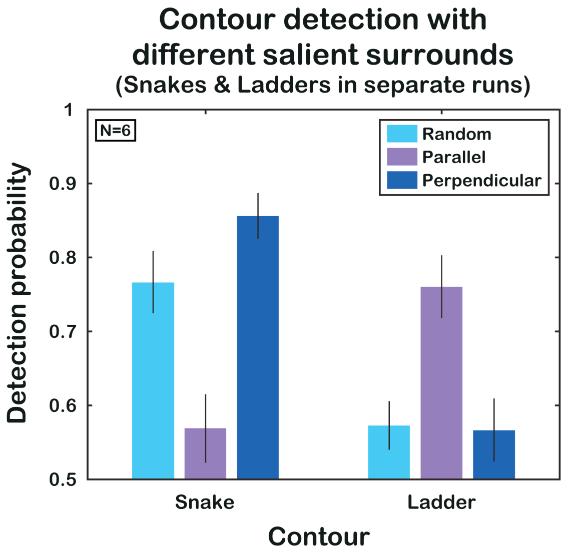

Figure 18. Results obtained in Experiment 5. Plotted data are detection-probabilities for snakes and ladders in parallel (violet bars), perpendicular (blue bars) and random (light blue bars) surrounds. Error bars represent standard errors. Snake-localisation is facilitated in the presence of perpendicular surrounds and impaired if the surround is parallel (both compared to random surrounds). Ladder-localisation is higher with parallel compared to random surrounds, but no effect at all can be observed with perpendicular surrounds.

Experiment 6

The effect of context is stimulus-independent

In Experiment 5 we did not report any effect from perpendicular surround on ladder-localisation. On the opposite, in Study 1 we showed better ladder-localisation in the presence of near-perpendicular than random surrounds. Note that the stimuli of the first study and those of Experiment 5 differ on several aspects, which – independently from the higher or lower probability of emergence of global structures in the surround – may have affected the pattern of results, especially for ladders. To rule out this possibility, in Experiment 6 we manipulated the orientation of just the contour's immediate surrounding-elements (similarly to Study 1). A pattern of results similar to that reported in the first study would argue for a *stimulus-independence* of the effects of context on contour-localisation.

Methods

Observers

Eight observers (AP, RB, CV, GR, VR, CC, SR, SS) – of which six naïve to the purposes of the study (AP, RB, CV, GR, SR, SS) – participated in Experiment 6. All had normal or corrected-to-normal vision. Three of them (RB, VR, CC) were experienced psychophysical observers and participated also in Experiment 5.

Apparatus

We used the same apparatus as in Experiment 5.

Stimuli

Stimuli were as in Experiment 5 but now we manipulated just the contour's immediate surround, as done in the first study. In particular, we manipulated the orientation of just those surrounding-elements that were the closest to the contour-elements (i.e. 5 Gabors on the circle with radius subtending 5.27 deg. and 3 Gabors on the circle with radius subtending 2.64 deg., see Figure 19). As before we tested parallel, perpendicular and random surround conditions, both for snake- and ladder-contours.

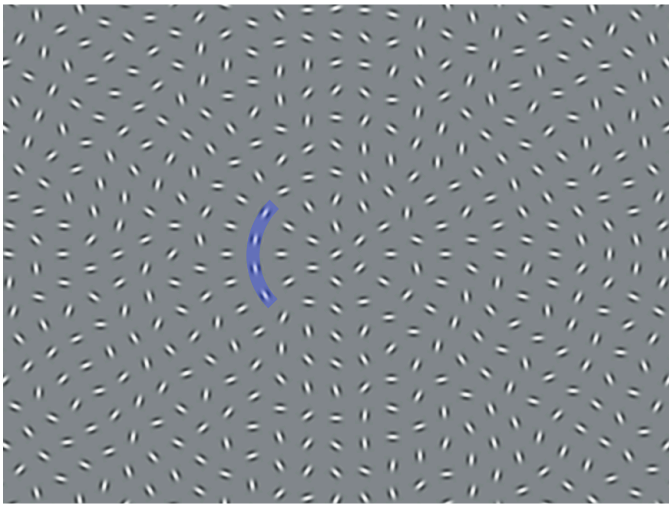

Figure 19. An example of the stimuli from Experiment 6 (with contour-elements shaded in blue to assist the reader in finding the contour). As before, observers were required to report which side of the screen contained the structured contour (either snake or ladder). In this example there is a snake on the left side of the display, embedded in *perpendicular* surround. Note that now the manipulation of context only involves elements in the immediate surround of the contour (similarly to what has been done in Study 1). Trial procedure was as in Experiment 5.

Design, Procedure and Statistical Analysis

Design, Procedure and Statistical Analysis were as in Experiment 5.

Results and discussion

Figure 20 presents results from Experiment 6. Graphed data are detection-probabilities for snakes and ladders embedded in different surrounds (random, parallel, perpendicular). The ANOVA shows a significant main effect of the factors *contour* ($F_{1,7}$ = 18.79, p = 0.003) – indicating general lower performance with ladders than snakes – and *surround* ($F_{2,14}$ = 8.37, p = 0.004) as well as a significant *contour x surround* interaction ($F_{2,14}$ = 24.46, p < 0.001).

Comparing probabilities in the baseline conditions (random surrounds) with those measured with parallel and perpendicular surrounds, it is clear that the manipulation of context has a different effect on snakes and ladders. *Post-hoc* comparisons indicate that snake-localisation is lower when the surround is parallel compared to random (mean probabilities ± SE are 0.65 ± 0.03 and 0.75 ± 0.02, $t_7 = -3.99$, p = 0.021) but it is higher with perpendicular than random surrounds (mean probabilities ± SE are 0.87 ± 0.03 and 0.75 ± 0.02, $t_7 = 3.61$, p = 0.034). Note that this trend for snakes is very similar to that shown in Study 1 and in Dakin and Baruch [2009]. Also the pattern of results for ladders is consistent with our findings of Study 1 and also with Dakin and Baruch's [2009] results. We also find a general increase in ladder-localisation (compared to the baseline) both with parallel (mean probabilities ± SE are 0.69 ± 0.04 and 0.55 ± 0.03, $t_7 = 3.97$, p = 0.022) and perpendicular surrounds (mean probabilities ± SE are 0.63 ± 0.03 and 0.55 ± 0.03, t_7 = 3.44, p = 0.043).

These results further support and extend the notion that the effects of context on contour-localisation generalise across different performance-measures (and not just across threshold-based measures as shown in Study 1). The finding that context affects threshold-based measures and accuracy in a similar way is important to provide a closer link to the standard "path paradigms" that generally use per cent correct measure. Not only the effects of context generalise across performance-measures, but also they are stimulus-independent. Indeed, the stimuli used in Experiment 6 differ on many aspects from that of Study 1 and still we report that snake-localisation is better with perpendicular and worse with parallel surrounds (both compared to the random condition), whereas ladder-localisation is higher with any organized compared to random surrounds.

A likely explanation for the “parallel-advantage” for ladders could be that observers actually segment a salient uniform texture-region instead of localising the target-contour. However, it has to be noted that when the surround is parallel to the contour, the resulting texture is statistically equivalent for snakes and ladders (i.e. in both cases there is an orientation-gradient of 90° between texture and background). This implies that the two textures should be equally salient. From this a question follows straightforwardly: why should observers use a strategy based on the localisation of a salient texture (instead of the target-contour) for ladders but not for snakes? The different effect of parallel surrounds on snake- and ladder-localisation (i.e. interference vs. “advantage") could suggest the use of different strategies for the two types of contour and this could have been supported by the fact that we tested snakes and ladders in separate runs. To rule out this possibility, in Experiment 7 we tested snakes and ladders in the same run.

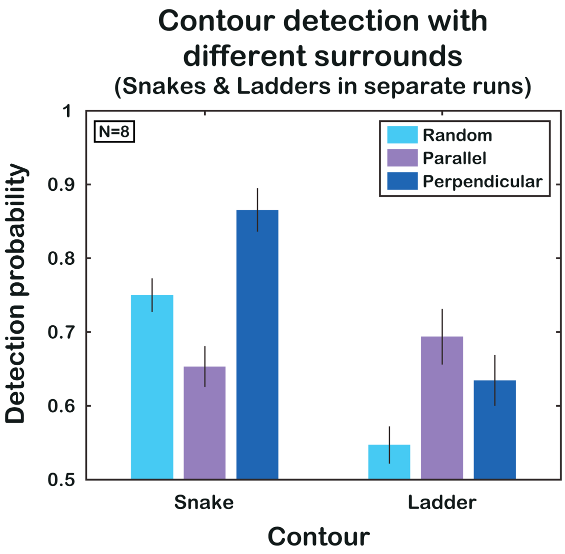

Figure 20. Results from Experiment 6 averaged across eight observers. Graphed data are detection-probabilities for snakes and ladders embedded in different surrounds (random, parallel, perpendicular).

Plotting conventions are as Figure 18. For both snakes and ladders the trend is very similar to that reported in Study 1 and in Dakin and Baruch [2009]: performance with snakes is higher in the presence of perpendicular surrounds but impaired with parallel surrounds, whereas performance with ladders is better in the presence of any organized compared to random surrounds. These findings support the notion that context affects contour-localisation, independently from stimuli and psychophysical procedure used for measuring performance.

Experiment 7

The parallel-advantage for ladders does not reflect the use of a texture-based strategy

As previously discussed, the segmentation of a salient texture-region could possibly account for the "parallel-advantage" for ladders we reported in Experiment 6. To rule out this possibility, in Experiment 7 we tested snakes and ladders within the same run. When snakes and ladders are tested in the same run it is unlikely that observers switch between different strategies (remember that the presentation-time is very short, i.e. 150 ms, and the stimulus is immediately followed by a masking-pattern). Therefore, if observers segment a salient texture-region (instead of localising the target-contour), we expect a "parallel-advantage" both for snakes and for ladders.

Methods

Observers

Four observers of Experiment 5 (VR, CC, RB, MM) and three more naïve observers (LB, RV, SS) participated in Experiment 7. All participants had normal or corrected-to-normal vision.

Apparatus, Stimuli and Design

Apparatus, stimuli and design were as in Experiment 6.

Procedure

Snakes and ladders were tested in the same run to avoid the possibility that observers use different strategies to perform the task with snakes and ladders.

Statistical analysis

As before, to test the effect of context on snake- and ladder-localisation we carried out a 2x3 repeated-measures ANOVA – with factors *contour* (snakes vs. ladders) and *surround* (random, parallel, perpendicular) – on the probability-values. Bonferroni correction has been used to adjust p-values for multiple comparisons. Alpha-value was set to 0.05.

Results and discussion

Figure 21 presents results from Experiment 7. As before, graphed data are detection-probabilities in the three surround conditions (random, parallel, perpendicular). We note that the effect of context on snake- and ladder-localisation is the same as in Experiment 6, where the two types of contours were tested in separate runs. This is confirmed by the results of the ANOVA, which shows a significant main effect of the factors *contour* ($F_{1,6} = 65.81$, $p < 0.001$) and *surround* ($F_{2,12} = 10.10$, $p = 0.003$) as well as a significant *contour x surround* interaction ($F_{2,12} = 30.39$, $p < 0.001$). *Post-hoc* comparisons confirm that snake-localisation is impaired in the presence of parallel compared to random surrounds (mean probabilities ± SE are 0.67 ± 0.03 and 0.77 ± 0.03, $t_6 = -7.33$, $p = 0.001$) but improves when the surround is perpendicular compared to random (mean probabilities ± SE are 0.86 ± 0.03 and 0.77 ± 0.03, $t_6 = 3.72$, $p = 0.039$). Additionally, *post-hoc* t-tests confirm also the pattern for ladders, namely higher accuracy (compared to the random surround condition) both with parallel (mean probabilities ± SE are 0.67 ± 0.04 and 0.55 ± 0.02, $t_6 = 3.85$, $p = 0.034$) and perpendicular (mean probabilities ± SE are 0.61 ± 0.02 and 0.55 ±

0.02, $t_6 = 4.11$, $p = 0.025$) surrounds.

The fact that the “parallel-advantage” for ladders is still present but no facilitation at all is seen for snakes in parallel surrounds (on the opposite data are consistent with interference from parallel surrounds) rules out any explanation based on observers segmenting a salient texture-region. Indeed, if observers were using such a strategy we should have shown a “parallel-advantage” also for snakes. These results suggest that the “parallel-advantage” for ladders is a genuine effect, which is not simply the consequence of observers segmenting a salient texture-region.

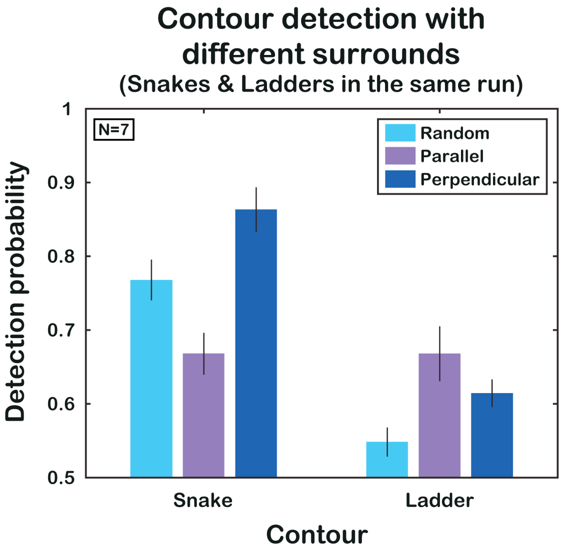

Figure 21. Mean detection-probabilities – averaged across seven observers – for snakes and ladders tested within the same run (Experiment 7). As before, the surround could be random, parallel or perpendicular. Plotting conventions are as Figure 18. Note similarity to Figure 20, which presents data for snakes and ladders tested in separate runs. These results suggest that the “parallel-advantage” for ladders cannot be the consequence of observers segmenting a salient texture-region.

GENERAL DISCUSSION

We investigated the role of *global* structures – which may arise in the surround of the target-contour – in the effects of context on contour-localisation. We report data consistent with a crucial role of global structures in the surround of the target-contour (Experiment 5). Specifically when salient global structures were present in the surround of the target-contour, contextual information did not facilitate at all (for ladder) or even interfered with the localisation-task (for snakes). We also find that the effects of context we reported in the first study are stimulus-independent (Experiment 6). Finally, our data of the second study further support the notion that context affects contour-localisation independently from the psychophysical procedure used for measuring performance (threshold-based measures in Study 1, probability/per cent correct in Study 2).

Context effect generalises across performance measures and is stimulus-independent

In Experiment 6 we did not use threshold-based measures but detection-probability (which is what the standard path paradigms usually measure) and still found contextual effects consistent with those reported in the first study. Taken together, results of the two studies provide evidence for a generality of the effects of context across different performance-measures, and not only within threshold-based measures of performance (as instead suggested in the discussion of the first study). Additionally, the comparison between our data from Experiment 6 and those from Experiments 1 and 2 indicate that the effects of context on contour-localisation are stimulus-independent. It is interesting to note that a similar pattern of contextual effects has also been reported for straight contours [Schumacher *et al.*, 2011], which further confirms the stimulus-independence of these effects.

*The effect of **parallel** surrounds on contour-localisation: our proposal*[‡]

In the general discussion of the first study we have described the current models of contour integration present in the literature. As previously discussed, the association field model [Field *et al.*, 1993] does not directly take into account contextual effects on contour-localisation and also cannot account for ladder-localisation. Thus, as it is, this model is not useful to account for the effects of context we reported both in Study 1 and in Study 2. A model that supports also ladder-localisation is the Yen and Finkel's [1998] model, where trans-axial connections (which run perpendicular to the local orientation of the contour-elements) nicely fit contours with elements orthogonal to the path. As it is, also this model does not entirely fit our data with parallel surrounds. Indeed, it fails to explain why ladder-localisation is better with parallel than random surrounds.

To account for the opposite effects of parallel surrounds on snake- and ladder-localisation (i.e. increased inhibitory effect for snakes and decreased inhibitory effect for ladders, both compared to random surrounds) we propose a two-stage process. For the sake of simplicity, here we will consider straight contours embedded in perfectly parallel or perpendicular surrounds. Note that we did not use straight contours in our experiments; however, contextual effects consistent with those we reported here have also been shown for straight contours [Schumacher *et al.*, 2011]. Consistent the stimuli we used in both Study 1 and Study 2 (and also with the stimuli generally used in contour integration paradigms) we will consider target-contours longer than any spurious linkage, which may arise between contour- and surrounding-elements.

Stage 1: formation of co-axial and trans-axial connections and emergence of global structures

In the first stage, consistent with the Yen and Finkel's [1998] model, we hypothesize the

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[‡] Note that our proposal makes no pretence of being an exhaustive model of the contextual effects on contour-localisation. It is simply meant to be a starting point for a new approach at the study of contour integration, in which also the effect of context is taken into account.

formation of *co-axial* and *trans-axial* connections between local elements (Figures 22a and 22c). As in the original model [Yen & Finkel, 1998], the strength of connection scales with distance and this occurs more rapidly for trans-axial than co-axial connections. This implies that at a given distance, trans-axial connections would be generally weaker than co-axial connections.

Let us first consider the case of a snake surrounded by parallel elements (Figure 22a) and, for the sake of simplicity, let us focus on the connections of the central contour-element (element #4 from left). This element would be strongly connected – through co-axial connections – with the two nearest contour-elements on both its sides (elements #3 and #5). Less strong co-axial connections would link the central contour-elements with elements #2 and #6. And so on, with the strength of connection decreasing as a function of elements' distance. Element #4 would also be linked – through trans-axial connections – to two surrounding-elements (elements #8 and #9). Note that these two trans-axial connections would be weaker (i.e. they would have a lower *connection strength*) than the co-axial connections between element #4 and element #3 or element #5. Indeed, although elements' distance is the same, the strength of connections scale more rapidly for trans-axial than co-axial connections [Yen & Finkel, 1998].

The formation of co-axial and trans-axial connections between *local* elements would then lead to the emergence of *global* structures. In particular, in the example in Figure 22b, the co-axial and trans-axial connections of the central contour-element with the other elements in the display would lead to the emergence of two global structures, one horizontally oriented (shaded in *blue* in Figure 22b) and one vertically oriented (shaded in *red* in Figure 22b). Note that the *red* global structure emerges as a consequence of false/spurious matching between contour- and background-elements.

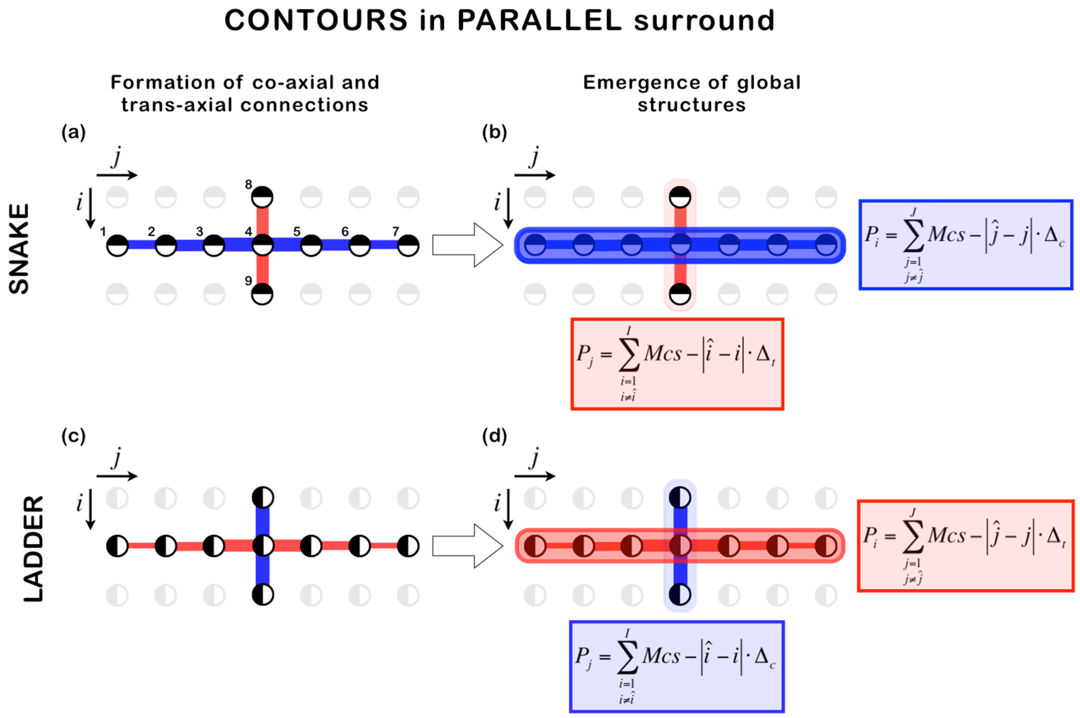

Figure 22. Formation of co-axial and trans-axial connections with the emergence of global structures, separately for snake (a, b) and ladder (c, d) in parallel surrounds. Here only co-axial and trans-axial connections of the central element of the display are shown. The thickness of the red and blues lines represents the strength of connection between local elements. We suggest that the *perceptual salience* of each global structure can be expressed as the sum of the connection-strength values of all the connections of a given type (e.g. co-axial) spreading out from a specific local element (see text for more details).

We hypothesise that the connection-strength values of all the connections spreading out from a given element (e.g. the central contour-element in our example) are summed[§], separately for type of connection (i.e. co-axial vs. trans-axial). These sums would express the *perceptual salience* of each global structure. We can express the perceptual salience of these global structures with a mathematical formula. Specifically, the perceptual salience P_i of the global structure shaded in *blue* in Figure 22b (which follows the

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[§] We chose the function *sum* because this is the simplest possible algorithm to compute salience (see also the cortical-based model proposed by Yen and Finkel [1998], where salience is computed as the sum of the activity of all the synchronized cells). Note also that this function allows us to express the fact that longer contours are generally more salient than shorter ones, which would have not been possible if we have computed an *average*.

formation of co-axial connections) would be:

$$P_i = \sum_{\substack{j=1 \\ j \neq \hat{j}}}^{J} Mcs - \left| \hat{j} - j \right| \cdot \Delta_c$$

where Mcs is the maximum connection-strength (i.e. when elements' distance is equal to zero) and Δ_c is a constant specific to the co-axial connections. Note that the term $\left| \hat{j} - j \right|$ represents the distance between two connected elements, in our example between the central contour-element (element #4) and each other element to which it is connected.

In a similar way, the perceptual salience P_j of the global structure shaded in *red* in Figure 22b (which follows the formation of trans-axial connections) can be expressed with the following formula:

$$P_j = \sum_{\substack{i=1 \\ i \neq \hat{i}}}^{I} Mcs - \left| \hat{i} - i \right| \cdot \Delta_t$$

where Δ_t is a constant specific to the trans-axial connections and

$$\Delta_t > \Delta_c$$

which expresses the fact that the strength of connection scales more rapidly with distance for trans-axial than co-axial connections [Yen & Finkel, 1998]. In our example (Figure 22b), the global structure shaded in *blue* is more salient than that highlighted in *red* (see the *Appendix* for a numerical example). This is mainly due to the higher number of co-axial than trans-axial connections. Certainly an important role is also played by the fact that co-axial connections are generally stronger than trans-axial connections.

In the case of a ladder in parallel surrounds (Figure 22c, again let us consider the central contour-element) the formation of trans-axial connections would lead to the emergence of a global structure (shaded in *red* in Figure 22d), which is more salient than the structure following linkages through co-axial connections (in *blue* in Figure 22d). Again the perceptual salience of these global structures can be expressed through mathematical formulas similar to those reported above (see Figure 22). Note that in the case of ladder, the higher number of trans-axial compared to co-axial connections overcomes the generally weaker strength of trans-axial connections (see the *Appendix* for a numerical example). This is true whatever contour-element we consider.

Note that both for snakes and for ladders the probability of false matching between contour- and background-elements is higher in the parallel than in the random condition. From this follows that both snakes and ladder should be better localised in random than parallel surrounds. This is not what our data consistently show. Indeed, we report better localisation of ladder in parallel than random surrounds. Therefore, an explanation that takes into account only local false matches between contour- and background-elements can at least in part account for the inhibitory effect of parallel surrounds on snake-localisation (in Study 2 we reported that also global mechanisms are possibly involved), but does not predict any reduction in the inhibitory effect of parallel surrounds (compared to random) on ladder-localisation. To fully account for these effects we hypothesise a second stage, where similar (both in terms of salience and local connections, e.g. co-axial, which they originated from) global structures actively compete.

Stage 2: competition between similar global structures

The second stage is based on the fact that global structures will emerge also in the surround. In particular, these structures will be similar (both in terms of salience and local connections, which they originated from) to that arising thanks to local connections between contour-elements. We hypothesise that these similar global structures actively compete (Figure 23), inhibiting one another – with each structure's strength of inhibition proportional to its salience. Note the similarity of this inhibitory effect amongst similar global structures to the suppressive effect of local iso-oriented surrounding-elements on the salience of a singleton – whereby the response of a V1 neuron to a target-line falling in its classical receptive field is suppressed if the target-line is embedded in identical, iso-oriented lines [Knierim & van Essen, 1992].

In the case of a snake in parallel surround we will have three snake-consistent very salient global structures, which, for this reason, will strongly inhibit each other (Figure 23a). This reciprocal strong inhibition between similar global structures can account for the poor localisation of snakes embedded in parallel compared to random surrounds. Indeed, the probability that similar global structures emerge in the surround is lower in the random than in the parallel surround condition.

For a ladder in parallel surrounds (Figure 23b), instead, we will have three ladder-consistent global structures, which will be generally less salient than snake-consistent structures (Figure 23a), and for this reason will weakly inhibit each other. As a consequence, the three ladder-consistent global structures will perceptually persist, thus accounting for the better localisation of ladder in parallel compared to random surrounds. Note that by stating this we are not saying that weak inhibition turns into facilitation between global structures. Instead, the better localisation of ladder in parallel compared to random surrounds likely occurs because three (rather than just one) ladder-consistent global structures are present (thus possibly relying on a mechanism of *probability summation*).

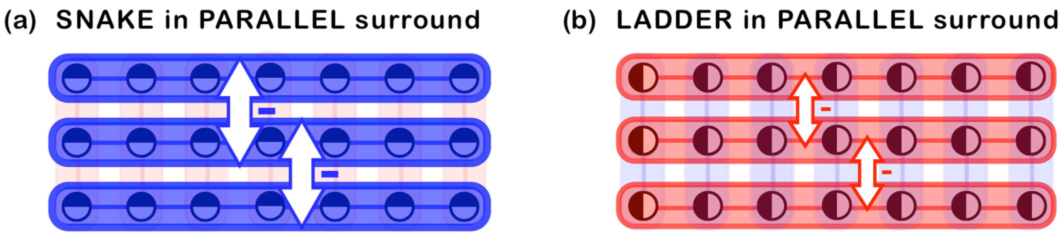

Figure 23. (a) Three very salient snake-consistent global structures strongly inhibit each other, thus accounting for the poor localisation of snakes in parallel compared to random surrounds (where the

probability of the emergence of global structures in the surround is low). (b) Three ladder-consistent global structures, which are generally less salient than snake-consistent structures (a), weakly inhibit each other. This possibly allows the three structures to perceptually persist, thus accounting for the better localisation of ladder in parallel than random surrounds.

Note that the two-stage process we propose here accounts for both local and global effects of context on contour-localisation. Indeed, in the first stage, where local elements are linked through co-axial and trans-axial connections, there is space for disruptive effects of local false matches between contour- and background-elements. Global effects due to interactions between spatially extended similar structures occur instead in the second stage. What is new in our proposal (compared to Yen and Finkel's [1998] model) is the importance given to inhibitory interactions between similar global structures, in addition to the crucial role of local effects.

The effect of ***perpendicular*** *surrounds on contour-localisation: our proposal*

In Experiment 5 we reported no effect on ladder-localisation by perpendicular (compared to random) surrounds when global structures in the immediate background were very salient. It is interesting to speculate what can account for this lack of effect. Interactions between *non-similar* global structures – with more salient structures inhibiting the less salient ones – could potentially account for this finding.

That we did not report any effect on ladder-localisation when the surrounding structures were very salient (Experiment 5) points to the direction that the facilitatory perpendicular-effect on ladder-localisation we reported in Study 1 and Experiment 6 should be mostly driven by local factors – such as lower probability of local false matches between contour- and surrounding-elements compared to the random surround condition. Indeed, the probability of false matches between contour- and background-elements is 0 if the surround is perpendicular to the contour-path. In the random surround conditions, instead, it is likely that some surrounding-elements will align with contour-elements, thus interfering with contour-localisation. This can account for the better localisation of ladders with perpendicular compared to random surrounds. Note that, for the sake of simplicity, here we have considered perfectly perpendicular surrounds. The same explanation in terms of interference from the emergence of false matches holds also for near-perpendicular surrounds (in which case the probability of false matches between contour- and background-elements will approach 0).

Whereas the perpendicular facilitatory effect on ladder-localisation can be explained without involving competition between global structures, the better localisation of snakes with perpendicular than random surround likely involves both local and global processes. Indeed, in Study 1 we showed that local factors cannot fully account for the perpendicular-effect on snake-localisation (Experiment 4). Here we propose that the effect is based on both lower probability of local false matches between contour- and surrounding-elements (compared to the random surround condition) and lower probability of the emergence of snake-consistent global structures in the perpendicular compared to random surround. Specifically, when the surround is random it is more likely that some surrounding-elements will align with contour-elements, thus supporting the emergence of local false matches, which may interfere with contour-localisation. Additionally, also the probability of the emergence of snake-consistent global structures in the surrounds will be higher with random than perpendicular surrounds. This would lead to reciprocal inhibition between similar global structures, thus making contour-localisation more difficult than in the perpendicular surround condition.

CONCLUSION

Results of the second study further confirm that context massively influences contour-localisation. Specifically, snake-localisation is better in the presence of perpendicular surrounds and worse with parallel surrounds (both compared to the random surround condition). Ladders are instead better localised in the presence of any of the two organized surrounds than with random surrounds. These effects generalise across performance-measures and are stimulus-independent. Finally, we report that global structures in the surround of the contour play an important role in these effects. These findings are consistent with the suggestion that both local and global mechanisms likely contribute to the effects of context on contour-localisation.

CLINICAL STUDIES

STUDY 3: CONTOUR INTEGRATION AND SEGMENTATION IN AGEING[**]

INTRODUCTION

Human visual functions degrade with age. Although there are age-related degenerations of the optics of the eye [Pierscionek & Weale, 1995; Winn, Whitaker, Elliott, & Phillips, 1994], those optical changes are insufficient to explain the decline of both low-level visual abilities (acuity [Kline, Culham, Bartel, & Lynk, 2001], contrast sensitivity for spatial or chromatic patterns [Bennett, Sekuler, & Ozin, 1999; Elliott, Whitaker, & MacVeigh, 1990; Hardy, Delahunt, Okajima, & Werner, 2005], orientation discrimination [Betts, Sekuler, & Bennett, 2007; Delahunt, Hardy, & Werner, 2008]) and more complex visual functions (motion perception [Bennett, Sekuler, & Sekuler, 2007; Betts, Sekuler, & Bennett, 2009; Betts, Taylor, Sekuler, & Bennett, 2005; Billino, Bremmer, & Gegenfurtner, 2008], bilateral symmetry perception [Herbert, Overbury, Singh, & Faubert, 2002], spatial integration and segregation [Andersen & Ni, 2008; Del Viva & Agostini, 2007; Roudaia, Bennett, & Sekuler, 2008]). Here we investigated the complex visual functions that involve deriving a meaningful percept from fragmented visual information in the retinal image. In particular, we sought to analyse whether ageing affects the integration of local fragments into contours and the segmentation of contours from the background.

The ability of the visual system to reconstruct contours from a fragmented retinal image has been extensively investigated in young adults using contours made of oriented disconnected elements. Numerous studies have examined the detection of linear

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[**] Based on Casco, C., **Robol, V.**, Barollo, M., Cansino, S. Effects of Aging on Visual Contour Integration and Segmentation. *Investigative Ophthalmology & Visual Science*, 52**,** 3955-3961, ISSN: 0146-0404, doi:10.1167/iovs.10-5439.

[Caputo & Casco, 1999; Casco, Campana, Han, & Guzzon, 2009; Casco, Grieco, Campana, Corvino, & Caputo, 2005; Polat & Bonneh, 2000], curvilinear [Field *et al.*, 1993; Hess, Beaudot, & Mullen, 2001], or closed contours [Achtman, Hess, & Wang, 2003; Altmann *et al.*, 2003; Kovacs & Julesz, 1993; Mathes & Fahle, 2007] embedded in a cluttered background of elements of different orientation from those forming the contour [R. F. Hess & D. Field, 1999; Hess, Hayes, & Field, 2003]. Those studies highlighted the spatial parameters that affect contour integration and segmentation, the most powerful being the orientation-jitter of nearby contour-segments (which makes them not aligned to the contour-path) and the relative distance between contour-segments [R. F. Hess & D. Field, 1999]. In particular, many studies have shown better detectability of contours whose elements were aligned along the global contour-orientation, both in the absence [Bonneh & Sagi, 1998; Saarinen & Levi, 2001] and in the presence of background-noise [Casco *et al.*, 2009; Polat & Bonneh, 2000].

The comparison of the ability to detect a fragmented contour with and without noise is important because it highlights the combined action of the two mechanisms involved: one *facilitatory* and the other *suppressive*. The facilitatory mechanism mediates the integration of oriented contour-segments. According to the association field model [Field *et al.*, 1993], the linking between contour-elements is strongest when they are aligned along their axis of preferred orientation [Field *et al.*, 1993; Roncato & Casco, 2003, 2009; Shipley & Kellman, 2003]. The suppressive mechanism mediates a reduction in the number of local *false matches* between contour- and background elements (which possibly emerge at the first stage of the two-stage process we proposed in Study 2 to account for the effect of surrounding-elements on contour-localisation). Note that to efficiently detect contours in noise it is also crucial to discard irrelevant orientation information along the contour. Facilitation probably relies on long-range excitatory horizontal connections between cells in V1 [Field & Hayes, 2004; Heeger, 1992]. Local false matches suppression and the process of discarding irrelevant information along the contour are instead more likely to result from short-range inhibitory connections [Das & Gilbert, 1999].

Despite the large number of previous studies on contour integration and segmentation, little is known about how ageing affects the facilitatory and suppressive mechanisms involved in those tasks. Neurophysiological studies in cats and monkeys indirectly suggest that ageing may affect facilitation and suppression. In particular, two age-related deficits reported by these neurophysiological studies may affect the facilitatory and suppressive mechanisms: (1) decreased selectivity to orientation in senescent V1 neurons caused by reduced lateral inhibition and (2) increased spontaneous activity [Hua *et al.*, 2006; Schmolesky *et al.*, 2000]. Both deficits may result from reduced γ-aminobutyric acid (GABA)–mediated inhibition [Leventhal *et al.*, 2003]. Human studies provide no evidence of reduced orientation selectivity [Delahunt *et al.*, 2008; Govenlock, Taylor, Sekuler, & Bennett, 2009], whereas there is an age-dependent increase in equivalent input noise or internal noise that may be related to increased spontaneous activity [Betts *et al.*, 2007]. If ageing reduces the efficiency of neural inhibition, this could affect not only the response of individual channels but also the efficiency of lateral interactions between channels accounting for contour integration and segmentation.

Two recent studies [Del Viva & Agostini, 2007; McKendrick, Weymouth, & Battista, 2010] examined the effect of ageing on contour integration and segmentation within noisy backgrounds, but with contradictory results. Specifically, McKendrick *et al.* [2010] did not find evidence for a deficit in segmentation. Indeed, the authors showed that the detrimental effect of adding background-noise was the same for older and younger observers. Del Viva and Agostini [2007], instead, showed reduced ability of older observers to detect closed circular contours embedded in noisy backgrounds, with greater effect for small than large inter-element distances. The results of these two studies are contradictory perhaps because the different tasks used – *shape discrimination* [McKendrick *et al.*, 2010] vs. *contour detection* [Del Viva & Agostini, 2007]) – affect different levels of processing involved in visual integration and segmentation, spanning from contextual influences in V1 to top-down influences such as attention and task demands [Casco *et al.*, 2009; Casco *et al.*, 2005].

To interpret the contour-detection results reported by Del Viva and Agostini [2007], two questions have to be answered. The first regards the relative contribution of facilitatory and inhibitory lateral interactions [Casco *et al.*, 2009] in accounting for reduced sensitivity to circular contours. The reduced ability of older observers to detect closed circular contours in noisy backgrounds may be attributable to a reduced capability of suppressing false matches between contour- and background-elements, particularly when integration signals are weak. Alternatively, and regardless of the presence of background-noise, older individuals may be less efficient in integrating elements belonging to the contour. The paradigm used by Del Viva and Agostini [2007] does not allow a distinction between these two explanations. The second question directly follows from the fact that Del Viva and Agostini [2007] only manipulated inter-element distance. As a consequence, it is unclear whether there is an ageing effect on contour integration that depends on the relative orientation of contour-elements in addition to their mutual distance.

One previous study [Roudaia *et al.*, 2008] examined the effect of relative local orientations on contour integration across different age-groups. The results show that the contrast threshold for detecting and discriminating the global orientation of a C-shaped contour against a blank background depends on the orientation of the local elements for younger but not for older observers. However, this result cannot be generalized to supra-threshold stimuli. Indeed, it is well established that facilitation by alignment in contrast detection is a low-level, monocular phenomenon [Huang, Hess, & Dakin, 2006], and its role in higher-level tasks – such as detection of a smoothly curved supra-threshold path – has been often questioned [Hess *et al.*, 1998; Williams & Hess, 1998]. In other words, the contrast-detection paradigm used by Roudaia *et al.* [2008] may have pinpointed age-differences in local low-level facilitatory mechanisms of contrast enhancement instead of, or in addition to, age-differences in the global long-range facilitation involved in supra-threshold circular contour integration [Loffler, 2008].

To summarize, a still open question is whether ageing affects the dependence of contour-detection mechanisms on the relative orientation of elements along the contour and in the background. Such dependence could be accounted for by the reduced orientation selectivity highlighted in primate studies [Hua *et al.*, 2006; Schmolesky *et al.*, 2000], in which case possibly both facilitatory and inhibitory interactions necessary to efficiently detect contours in noise would be affected. However, the effect of ageing could be selective for either facilitatory or inhibitory low-level cortical lateral interactions, thus specifically affecting either the integration- or the segmentation-process.

To compare the efficiency of integrative and segregative operations in younger and older adults we measured the detectability of deviation from circularity (DFC) in the shape of supra-threshold circular contours [Keeble & Hess, 1999; Levi & Klein, 2000], defined by oriented Gabor elements. The comparison between age-groups in a condition where Gabors were aligned along the contour allowed us to investigate how contour-integration is affected by ageing. Additionally, we also compared the condition with aligned Gabors with another condition where Gabors had alternating tangential and orthogonal orientations, to establish how ageing affects the capacity to discard irrelevant orientation information along the contour. Finally, by comparing performance with and without background-noise in the two age-groups we specifically aimed at establishing whether the capacity to suppress false matches arising between contour- and background-elements is affected by ageing. Contrast sensitivity was also measured to confirm that the contrast of the carrier was above threshold for both age-groups. Indeed, there is evidence of an age-related loss in sensitivity at high and middle spatial frequencies in photopic vision [Owsley, Sekuler, & Siemsen, 1983], whereas only in scotopic vision does an age-related decline occur for spatial frequencies < 1.2 c/deg, consistent with age-related changes in the magnocellular pathway [Schefrin, Tregear, Harvey, & Werner, 1999].

Experiment 8

Spatial suppression but not integration is impaired in ageing

Methods

Observers

Participants were fourteen younger observers (mean age: 24.8 ± 3.4 years; range: 19–33 years) and fourteen older observers (mean age: 66.9 ± 6.3 years; range: 60–78 years). All participants had normal or corrected-to-normal vision such that binocular visual acuity was ≤ 0.10 logMAR at a distance of 70 cm (younger mean visual acuity [logMAR]: −0.11 ± 0.07; older mean visual acuity [logMAR]: −0.00 ± 0.09). Older observers did not have eye defects (such as cataract and glaucoma) or neurologic deficits (such as Alzheimer's disease or other forms of age-associated dementia). Both groups had similar socioeconomic status and educational background.

In nine younger (mean age: 24.8 ± 3.6 years; range: 20–33 years) and eight older (mean age: 65.9 ± 7.5 years; range: 60–78 years) observers we also measured contrast sensitivity (see Figure 25) in addition to visual acuity (younger mean visual acuity [logMAR]: −0.11 ± 0.08; older mean visual acuity [logMAR]: −0.02 ± 0.10).

Apparatus

The main experiment (*spatial integration and suppression*) was run on a Pentium 4 (Intel, Santa Clara, CA) computer under the E-Prime programming environment (Psychology Software Tools, Inc., Sharpsburg, PA). Stimuli were generated under the Matlab programming environment (MathWorks, Natick, MA) with incorporated elements of the

Psychophysics Toolbox extensions [Brainard, 1997; Kleiner *et al.*, 2007; Pelli, 1997] and presented on a 17-in. cathode ray tube (CRT) monitor (P70f ViewSonic, Walnut, CA). The monitor was calibrated with a Minolta photometer, giving a mean luminance of 38.9 cd/m^2. The display resolution was 1024 x 768 pixels and the refresh rate was 100 Hz.

Contrast sensitivity was measured using the software application tool CRS Psycho (Cambridge Research Systems Ltd, Rochester, UK). The stimuli were generated by a VSG2/3 graphics card (Cambridge Research Systems Ltd, Rochester, UK) and displayed on a 17-in. CRT monitor (Brilliance 107P; Philips [Amsterdam, The Netherlands]; resolution: 1024 x 768 pixels; refresh rate: 70 Hz).

Stimuli

Stimuli of the *spatial integration and suppression experiment* were composed of cosine-phase Gabor patches. The Gaussian envelope σ subtended 0.16 deg. and the sinusoidal grating had a wavelength λ of 0.32 deg. (spatial frequency = 3.13 c/deg). Stimuli were achromatic with a Michelson contrast of 0.87 and presented on a background with mean luminance of 38.9 cd/m^2.

We first created a circular contour by placing eight equally spaced Gabors (center-to-center distance = 74.4 arcmin or 3.9λ) along a notional path (radius = 97.2 arcmin) centred on the screen. Gabors were co-aligned to the local orientation of the underlying path (*tangential* condition, Figures 24a and 24d). We then positioned one of these Gabors on a notional path of larger radius (five levels: 98.7, 103.1, 107.5, 112.0, and 116.4 arcmin) while keeping its orientation consistent with the underlying contour. In this way we obtained five DFC-levels: 1.5, 5.9, 10.3, 14.8, and 19.2 arcmin. We selected these DFC-levels because pilot experiments showed they bracketed the psychometric function for observers tested under these conditions. On each trial the displaced Gabor could appear, with equal probability, in one of four locations along the circle (0°, 90°, 180°, and 270°).

We then created a second stimulus condition – which we refer to as *mixed* condition

(Figures 24b and 24e) – where Gabors not falling on either candidate target-positions (i.e. 0°, 90°, 180°, and 270°) were orthogonal to the notional circular path. In this way we obtained a stimulus where Gabors had alternating tangential and orthogonal orientations (relative to the underlying path).

A third stimulus condition (Figures 24c and 24f) was created by adding randomly oriented background-noise to the *tangential* stimuli. Specifically, sixteen distracting background-Gabors were placed along two notional paths centred on the screen. Four of these Gabors were placed along a circular path with radius of 41.3 arcmin. The remaining twelve Gabors were placed on a path with radius of 153.2 arcmin. We refer to this stimulus condition with background-elements as *noise* condition.

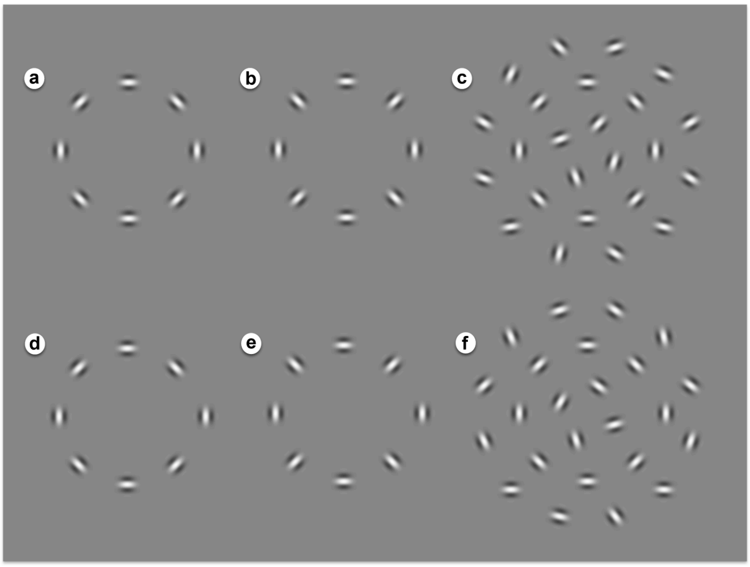

Figure 24. Example of the stimuli used in Experiment 8. (a,d) *tangential* condition; (b,e) *mixed* condition; (c,f) *noise* condition. Stimuli on the bottom of the figure show three examples where the element on the right is displaced from the contour-path (here only a DFC of 14.8 arcmin is shown). On the top instead perfectly circular contours are shown. Observers indicated which interval contained a DFC.

Since we used a two-interval, two-alternative forced choice (2I-2AFC) task in which observers indicated which intervals contained a DFC, our reference stimulus was a perfectly circular contour (with elements all co-aligned to the underlying path in the *tangential* and *noise* conditions and alternating in orientation in the *mixed* condition).

Stimuli for the contrast sensitivity measurement consisted of full-screen vertical sinusoidal gratings. Eight spatial frequencies (0.10, 0.19, 0.42, 0.90, 1.99, 4.41, 9.91, and 19.82 c/deg) were tested. We used the method of limits with three ascending (from lower to higher grating contrast) and three descending (from higher to lower grating contrast) series. On each trial, observers indicated whether they could detect the grating. For each participant contrast sensitivity at each spatial frequency was calculated by averaging across series.

Design

We used a within-subjects design. For each condition tested (*tangential*, *mixed, noise*), the independent variable was the DFC-level (1.5, 5.9, 10.3, 14.8, or 19.2 arcmin) and the dependent variable was the probability to correctly detect the DFC (first vs. second interval).

Procedure

For all measurements (spatial integration and suppression and contrast sensitivity) stimuli were viewed binocularly in a darkened room at a viewing distance of 70 cm. In each trial of the spatial integration and suppression experiment, a fixation cross (200 ms) was followed, after 300 ms, by two stimuli presented for 400 ms each. Inter-stimulus interval was 600 ms. We used a 2I-2AFC detection task in which observers had to choose – by pressing one of two alternative keys on the computer keyboard – which presentation contained a displaced Gabor (relative to the notional circle). The contour with the displaced Gabor was presented, with equal probability, either in the first or in the second stimulus interval. The other stimulus displayed a perfectly circular contour.

Observers completed one session for each condition (*tangential*, *mixed, noise*). Each session consisted of 80 randomly presented trials (5 DFC-levels x 2 presentation-intervals x 8 trials per DFC-level). Contrast sensitivity was measured after the third session of the main experiment.

Statistical analysis

Raw data from each participant in each condition of the main experiment were fit with Probit functions [Finney, 1971], to give an estimate of *DFC-threshold* (i.e. the DFC-level that supported 75% correct performance). To test the effect of ageing on spatial integration we performed a two-way repeated-measures ANOVA on threshold-values – with factors *stimulus condition* (tangential vs. mixed) and *group* (younger vs. older). Note that this analysis allowed us to investigate also the effect of ageing on the ability to discard irrelevant orientation information along the contour. To test how aging affects the ability to suppress false matches arising between contour- and background-elements we performed another two-way repeated-measures ANOVA on the threshold-values of the two age-groups – with *tangential* and *noise* as levels for the factor *stimulus condition*. Degrees of freedom have been corrected with the Greenhouse–Geisser procedure and corrected probability levels are reported. *Post-hoc* pairwise comparisons have been computed with Bonferroni correction. Alpha level was set to 0.05 for all statistical tests.

Results and discussion

Contrast sensitivity

Figure 25 presents mean binocular sensitivity functions for younger (blue line) and older observers (red line). In agreement with previous findings [Owsley *et al.*, 1983], we found that at the spatial frequency of the carrier we used (3.13 c/deg) sensitivity was lower for older than younger observers. However, since the contrast of our Gabors was very high, the low sensitivity to the carrier cannot account for group differences in the detection of the DFC (even if one considers that a grating viewed through a Gaussian window produces a sensitivity reduction of approximately 0.5 log units [Peli, Arend, Young, & Goldstein, 1993]).

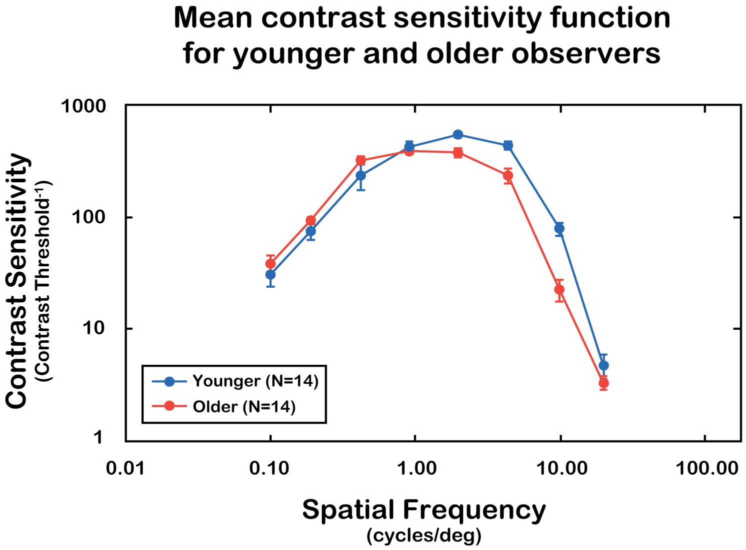

Figure 25. Mean contrast sensitivity functions for younger (blue line) and older observers (red line). Error bars represent standard errors.

Spatial integration

Figure 26 presents mean DFC-thresholds in the *tangential* and *mixed* conditions for younger and older observers. We first note that older observers have generally higher thresholds compared to younger participants. Additionally, the graph clearly indicates that, whereas younger observers are not affected by the perturbation of co-alignment of elements along the contour-path, older observers are.

This pattern of results is confirmed by the ANOVA on the threshold-values of the tangential and mixed conditions, which shows a significant effect for the factors *group* ($F_{1,26} = 16.21$, $p < 0.001$) and *stimulus condition* ($F_{1,26} = 6.29$, $p = 0.019$), as well as a significant interaction of the two factors ($F_{1,26} = 7.71$, $p = 0.01$). *Post-hoc* comparisons reveal that the difference between tangential and mixed conditions is not significant in the younger group ($t_{26} = 0.19$, $p = 0.852$), but it is for older participants ($t_{26} = -3.74$, $p = 0.001$). Additionally, *post-hoc* comparisons indicate a statistically significant difference between groups in the mixed ($t_{26} = -4.98$, $p < 0.001$) but not in the tangential condition ($t_{26} = -1.58$, $p = 0.127$).

Taken together, these results suggest that ageing affects the ability to discard irrelevant orientation information along the contour, but not the capacity to integrate local elements into global structures.

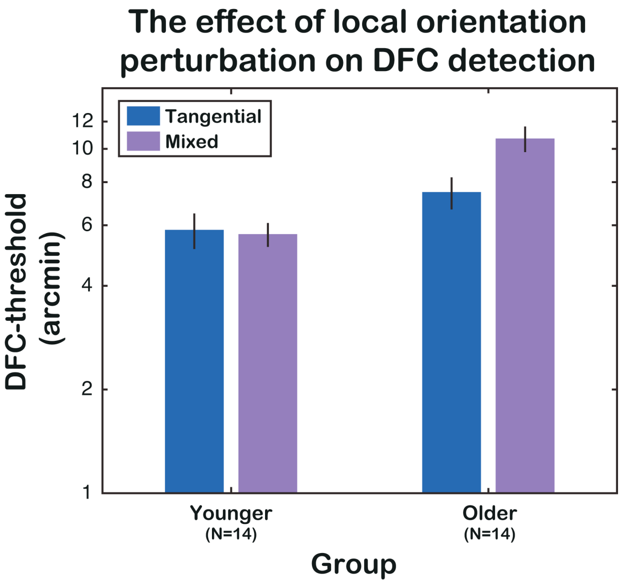

Figure 26. Mean DFC-thresholds in the tangential (blue bars) and mixed conditions (violet bars) for younger (*left*) and older observers (*right*). Only older observers are strongly affected by the perturbation of co-alignment of local elements along the contour-path. Note that thresholds in the tangential condition do not differ between groups, suggesting that ageing affects the ability to discard irrelevant orientation information along the contour, but not the capacity to integrate local elements into global structures.

Spatial suppression

Figure 27 presents mean DFC-thresholds in the *tangential* and *noise* conditions for younger and older observers. The ANOVA on the threshold-values from the tangential and noise conditions shows a significant effect of the factor *group* ($F_{1,26} = 8.95$, $p = 0.006$), indicating a general increase in thresholds with ageing. Also the effect of the factor *stimulus condition* is significant ($F_{1,26} = 17.90$, $p = 0.001$), indicating that thresholds are generally affected by the presence of background-noise. The interaction between the two factors is also significant ($F_{1,26} = 5.52$, $p = 0.027$). *Post-hoc* comparisons indicate that the presence of background-noise significantly increases thresholds in the older group ($t_{26} = -4.65$, $p < 0.001$) but not in the younger group ($t_{26} = -1.33$, $p = 0.195$). Furthermore, an interesting result can be observed at the largest DFC-level. Indeed, although both groups are generally affected by the presence of background-noise, only older observers are strongly impaired at the largest DFC-level: t-tests on detection probability-values show indeed that the difference between the tangential and noise conditions at the largest DFC-level is non-significant in the younger group ($t_{13} = 1.22$, $p = 0.246$) but it is significant in the older group ($t_{13} = 4.88$, $p = 0.001$).

Taken together, these results suggest that ageing affects the ability to suppress local *false matches*, which may arise between contour- and background-elements (possibly in the first stage of the two-stage process we proposed in Study 2).

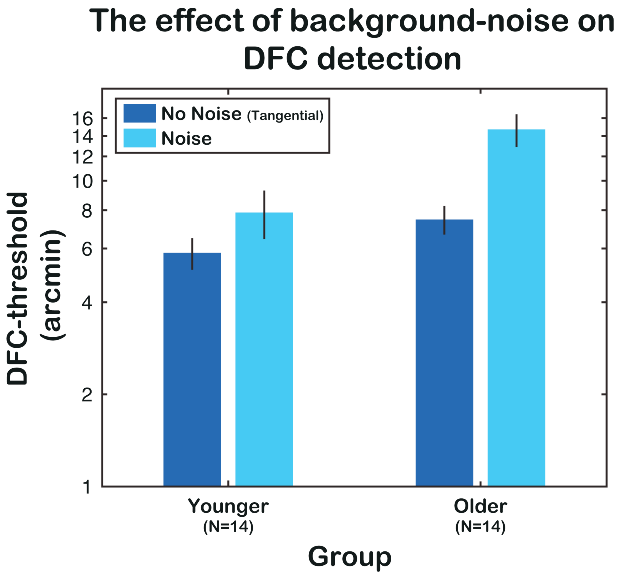

Figure 27. Mean DFC-thresholds in the tangential/no noise (blue bars) and noise conditions (light blue bars) for younger (left) and older observers (right). Only older observers are strongly affected by the presence of background-noise. This result suggests an effect of ageing on the ability to suppress *false matches*, which may arise between contour- and background-elements.

GENERAL DISCUSSION

Taken together, results of the third study indicate a disruptive effect of background-noise on older observers' ability to detect the DFC in a disconnected contour. Additionally, older observers' performance is impaired if elements not co-aligned with the path are present along the contour. These findings are consistent with an effect of ageing on the ability to suppress local *false matches* that may arise between contour- and background-elements as well as on the capacity to discard irrelevant orientation information along the contour. However, ageing does not affect the ability to integrate contours (thresholds in the tangential condition do not differ between groups).

Spatial integration

Results of Experiment 8 show that older observers are strongly impaired in detecting the DFC when the contour contains mixed orientations. Nevertheless, performance of the two groups does not significantly differ when only tangential Gabors define the circular contour. These results are relevant to the issue of whether ageing affects the efficiency of integrative operations and whether this effect might depend on reduced orientation discrimination.

In order to be integrated, oriented elements lying along a curved contour have to stimulate cells with relative orientations and spatial positions that optimize their encoding of the contour [Field & Hayes, 2004]. This means that the association of one cell with another is strong not only along the axis given by the cell's orientation but also along a curved contour, as long as the orientation of the two cells is tangential to the contour. In this case, an association field is formed that integrates the response of the two cells through excitatory connections. This is possible for orientation differences up to ±60° among elements along the contour. Conversely, if oriented elements lying along the contour stimulate cells with relative orientations and positions that do not optimize their encoding of the contour, inhibitory connections are activated [Field & Hayes, 2004; Heeger, 1992]. The "association field model" [Field *et al.*, 1993] predicts detection of curved contours but does not account for the difference between open and closed contours. Closed contours are better detected than open contours [Kovacs & Julesz, 1993]. Moreover, the integration of elements lying along a closed contour tolerates larger inter-element distances than the integration of elements along an open contour [Kovacs & Julesz, 1993]. Finally, for closed contours integration occurs with as few as four/five tangential signal elements, even when there are, as in our stimuli, four noise elements with non-tangential orientation between each pair of tangential elements along the contour [Achtman *et al.*, 2003; Keeble & Hess, 1999; Levi & Klein, 2000; Loffler, 2008].

To account for the relative insensitivity to the perturbation of local orientations in younger observers, some authors have suggested that the detection of circular contours involves the comparison of the centroid of the contrast envelope, which does not vary with Gabor orientation [Hess & Holliday, 1996]. Performance in our task could be based on this strategy. However, if older observers were less efficient in using this centroid-based strategy, they should be impaired also in the tangential condition. Another plausible explanation for the insensitivity to local orientation perturbations could rely on the activation of a *shape-specific mechanism* that integrates relevant orientations along the closed contour, while discarding interposed non-tangential (therefore irrelevant) orientations. This mechanism may involve extrastriate areas in the ventral stream [Pasupathy & Connor, 2001]. The specific impairment in the mixed condition indicates that ageing may reduce the efficiency of this shape-specific mechanism. However, it is unlikely that this impairment is the consequence of older observers requiring more than four relevant orientations. Although it has been claimed that older observers need more elements for shape-integration [Del Viva & Agostini, 2007; McKendrick *et al.*, 2010], the evidence produced is not indisputable. Indeed, Del Viva and Agostini [2007] found a group difference in the slope of the linear regression line fitting average sensitivity data as a function of the number of elements in the target. The shallower slope they observed for older adults reflects a lower rate of sensitivity improvement as the number of elements increases. Importantly, McKendrick *et al.* [2010] found that thresholds (i.e. the minimum number of contour-elements required for shape-discrimination) were very similar in the two groups and did not differ from those of four/five elements needed to activate a shape-specific mechanism [Loffler, 2008].

With these results in mind, here we propose that ageing affects the ability to discard non-relevant orientations along the contour, but not the efficiency of integrative operations.

Spatial suppression

The comparison between the results obtained in the tangential and noise conditions indicates that older observers are more impaired than younger participants in detecting the DCF when background-noise surrounds the contour. Additionally, at the largest DFC-level only older observers are significantly impaired, indicating that they do not take advantage of the largest Gabor-displacement. We suggest that this is because although Gabors with large displacements from the circular contour are easily detected, they are also easily embedded in the background-noise. This “masking effect” is higher in older observers because of reduced suppression of local false matches between contour- and background-elements.

Reduced suppression of local false matches or lower efficiency in detecting local density irregularity?

The presence of a displaced Gabor in the display creates a local density irregularity in that location. As such, rather than a reduced suppression of local false matches between contour- and background-elements, higher DFC-thresholds in the older group may indicate reduced efficiency in detecting which interval contains a local density irregularity.

To check for this second possibility we performed a control experiment with stimuli made of randomly oriented Gabors that were placed along three circles. Specifically, we modified the stimuli used in the noise condition of the main experiment, by randomizing the orientation of the element that defined our circular contour (without changing their position). As before the independent variable was the DFC-level. Procedure was as in the main experiment. We asked six younger observers (who did not participate in the main experiment) to indicate (2I-2AFC task) in which of the two presentations there was a density irregularity. To test whether accuracy was significantly different from 50% (chance level), we performed a t-test for each DFC-level. Results show that accuracy was never different from chance ($t_5 = 1.94$, $p = 0.111$; $t_5 = 0.00$, $p = 1.000$; $t_5 = 1.28$, $p = 0.256$; $t_5 = 0.47$, $p = 0.661$; $t_5 = 2.10$, $p = 0.090$ for DFC-levels equal to 1.5, 5.9, 10.3, 14.8, and 19.2 arcmin, respectively). These results rule out the possibility that higher DFC-thresholds for the older group in the noise condition indicate lower efficiency in detecting which interval contains the local density irregularity.

Suppressive mechanism, attention, or working memory?

To summarize, we have shown that ageing reduces the ability to suppress local false matches between contour- and background-elements as well as the efficiency in discarding irrelevant information along the contour. These results suggest an age-dependent reduction in the efficiency of an inhibitory circuitry, which likely relies on short-range inhibitory connections [Das & Gilbert, 1999]. Neurophysiological studies in cats and monkeys provide indirect support for this suggestion. These studies show reduced lateral inhibition as well as increased spontaneous activity in senescent V1 neurons selective for orientation and direction of motion [Hua *et al.*, 2006; Schmolesky *et al.*, 2000]. Those changes might result from reduced GABA-mediated inhibition [Leventhal *et al.*, 2003]. This could specifically affect the suppression of local false matches (and possibly also the discard of irrelevant information along the contour), while leaving the integrative mechanism unperturbed. Indeed, the intra-cortical interactions, which underlie these visual operations, are different. Specifically, the majority of the postsynaptic excitatory effects – amongst which are those supporting contour-integration – results from long-range intra-cortical interactions [Field & Hayes, 2004; Heeger, 1992]. Inhibitory effects – which may support the suppression of local false matches between contour- and background-elements and possibly also the discard of irrelevant information along the contour – are instead mediated by short-range intra-cortical inhibitory interactions between GABA-ergic cells [Das & Gilbert, 1999].

It is also interesting to speculate whether our data can be explained by declining attentional capacity with age. Attentional factors cannot be excluded because they may affect the relatively low-level perceptual operations investigated here. Indeed, it has been demonstrated that attention modulates both facilitatory and inhibitory contextual influences on contour integration and segmentation [Casco *et al.*, 2005; Kourtzi & Huberle, 2005] and exclusion of distracters [Cameron, Tai, Eckstein, & Carrasco, 2004]. Declining attentional capacity with age should negatively affect all conditions tested in the present study and not only mixed and noise conditions. Thus, the reduction of attentional resources with age cannot be the only explanation for our findings. Similarly, differences in working memory cannot account for our results; indeed a general effect on all conditions tested should have emerged.

CONCLUSION

To conclude, we suggest that in older observers reduced inhibitory intra-cortical lateral connections may account for the increased disruptive effect of background-noise. In particular, the reduction in the efficiency of an inhibitory circuitry would result in lower ability to suppress local false matches that may arise between contour- and background-elements. A deficit in intra-cortical inhibition can also account for the reduced performance of a shape-specific mechanism that integrates only a few relevant local elements along a contour while discarding non-relevant ones.

STUDY 4: CONTOUR-LOCALISATION AND CONTEXT PROCESSING IN SCHIZOPHRENIA[††]

INTRODUCTION

Convergent evidence from psychophysics, electrophysiology and functional brain imaging indicates that people with schizophrenia (SZ) exhibit persistent deficits in visual processing (for review see [Butler *et al.*, 2008]). Patients show poorer detection of low compared to high spatial frequency (SF) gratings (for review see [Keri, Antal, Szekeres, Benedek, & Janka, 2002; Slaghuis, 1998]), a finding that is mirrored in patients exhibiting noisier visual evoked potentials (VEPs) in response to low SF stimuli [Butler, Martinez, Foxe, Kim, Zemon, Silipo, Mahoney, Shpaner, Jalbrzikowski, & Javitt, 2007; Butler, Zemon, Schechter, Saperstein, Hoptman, Lim, Revheim, Silipo, & Javitt, 2005]. Such findings have sometimes been attributed to a selective deficit in the magnocellular visual pathway (although see e.g. Skottun and Skoyles [2011]).

Another way in which contrast-processing differs in SZ is in the effect of *context*. Dakin, Carlin and Hemsley [2005] showed that the dramatic reduction in perceived contrast of a target-patch that occurs when it is embedded in a high contrast background [Chubb, Sperling, & Solomon, 1989] is greatly reduced in patients with SZ. That patients are less prone to this illusion results in superior (less biased) performance and allows one to be confident that this is a consequence of a particular mechanism (rather than poorer performance, which could reflect e.g. general attentional deficit). Dakin *et al.* [2005] interpreted this finding as a manifestation of decreased *gain control*, the inhibitory

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[††] Based on **Robol, V.**, Anderson, E.J., Tibber, M.S., Bobin, T., Carlin, P., Shergill, S., Dakin, S.C. (In Prep) Reduced crowding and poor contour detection in schizophrenia are consistent with weak surround inhibition. *Neuron*.

cortical processes that allow neurons to optimise their limited operating range. Reduced centre-surround interactions on perceived contrast have been replicated [Barch *et al.*, 2012; Yoon *et al.*, 2009] and have also been observed for motion processing [Tadin *et al.*, 2006] and for the processing of size [Uhlhaas *et al.*, 2006a; Uhlhaas *et al.*, 2006b] and orientation [Dakin *et al.*, In Prep]. The ubiquitous nature of gain control in human visual processing means that it could provide a coherent framework for understanding the wide range of perceptual deficits observed in SZ [Dakin *et al.*, 2005].

In a similar vein it has also been proposed that impaired *cognitive coordination* underlies various deficits in the processing of visual context in SZ [Phillips & Silverstein, 2003]. Cognitive coordination refers to those processes involved in modulating the salience of visual structure – e.g. through changes in the timing of neural signals – and is manifest through phenomena labelled e.g. selective attention and, in particular, *grouping*. Grouping refers to the rules governing the perceptual association of simple local-features into more complex global-structures (e.g. Wertheimer [1923]). The balance of evidence suggests that people with SZ have a deficit in visual grouping compared to unaffected controls (reviewed in Uhlhaas and Silverstein [2005]). In particular people with SZ have difficulty with tasks that require integration to reveal global spatial form [Doniger, Silipo, Rabinowicz, Snodgrass, & Javitt, 2001; Kimhy, Corcoran, Harkavy-Friedman, Ritzler, Javitt, & Malaspina, 2007; Silverstein *et al.*, 2000] or global motion (for review see Chen [2011]) including biological motion [Kim, Park, & Blake, 2011] and the inference of causality [Tschacher & Bergomi, 2011]. This deficit can again lead to *superior* performance in SZ – for example, at ignoring the presence of irrelevant groupings when enumerating line segments [Place & Gilmore, 1980] – ruling out a more generalised explanation based on e.g. an attentional deficit.

Here we focus on two tasks involving the perception of orientation. The first is c*ontour integration*: the linking of the oriented elements of a contour across space (for review see Hess and Field [1999]). This is probed using a psychophysical paradigm where the observer must detect a contour composed of discrete oriented patches (Gabors), embedded in an array of randomly oriented distractor-elements (Figure 28a for an example; Field, Hayes et al. [1993]). This paradigm has been used to uncover the rules governing linkage; e.g. that it is tuned for the SF of elements [Dakin & Hess, 1998; Hess & Dakin, 1999] and is much cruder in the peripheral visual field, apparently relying on the output of large spatial filters [Hess & Dakin, 1997]. Furthermore, the immediate *context* that a contour arises in matters: observers have more difficulty finding contours embedded in distractors that are near-parallel than near-perpendicular to the local contour orientation [Dakin & Baruch, 2009; Robol, Casco, & Dakin, Under Review]. Contour integration paradigms have proven invaluable for probing the specific nature of the grouping deficit in SZ. Patients require closer spacing of elements to detect contours [Silverstein, Hatashita-Wong, Schenkel, Wilkniss, Kovacs, Feher, Smith, Goicochea, Uhlhaas, Carpiniello, & Savitz, 2006; Silverstein *et al.*, 2000; Uhlhaas *et al.*, 2006a; Uhlhaas *et al.*, 2006b] assessed using contour card system [Kovacs, Polat, Pennefather, Chandna, & Norcia, 2000]. This deficit has been linked to a specific subtype of SZ characterized by thought disorder (as assessed using the positive and negative syndrome scale, PANSS [Kay, Fiszbein, & Opler, 1987]). These deficits are particularly manifest for tasks where top-down cognitive control is required [Silverstein *et al.*, 2006].

The collapse in our ability to see complex/curved contours in the periphery [Hess & Dakin, 1997] relates to the second visual phenomenon we consider: *crowding*. Crowding refers to the disruptive effect of “clutter” (task-irrelevant flanking features) on our ability to recognise target-objects (for review see Whitney and Levi [2011]). Crowding can affect our ability to determine the local orientation of features, with observers making reports that are consistent with the target-orientation having been averaged with the orientation of the flankers [Parkes *et al.*, 2001]. Crowding of orientation is more pronounced within contours [Livne & Sagi, 2007] leading some to propose that crowding is contour grouping “gone awry” [Dakin *et al.*, 2010; Livne & Sagi, 2007, 2010; May & Hess, 2007]. Recently we have linked crowding to the effects of context on contour integration [Robol *et al.*, Under Review]. These results accord with the notion that spurious grouping of background-elements – with one another and with the contour-elements – is the primary limitation on contour grouping rather than the limits of a particular model *per se* [Watt *et al.*, 2008]. In short the balance of evidence is that performance on contour integration tasks reflects an inter-play of limits set by visual integration (of contour elements) and interactions of individual elements with their surrounding context. Such interactions can improve or interfere with contour-localisation, with interference effects being in part attributable to crowding.

With that in mind, the contour-grouping deficit in SZ has largely been attributed to differences in integration. In this paper we explore how abnormal processing of *visual context* may contribute to patients' poor performance with tasks involving visual contour integration. We begin by assessing people with SZ's ability to localise contours in the presence of random variation in the local orientation of path-elements and how their performance is affected by the presence of contextual information that either helps or hinders performance in healthy controls [Dakin & Baruch, 2009; Robol *et al.*, Under Review]. As well as replicating previous deficits in contour-localisation, we find that while near-perpendicular surrounds facilitate localisation in both patients and controls, near-parallel surrounds disrupt performance less in the clinical than in the unaffected group. The second experiment explores the idea that this pattern of performance could arise from differences in the way local elements of the stimuli are processed. In particular, based on our previous results [Robol *et al.*, Under Review] showing that the disruptive effect of near-parallel surrounds may in part be attributed to contours (frequently) falling in the peripheral field where recognition is prone to *visual crowding*, we tested the paradoxical prediction that patients should show less crowding of local contour-elements. We show that patients are poorer at reporting local orientation – of isolated Gabor elements – but show proportionally less crowding from flanking elements. Taken together these results indicate that differences in processing of surrounding context contribute significantly to the contour integration deficit in SZ. The influence of weaker contextual interactions could be direct – e.g. reduced ability to use context to localise contours – or indirect – e.g. leading to broader tuning for orientation in primary visual cortex, which in turn would reduce sensitivity to local orientation.

Experiment 9

Contour-localisation and sensitivity to context

Several studies have reported poor contour detection in people with SZ [Kozma-Wiebe, Silverstein, FehÈr, Kovacs, Ulhaas, & Wilkniss, 2006; Schenkel, Spaulding, DiLillo, & Silverstein, 2005; Schenkel, Spaulding, & Silverstein, 2005; Silverstein, Berten, Essex, Kovacs, Susmaras, & Little, 2009; Silverstein *et al.*, 2006; Silverstein *et al.*, 2000; Uhlhaas *et al.*, 2006a; Uhlhaas *et al.*, 2006b; Uhlhaas, Phillips, & Silverstein, 2005], a deficit largely attributed to differences in integration. In Experiment 9 we tested the hypothesis that poor contour detection may be related to differences in the processing of context. To this end we measured SZ people's performance in localising contours embedded in different surrounds. Specifically, we assessed whether patients were affected by the presence of contextual information that either helped or hindered performance in healthy controls [Dakin & Baruch, 2009; Robol *et al.*, Under Review].

Methods

Observers

Participants were 18 patients [12 males; mean age 39.2 years (σ = 8.0 years); mean IQ 104.3 (σ = 9.3)] diagnosed with schizophrenia (1 male and 2 females) or paranoid schizophrenia (15 patients). All were diagnosed independently of this study according to DSM-IV criteria. IQ was assessed with the *Revised National Adult Reading Test* (NART [Nelson & Willison, 1991]) and patients' clinical state was evaluated with the *Positive and Negative Syndrome Scale* (PANSS [Kay *et al.*, 1987]). Sixteen patients were treated with atypical antipsychotics, one with typical antipsychotics and one was unmedicated. The non-clinical control group comprised 12 male and 6 female participants recruited from university offices [mean age 40.7 years (σ = 9.4); mean IQ 109 (σ = 9.3)]. The two groups did not differ significantly for age ($t_{34} = -0.51$, $p = 0.611$) or for IQ ($t_{34} = -1.51$, $p = 0.141$).

Apparatus

Experiments were run on an Apple MacBook computer under the Matlab programming environment (MathWorks, Natick, MA) and incorporated elements of the Psychophysics Toolbox extensions [Brainard, 1997; Kleiner *et al.*, 2007; Pelli, 1997]. Stimuli were presented on CRT monitors (LaCie [Paris, France] Electron Blue 22″ and Sony [Tokyo, Japan] Trinitron Multiscan E400 19″). Both monitors were calibrated with a Minolta photometer and linearized using custom-written software, giving a mean and maximum luminance of 50 and 100 cd/m^2, respectively. In both cases the display resolution was 1024 x 768 pixels and the refresh rate was 75 Hz.

Stimuli

Test stimuli (Figure 28) consisted of contours composed of seven spatial-frequency band-pass Gabor micro-patterns (Gabors co-aligned with an underlying contour-spine), embedded in a field of distracter-Gabors [Field *et al.*, 1993]. The separation of contour elements was 56 arcmin and the whole-stimuli subtended a 12.8x12.8 deg. square containing on average 220 elements ($\sigma = 3.9$ elements). All elements were in cosine phase, had a peak spatial frequency of 3.75 c/deg with an envelope σ of 5.7 arcmin, and were presented at 95% contrast.

Stimuli were generated as in Robol *et al.* [Under Review]. In brief, we used standard contours with a 15° path angle where the sign of the orientation difference between subsequent elements was randomised. As before, stimuli were manipulated so that contour-elements were clearly located in either the left or the right half of the image. This was achieved by forcing the middle contour-element to (a) pass through a region within ±0.53 deg. of the centre of a given image-half and (b) to have an orientation within ±45° of vertical. Further, no single contour-element could pass within 0.9 deg. of the edge of the image; nor could the contour cross itself.

Stimuli were made by first inserting two contours – one in the left and one in the right half of the image – and then dropping distracter-elements on to the background. A minimum inter-element separation of 40 arcmin was maintained, thereby matching the mean-distance of any element – within contour or background – to its nearest neighbour. The orientation of distracter-elements was manipulated to obtain three surround conditions: *random*, *near-parallel* and *near-perpendicular* (Figure 28). We used the inverse of the Gaussian function (σ = 1.0 deg.) of the distance between distracters and contour-elements to set the orientation of distracter-elements – offset by 0° (near-parallel) or 90° (near-perpendicular). In the random condition (our baseline) the orientation of the distracting surrounding-elements was randomised.

At this stage of the stimulus generation procedure we have an image containing two contours, one on either side of fixation, for which the distracter-elements surrounding each have been subjected to the same contextual constraints (w.r.t. the contour on each side). We subsequently made our "random contour" by simply randomising the orientation of the elements within one of these contours. The observers' task was then to report the side of the image containing the structured contour. Figure 28 shows an example (with the contrast of surround reduced for the purpose of illustration).

Prior to stimulus presentation we jittered the orientation of the elements within the structured contour. We did this by generating Gaussian random offsets with a standard deviation in the range 0-90° (note that this is the generating standard deviation – the true/wrapped standard deviation will be lower). A generating Gaussian standard deviation of 90° will produce a near-isotropic distribution of orientations. The level of orientation-jitter was under control of an adaptive staircase procedure (QUEST [Watson & Pelli, 1983]), as described in the *Procedure* section below. The orientation of distracter-elements was not modified further based on the new (noisy) contour orientation structure. Thus, in the near-parallel condition for example, the immediate surround was near-parallel to the contour-spine even if the orientation of each contour-element had been drastically altered.

Stimulus presentation was immediately followed by a mask composed of a field of randomly oriented elements (with on average the same number and separation of Gabors as the test stimulus). This display persisted until observers gave a response.

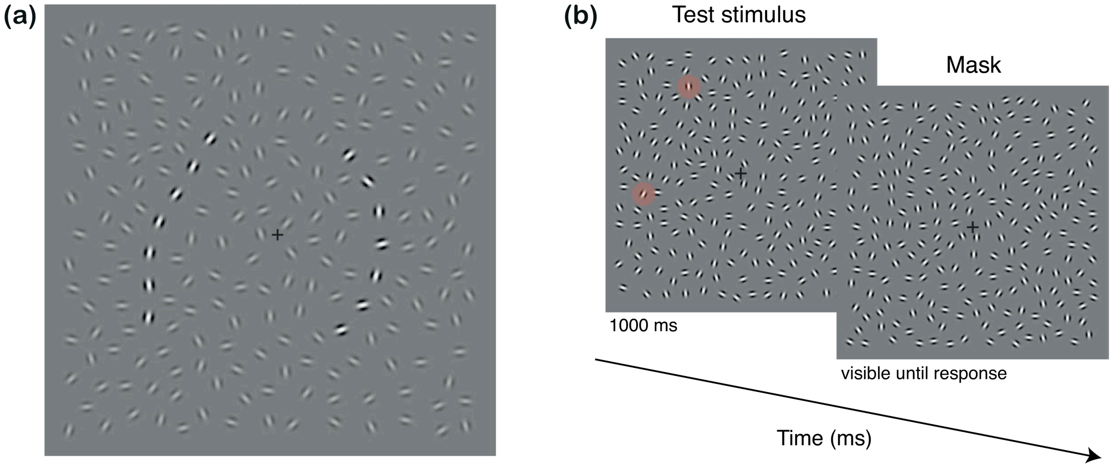


Figure 28. An example of the stimuli from Experiment 9 (with the contrast of distracters reduced for illustrative purposes). Observers had to report which side of the image contained a structured contour. In this case the contour is surrounded by near-perpendicular elements, which generally enhance detectability. Note that the random path on the right was generated in essentially the same way as the structured contour – except that the orientation of path-elements was randomised prior to presentation. Because of this the orientation of distracters surrounding the random-path is comparable to the context of the structured contour in that elements are near-perpendicular to the contour-spine used to *generate* the random path.

Design

The experiment had a within-subjects design. The independent variable was the orientation offset of the contour’s immediate context, defined as the mean orientation of the surrounding-elements relative to the contour-spine. We tested three levels of orientation offset: 0° (surrounding elements near-parallel to the contour-spine), 90° (surrounding elements near-perpendicular to the contour-spine), and random (surrounding elements randomly oriented). The dependent variable was the maximum orientation-jitter along the contour-path supporting 75% correct contour-localisation (*threshold orientation-jitter*, see *Procedure*).

Procedure

Stimuli were viewed binocularly at a distance such that the whole-stimuli subtended 12.8x12.8 deg. square (129 and 116 cm for the LaCie and Sony monitors, respectively). Observers fixated a centrally presented marker during presentation of test and masking stimuli. We monitored eye position during the experiment; observers were able to maintain good fixation. Participants were presented a test stimulus (for a fixed exposure-duration of 1000 ms) containing a structured and a random contour embedded within distracter-elements and located right and left of the fixation marker. This screen was immediately followed by a mask, which contained randomly oriented Gabors and remained on the screen until observers gave a verbal response to the question "Which side of the stimulus contained the contour?". We selected a relatively long fixed exposure-duration of 1000 ms because pilot experiments revealed that the minimum exposure-duration for experienced observers to perform contour-localisation at 75% correct with high level of orientation-jitter (~15°) was around this value. The orientation variability along the contour-path was controlled by an adaptive staircase procedure (QUEST [Watson & Pelli, 1983]) with correct and incorrect responses causing respectively an increase and a decrease in orientation variability. The procedure converged on the orientation variability that led to 75% correct contour-localisation. We refer to this measure as the *threshold orientation-jitter*. Observers completed at least three runs of 135 trials each (45 trials per surround condition). In this way, for each observer we obtained the mean threshold orientation-jitter in each surround condition over at least 135 trials. Each run comprised all three surround orientation conditions (random, near-parallel, near-perpendicular). Before data collection every observer completed a practice session with doubled exposure-duration. In addition, all observers gave informed written consent in accordance with the Declaration of Helsinki.

Statistical analysis

To test the effect of context on contour-localisation and whether this was different in patients and healthy controls, we first carried out a repeated-measures analysis of variance on threshold-values (which are a measure of tolerance to orientation-jitter), with *group* (patients, controls) as between-subjects factor and *condition* (random, near-parallel, near-perpendicular) as within-subjects factor. To examine whether SZ patients showed less *inhibition* from the surround we then calculated log-ratios between thresholds with organized and random surrounds (i.e. log[near-parallel/random] and log[near-perpendicular/random]) and carried out a repeated-measures analysis of variance on these values, with factors *group* (patients, controls) and *condition* (near-parallel, near-perpendicular). P-values for all *post-hoc* t-tests have been corrected for multiple comparisons using the Bonferroni procedure and corrected p-values are reported. Alpha-value was set to 0.05 for all statistical tests.

Results and discussion

Figure 29a presents results from Experiment 9 for patients (red) and non-clinical controls (blue). Graphed data are *thresholds orientation-jitter* measured with random, near-parallel and near-perpendicular surrounds. Note that these thresholds represent a measure of tolerance to orientation-jitter along the contour-path. This means that the higher the number the more orientation-jitter observers tolerate and the better their performance. Analysis of variance on threshold-values shows a significant main effect of *group* ($F_{1,34}$ = 22.73, $p < 0.001$) and *condition* ($F_{2,68}$ = 122.56, $p < 0.001$) as well as a significant interaction ($F_{2,68}$ = 12.73, $p < 0.001$). *Post-hoc* comparisons show a significant difference between patients and controls only in the random (t_{34} = 4.34, $p < 0.001$) and in the near-perpendicular surround conditions (t_{34} = 5.44, $p < 0.001$). That in the baseline condition (random surround) patients have lower thresholds than healthy controls (their tolerance is halved compared to controls: mean tolerance (± SE) is 4.11° ± 0.74° vs. 9.99° ± 1.14°) indicates generally poor contour-localisation in SZ people. In addition, *post-hoc* comparisons indicate a different relative effect of near-parallel but not near-perpendicular surrounds in the two groups. Near-perpendicular surrounds increase tolerance (compared to the random surrounds) both in controls (19.97° ± 0.69° vs. 9.99° ± 1.14°, t_{17} = 10.03, $p < 0.001$) and patients (11.23° ± 1.45° vs. 4.11° ± 0.74°, t_{17} = 6.10, $p < 0.001$). On the contrary, near-parallel surrounds decrease tolerance in controls (4.91° ±

0.78° vs. 9.99° ± 1.14°, $t_{17} = -5.03$, $p < 0.001$), but not in patients (3.69° ± 0.96° vs. 4.11° ± 0.74°, $t_{17} = -0.453$, $p > 1$).

These data may suggest the presence of less *inhibition* from the surround (which may also be consistent with increased *facilitation*) in SZ patients compared to healthy controls. To examine this prediction we performed a repeated-measures analysis of variance on log-ratios between thresholds with organized and random surrounds (as described in the *Methods* section). Note that log-ratios = 0 means no effect of organized surround, log-ratios < 0 indicate worse performance with organized than random surrounds (consistent with increased *inhibition* from the surround), and log-ratios > 0 reflect better performance in the presence of organized than random surrounds (consistent with reduced *inhibition* or even *facilitation* from the surround).

As shown in Figure 29b and confirmed by the ANOVA results, in both groups log-ratios with perpendicular surrounds are positive and higher than with parallel surrounds (significant main effect of the factor *condition*, $F_{1,34} = 114.94$, $p < 0.001$, one-tailed), consistent with facilitation from perpendicular surrounds. Additionally, log-ratios are generally higher in patients than controls (significant main effect of the factor *group*: $F_{1,34} = 3.26$, $p = 0.040$, one-tailed). Note this effect is likely to be weakened by the fact that patients exhibit significantly higher log-ratios compared to controls only in the near-parallel condition ($t_{34} = -1.83$, $p = 0.038$, one-tailed). No significant interaction was observed ($F_{1,34} = 1.08$, $p = 0.153$, one-tailed), consistent with performance in the two surround conditions being affected in the same way by the factor *group*.

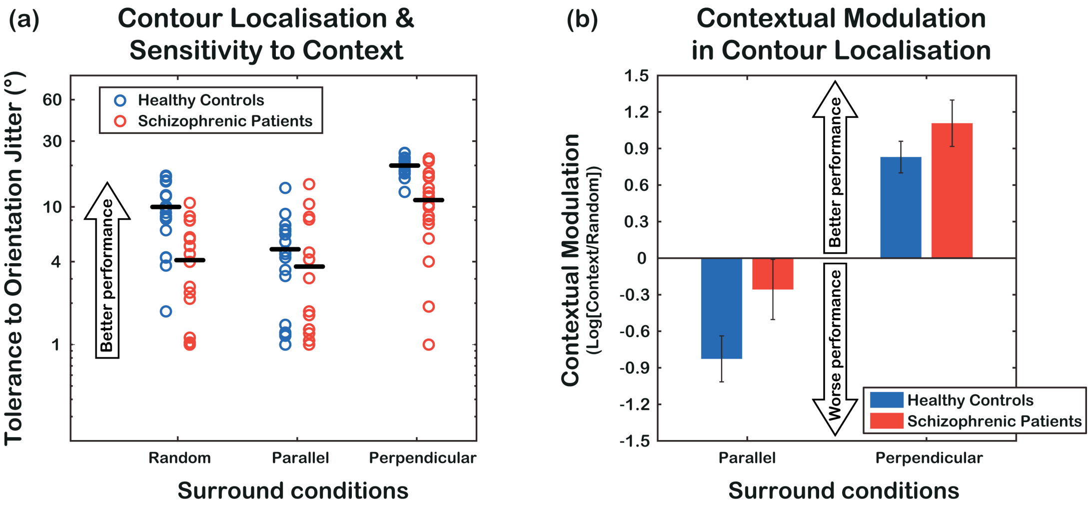


Figure 29. (a) Tolerance to orientation-jitter for SZ patients (red) and healthy controls (blue), measured with random, near-parallel and near-perpendicular surrounds. Black horizontal lines represent mean tolerance. Patients generally tolerate less orientation-jitter than controls and are not affected by near-parallel surrounds. (b) Log-ratios between tolerance with organized and random surrounds (i.e. log[near-parallel/random] and log[near-perpendicular/random]). Patients show less disruption from near-parallel surrounds compared to controls.

Taken together, results for controls confirm our previous findings [Dakin & Baruch, 2009; Robol *et al.*, Under Review], showing facilitation (higher tolerance) from near-perpendicular surrounds and suppression (lower tolerance) from near-parallel surrounds. The pattern of results for SZ patients indicates poor contour-localisation and an *abnormal* processing of context. Indeed, although patients are poor at localising the contour embedded in random surrounds, they are also proportionally less disrupted by the presence of near-parallel surrounds than healthy controls. It is not the case that people with SZ are generally less influenced by any contextual information since they exhibit as much facilitation by near-perpendicular surrounds as healthy controls. Consistent with earlier findings [Place & Gilmore, 1980] we find that differences in context-processing in SZ can impact on form detection in a positive way: in the near-parallel surround condition we see less disruption in the SZ group. A reduced influence of near-parallel surrounds is generally consistent with earlier reports of reduced surround suppression [Barch *et al.*, 2012; Dakin *et al.*, 2005; Tadin *et al.*, 2006; Uhlhaas *et al.*, 2006a; Uhlhaas *et al.*, 2006b; Yoon *et al.*, 2009] although earlier results focused on the processing of contrast.

Previously Robol, Casco *et al.* [Under Review] have shown that the disruptive effect of near-parallel surrounds may in part be attributed to contours (frequently) falling in the peripheral field where recognition is prone to *visual crowding* (the disruptive effect of clutter on object recognition). This notion leads to the paradoxical prediction that patients should be less affected by the disruptive influence of distracter-elements on object recognition in the periphery (a paradigm known as *visual crowding*). In particular, patients should show less crowding of *local* contour-elements by surrounding-elements. Experiment 10 directly examines this prediction, by measuring orientation discrimination in isolated and crowded stimuli.

Experiment 10

Local processing of orientation in isolated and crowded stimuli

Previous studies [Carter, Robertson, Nordahl, Chaderjian, & Oshora-Celaya, 1996; Granholm, Perry, Filoteo, & Braff, 1999] have reported local processing deficits in SZ, manifested both in slower detection and in poorer discrimination of local compared to global targets. In Experiment 10 we tested whether the pattern of contour-detection performance reported in Experiment 9 could arise from differences in the way local elements of the stimuli are processed. In particular, we tested the prediction that patients should show less crowding of the local components of our contours by surrounding-elements. We did this by measuring observers' local processing of orientation in isolated and crowded stimuli. Observers reported if the orientation of either an isolated Gabor or a Gabor presented with two flankers (Figure 30) was clockwise or anticlockwise of vertical. Stimuli were of a similar size, eccentricity and (where applicable) spacing, to the contour-elements in Experiment 9.

Methods

Observers

Thirteen of the SZ patients (and their matched healthy controls) of Experiment 9 also participated in Experiment 10.

Apparatus

We used the same apparatus and display parameters as in Experiment 9.

Stimuli

In Experiment 10 we used Gabors with the same parameters as those in Experiment 9 (cosine phase, peak spatial frequency = 3.75 c/deg, envelope σ = 5.7 arcmin, 95% contrast). The target for the orientation judgement (clockwise or anticlockwise of vertical) was a Gabor presented in the parafovea (either upper or lower side of the screen, 3.2 deg. eccentricity), with or without similar flankers (Figure 30).

We tested three conditions: *isolated Gabor*, *random flankers*, *contour-fragment*. In the *isolated Gabor* condition, the target element was presented at an eccentricity of 3.2 deg. either above or below the fixation cross. When there were flankers (*random flankers* and *contour-fragment* conditions), Gabor elements' separation was 56 arcmin (so matching the contour-elements' separation used in Experiment 9). In the *random flankers* condition two randomly oriented similar elements flanked the isolated Gabor. Flankers were on the same horizontal axis as the target Gabor. In the *contour-fragment* condition we added two Gabors laying on a contour-spine defined using a vertical target orientation, thus forming a contour-fragment (vertically oriented). In this way flanker-orientation and position were not informative of the target orientation. Path angle was 15°, with the sign of the orientation difference between subsequent elements randomised.

We manipulated the target tilt (clockwise or anticlockwise of vertical), pre-selecting seven appropriate tilt values to fit psychometric functions (see *Design* section below). These values were selected based on pilot data that indicated they bracketed the psychometric function for observers tested under these conditions of crowding.

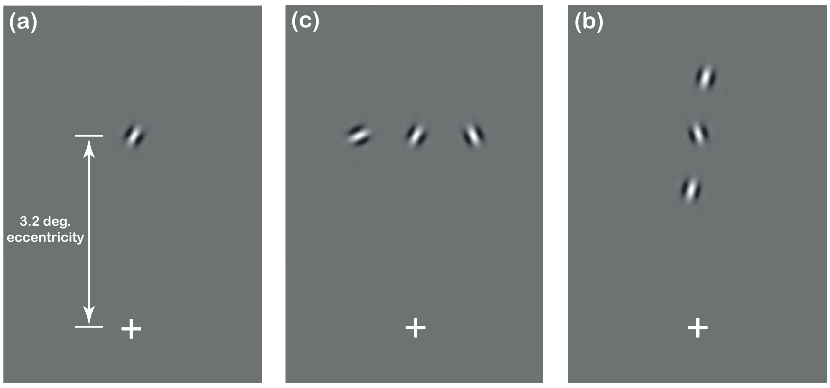


Figure 30. Examples of the stimuli from Experiment 10, where observes had to judge the orientation of the central Gabor (clockwise or anticlockwise of vertical). (a) Isolated target condition. (b) Random-flankers condition. (c) Contour-fragment condition.

Design

We used a within-subjects design and tested three conditions: (i) isolated target, (ii) target plus 2 randomly oriented flankers, (iii) contour-fragment. In each condition the independent variable was the degree of tilt of the target set according to a method of constant stimuli with seven levels: -6°, -4°, -2°, 0°, +2°, +4°, +6° (in the isolated Gabor condition), -9°, -6°, -3°, 0°, +3°, +6°, +9° (in the random-flankers condition) and -45°, -30°, -15°, 0°, +15°, +30°, +45° (in the contour-fragment condition). The dependent variable was the probability to report that the target was tilted clockwise of vertical.

Procedure

Stimuli were viewed monocularly (with observers' dominant/sighting eye) at the same viewing distance as Experiment 9 (i.e. 129 and 116 cm for the LaCie and Sony monitors, respectively). Observers fixated a centrally presented marker (a white cross) during presentation of the test stimulus. We monitored eye position during the experiment; observers were able to maintain good fixation. Stimuli were presented for 125 ms and appeared peripherally either in the upper or in the lower half of the screen (3.2 deg.

eccentricity). Observers indicated (verbally) whether the target was tilted clockwise or anticlockwise of vertical, and the experimenter recorded their response using the computer keyboard. Visual feedback (the contrast-polarity of the fixation marker) indicated a correct or incorrect response. Three conditions (each comprising seven target tilt-levels) were interleaved in a single run. Observers completed at least one run of 336 trials each (3 conditions x 7 levels per condition x 16 trials per tilt-level). Observers completed a practice session prior to data collection, where all target tilts were doubled. Raw data were fit with cumulative Gaussian functions, to give an estimate of response-variance (orientation discrimination threshold) and bias (point of subjective equality; PSE). Since there was no difference in correct responses for the upper and lower sides of the screen – for both patients ($t_{14} = -0.02$, $p = 0.981$) and healthy controls ($t_{14} = -0.63$, $p = 0.540$) – raw data were fit independently of stimulus position. There were no systematic trends in PSE data – both clinical and non-clinical groups were uniformly unbiased – and we do not consider these data further.

Statistical analysis

To compare the effect of flankers in patients and controls we first carried out a repeated-measures analysis of variance on threshold-values, with *group* (patients, controls) as between-subjects factor and *condition* (isolated target, random flankers, contour-fragment) as within-subjects factor. We then estimated the amount of crowding from random flankers and within contours in each group by calculating log-ratios between thresholds in the crowded and isolated stimuli (i.e. log[random/isolated] and log[contour/isolated]). To compare the amount of crowding in patients and controls and test the prediction that patients should show less crowding we performed a repeated-measures analysis of variance on log-ratios, with *group* (patients, controls) as between-subjects factor and *condition* (random flankers, contour-fragment) as within-subjects factor. The Bonferroni procedure has been used to correct p-values for multiple comparisons. Alpha-value was set to 0.05 for all statistical tests.

Results and discussion

Figure 31a presents mean orientation discrimination thresholds for patients (red) and non-clinical controls (blue) in the three conditions tested in Experiment 10 (isolated Gabor, random flankers, contour-fragment). We note that patients are poor at discriminating the orientation of an isolated element: thresholds are indeed doubled compared to controls (mean thresholds (± SE) are 5.61° ± 1.21° vs. 2.73° ± 0.30°, $t_{24} = -2.31$, $p = 0.03$). This indicates poor processing of local structure (the constituents of contours). Analysis of variance on threshold-values, with *group* (patients, controls) as between-subjects factor and *condition* (isolated target, random flankers, contour-fragment) as within-subjects factor, indicates a significant effect only for the main factor *condition* ($F_{2,48} = 36.20$, $p < 0.001$). That the *group x condition* interaction is not significant suggests that adding flankers increases thresholds both in healthy controls and in patients.

To quantify the amount of crowding from randomly oriented flankers and contour-consistent flankers, we calculated log-ratios between orientation thresholds in the crowded and isolated stimuli (i.e. log[random/isolated] and log[contour/isolated]). The mean log-ratios for patients and controls are presented in Figure 31b (note that in this figure we present log[Isolated/Flankers] in order to better compare graphically these results to those of Figure 29b). Analysis of variance on log-ratios, with *group* (patients, controls) as between-subjects factor and *condition* (random flankers, contour-fragment) as within-subjects factor, shows a significant main effect of group ($F_{1,24} = 9.16$, $p = 0.003$, one-tailed) and condition ($F_{1,24} = 78.11$, $p < 0.001$, one-tailed) with non-significant interaction ($F_{1,24} = 0.67$, $p = 0.211$, one-tailed). This indicates that patients show less crowding (i.e. better performance) compared to healthy controls both in the condition where the target is flanked by two randomly oriented elements and within contours. Note that this pattern of results does not reflect a ceiling effect. Indeed, in a control experiment on one healthy observer we measured a threshold in the contour-fragment condition that was 6 times higher than in the isolated Gabor condition (16.64° vs. 2.65°). With noise superimposed on the stimuli – to elevate the baseline threshold and thus mimic patients' performance in the isolated Gabor condition – we could still observe a 6X threshold-increase (37.09° vs. 5.89°). This shows that our paradigm was not limited in its ability to estimate the effect of crowding because of some elevation in baseline performance in patients.

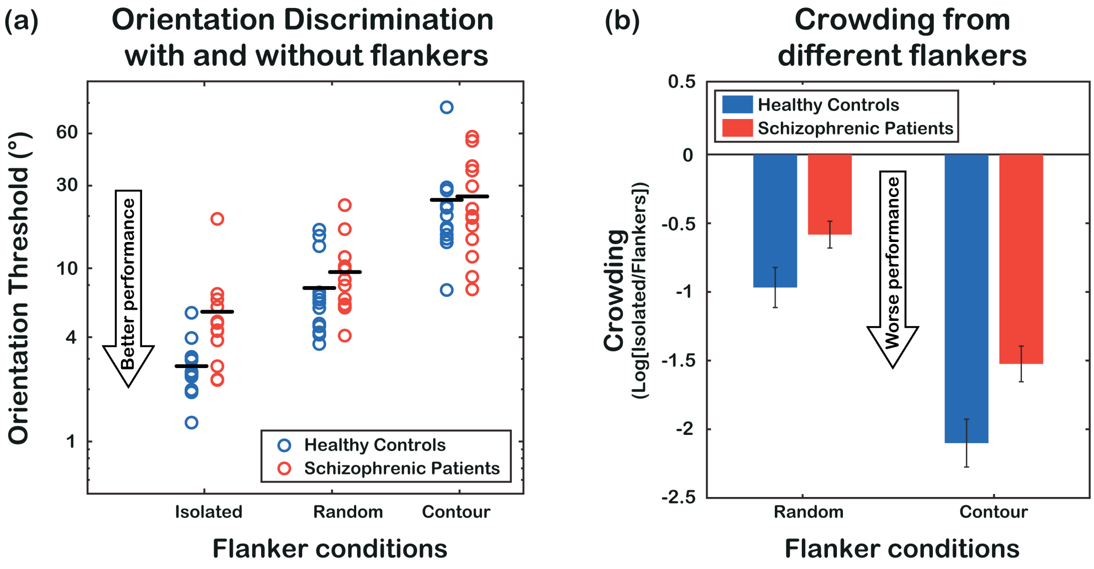


Figure 31. (a) Mean orientation discrimination thresholds for SZ patients (red) and non-clinical controls (blue) in the three conditions tested in Experiment 10 (isolated Gabor, random flankers, contour-fragment). Black horizontal lines represent mean orientation thresholds. Note that in this graph *better* performance corresponds to *lower* y-values, whereas in Figure 29a better performance corresponds to *higher* y-values. Patients' thresholds in the isolated Gabor condition are doubled compared to controls', indicating reduced sensitivity to local orientation. (b) Log-ratios between thresholds in the isolated and crowded stimuli (i.e. log[isolated/random] and log[isolated/contour]). Both in the random flankers condition and in the contour-fragment condition patients show less crowding compared to controls.

Taken together, the results of Experiment 10 indicate both reduced sensitivity to local orientation and relatively weaker crowding in SZ patients, confirming our prediction that they should be less affected by the disruptive influence of distractor elements on object recognition in the periphery. Additionally, these results suggest a role of poor local processing in the contour-localisation deficit shown by SZ people.

Note that, at least for the contour-fragment condition, we cannot rule out a role of the clinical state in the reduced crowding shown by patients. Indeed, we found a significant negative correlation between the total score of the PANSS Negative Scale and the effect of flankers (log-ratios) in the contour-fragment condition ($r_{11} = -0.684$, $p = 0.040$). In other words, patients who scored more highly on the PANSS Negative Scale experienced less crowding from flankers within contour.

GENERAL DISCUSSION

In Experiment 9 we measured SZ patients' ability to localise a contour embedded in different surrounds (random, near-parallel and near-perpendicular). We reported that, although patients were poorer at detecting contours embedded in random noise, they were proportionally less disrupted by the presence of near-parallel surrounds than healthy controls. We then measured SZ people's ability to discriminate the orientation of the local components of our contours (Experiment 10) and showed that although patients performed worse at this task (i.e. orientation discrimination thresholds were higher), they were less affected by the disruptive influence of distractor-elements (i.e. they were less prone to visual crowding).

Orientation tuning, gain control, GABA and NMDA-dysregulation

Gain control refers to the inhibitory cortical processes that allow neurons to optimise their limited operating range (for recent review see Carandini and Heeger [2012]). It has been proposed that gain control plays a substantial role in the *contrast-contrast* illusion. Dakin *et al.* [2005] have proposed that their finding that SZ patients are less prone to this illusion could be a consequence of reduced gain control. A reduction in these center-surround interactions in SZ has been widely reported for motion processing [Tadin *et al.*, 2006], for the processing of size [Uhlhaas *et al.*, 2006a; Uhlhaas *et al.*, 2006b] and recently also for orientation [Dakin *et al.*, In Prep]. Cortical levels of γ-aminobutyric acid (GABA) – the chief inhibitory neurotransmitter in humans, which is thought to play a crucial role in these center-surround interactions [Angelucci & Bressloff, 2006] – are lower in SZ people [Goto, Yoshimura, Moriya, Kakeda, Ueda, Ikenouchi-Sugita, Umene-Nakano, Hayashi, Oonari, Korogi, & Nakamura, 2009; Yoon, Maddock, Rokem, Silver, Minzenberg, Ragland, & Carter, 2010] and also correlate with the amount of visual surround suppression, as measured psychophysically [Yoon *et al.*, 2010]. Here we suggest that a reduction in the inhibitory interactions of this center-surround circuitry may also be involved in the poor local orientation discrimination in SZ we reported in Experiment 10. Data from studies of humans and non-human primates suggest a role of GABA-mediated inhibition in orientation discrimination. Physiological reports show that GABA-mediated inhibition modulates neuronal selectivity in the visual system [Alitto & Dan, 2010] and specifically the selectivity of visual cortical neurons to stimulus orientation [Crook & Eysel, 1992; Katzner *et al.*, 2011; Li, Yang, Liang, Xia, & Zhou, 2008; Sillito, 1975, 1979; Sillito *et al.*, 1980]. The specific action of GABA blockage (e.g. via administration of Gabazine) seems to be to elevate overall levels of activation of neurons [Katzner *et al.*, 2011]; some authors have interpreted this as a broadening of tuning while others have proposed that tuning is essentially unchanged but that response now sits on top of a pedestal of higher underlying spontaneous activity. In terms of human data, the importance of GABA-levels for orientation discrimination has recently been confirmed using magnetic resonance spectroscopy [Edden, Muthukumaraswamy, Freeman, & Singh, 2009] and preliminary evidence [Rokem, Yoon, Ooms, Maddock, Minzenberg, & Silver, 2011] indicates a negative correlation between human visual cortical levels of GABA and human orientation discrimination performance. A reduction in orientation selectivity of individual neurons due to decreased GABA-mediated inhibitory interactions in SZ could account for the poorer local orientation discrimination performance (relative to controls) we reported in Experiment 10.

Poor orientation discrimination could potentially be related also to the extensively reported N-methyl-D-aspartate (NMDA) receptor dysregulation in SZ (for a review see Moghaddam [2003]). NMDA receptors, indeed, seem to play a critical role in gain control mechanisms. Several neurophysiological studies and animal models have shown that NMDA-receptors amplify the responses to isolated stimuli and increase the effects of lateral inhibition (for a review see Daw, Stein and Fox [1993]). In the light of these results, NMDA-receptor dysregulation likely results in less amplification and decreased lateral inhibition. An indication of decreased signal amplification in SZ patients comes from the study by Butler *et al.* [2005], who reported that patients' visual evoked potential contrast response curves show decreased gain at low contrast as well as a lower plateau. Interestingly, studies on NMDA-receptor activity in cat visual cortex and lateral geniculate nucleus [Fox, Sato, & Daw, 1990; Kwon, Nelson, Toth, & Sur, 1992] have reported similar effects (i.e. decreased gain at low contrast and lower plateau), suggesting a substantial role of NMDA in gain control.

The role of inhibition in contour integration

As previously discussed (Studies 1 and 2), the near-parallel surround condition is characterized by a higher probability of local *false matches* between contour- and background-elements compared to the random surround condition. A deficit in visual grouping (reviewed in Uhlhaas and Silverstein [2005]) an/or imprecise local orientation discrimination in SZ patients (Experiment 10) could potentially lead to a reduction – across *all* stimulus-conditions – in the number of local false matches. This would predict a pattern of contextual effects similar to that shown by healthy controls and not reduced disruptive effect of near-parallel surrounds together with as much facilitation from near-perpendicular surrounds as healthy observers (as instead reported in Experiment 9).

Additionally, if, as suggested by Chapman and Chapman [1973], patients have problems in ignoring irrelevant stimuli, they should have particular problems with near-parallel surrounds (that could be characterized as presenting more plausible alternatives to the contour). We report the opposite: patients are better at ignoring such disruptive surrounds. Thus, the result that patients are relatively good in this condition cannot be accounted for by a general inability to ignore irrelevant stimuli but must be attributable to a more specific deficit that we propose is related to cortical inhibition.

A deficit in a circuitry that, from a computational point of view, is *inhibitory* is suggested not only by the reduced local orientation discrimination in patients (see previous paragraph), but also by the reduced disruptive effect of near-parallel surrounds on their ability to localise contours. Conceptually, this finding is indeed consistent with less suppression from iso-oriented surrounds.

The crucial role of inhibition in contour integration has been emphasized in Yen and Finkel's [1998] model. In this cortical-based model, contour integration reflects the level of synchronization of activity of units responding to interrelated contour-segments, which strongly depends on the balance of facilitatory and inhibitory inputs from contour- versus background-elements. In a first stage two sets of *facilitatory* connections operate, the *co-axial* and the *trans-axial* connections, which run parallel and orthogonal to the local orientation of the unit, respectively. After co-axial and trans-axial patterns of activity around a given point in space have been compared, *inhibitory* connections switch off the responses of all those units whose facilitation from other active cells falls below a given threshold. Finally, strongly facilitated units undergo temporal synchronization, with the sum of the activity of all synchronized units determining the perceptual salience of the contour. In Study 2 we proposed a two-stage process – based on the Yen and Finkel's [1998] model – to account for the effects of context we reported in healthy observers. The key point of our proposal is the hypothesis of inhibitory interactions between similar *global* structures.

In this framework, the disruptive effect of near-parallel surrounds would reflect strong suppression of the target-snake from similar snake-consistent global structures, which arise in the immediate surround. By extension, the reduced disruptive effect of near-parallel surrounds we reported for SZ patients (Experiment 9) would be the result of weaker inhibitory interactions between global structures (i.e. the target-snake structure and the snake-consistent global structures, which arise in the immediate surround). We cannot rule out a role of inhibition between global structures in the pattern of results we showed for SZ patients. However, given the difficulty shown by SZ people in tasks that require integration to extract *global* spatial form [Doniger *et al.*, 2001; Kimhy *et al.*, 2007; Silverstein *et al.*, 2000], further research is needed to establish whether inhibitory interactions between global structures can also play a role in the pattern of contextual effects we reported in Experiment 9. It could also be the case that patients' immunity to the near-parallel surrounds relies on decreased inhibitory inputs from *local* iso-oriented surrounding elements – consistent with reduced surround-suppression from iso-oriented distractors [Knierim & van Essen, 1992] – instead of (or in addition to) decreased inhibitory interactions between *global* structures.

Note that reduced inhibition can also account for patients' poorer localisation of contours in random surrounds. Two aspects of the Yen and Finkel's [1998] model are relevant in this regard: (i) the importance of the balance between facilitation and inhibition for contour integration and perceived contour salience and (ii) the fact that facilitation and inhibition operate in parallel over the scene and extract not only the target-contour, but also, other less salient contours. A reduced inhibition in SZ would lead patients to perceive more spurious contour-fragments arising in the background by chance. An inability to ignore these irrelevant contour-structures in the random-noise [Chapman & Chapman, 1973] would make them vulnerable to lots of "false alarms" in the background. This could also potentially predict increased susceptibility to hallucinatory experiences in noise – abnormal sensory experiences related to the loss of distinction between relevant and irrelevant stimuli [Frith, 1979; Hemsley, 1993; Kapur, 2003].

The role of inhibition in the reduced crowding in schizophrenia

Recent findings suggest that the attributes (e.g. orientation or position) of local stimuli in crowded displays are *averaged* or *pooled* together [Dakin *et al.*, 2010; Greenwood *et al.*, 2009; Parkes *et al.*, 2001]. For example, observers generally make reports that are consistent with the target-orientation having been averaged with the orientation of the flankers [Parkes *et al.*, 2001]. Pooling is more pronounced within contours [Livne & Sagi, 2007], which led to the proposal of a close link between crowding and contour grouping [Dakin *et al.*, 2010; Livne & Sagi, 2007, 2010; May & Hess, 2007]. Our results of Experiment 10 point to the direction that actually also inhibition might be involved in crowding (and not just pooling). Indeed, given the visual grouping deficit in SZ (reviewed in Uhlhaas and Silverstein [2005]) and the fact that pooling is more pronounced within contours, if just pooling was involved in crowding patients should have shown less disruption from flankers (compared to controls) specifically in the contour-fragment condition (but not with randomly oriented flankers). Note that also an explanation of crowding as excessive feature integration [Pelli *et al.*, 2004; Pelli & Tillman, 2008] would have lead to similar predictions. Our results are instead consistent with the notion that crowding relies also on inhibitory interactions between spatially adjacent mechanisms selective to similar visual features [Andriessen & Bouma, 1976; Bjork & Murray, 1977; Wilkinson *et al.*, 1997; Wolford, 1975]. Our suggestion is that reduced crowding in SZ may result from reduced inhibitory interactions from flanking-elements.

CONCLUSION

In conclusion, our data of Experiment 9 are consistent with reduced suppression rather than a general decrease in all contextual effects on contour-localisation in SZ. The poor local orientation discrimination and the reduced crowding in patients (Experiment 10) – which likely play a role in the abnormal contour-localisation in SZ – also are consistent with a reduction in inhibitory interactions. We suggest that this pattern could result from abnormal gain control, which is crucial both in orientation-selectivity and in surround suppression.

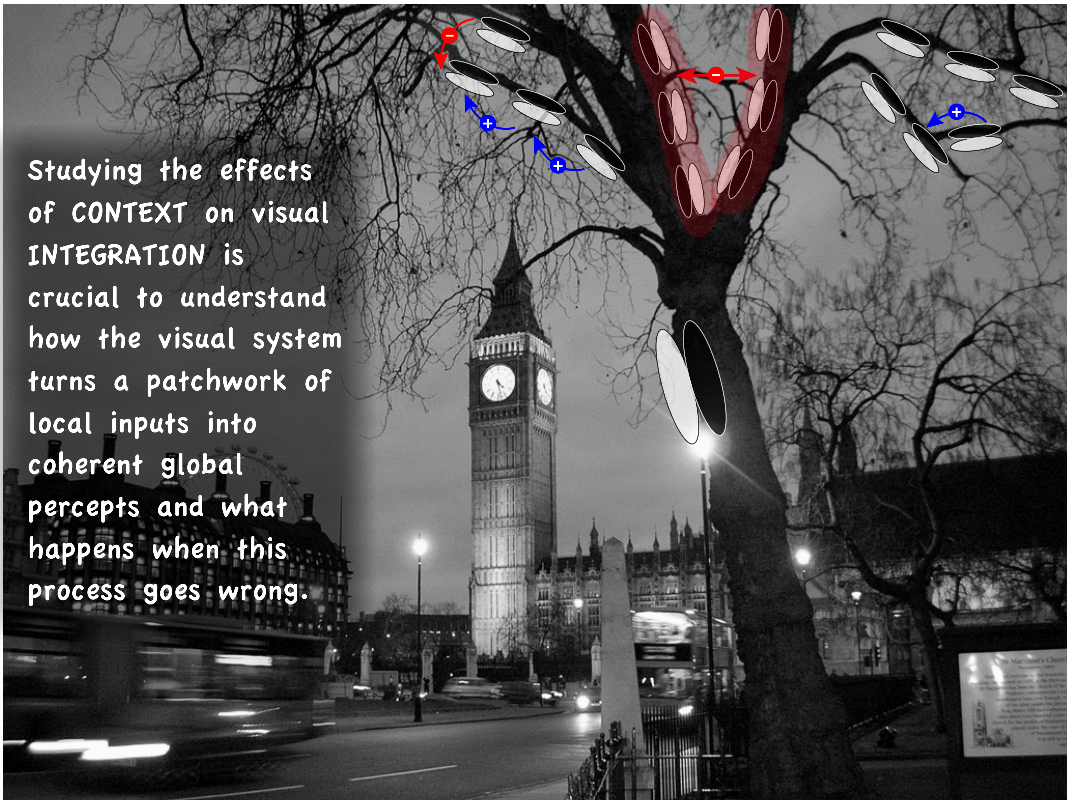
GENERAL CONCLUSION

Taken together, the results of the four studies indicate that context massively influences the localisation of contours embedded in background-noise. The relevance of this finding is twofold.

First of all, it extends our knowledge of how the visual system extract perceptually salient global structures embedded in background-noise and what can affect or contribute to this process. In particular, the results of the two psychophysical studies are relevant in the light of the current models of contour integration [Elder & Goldberg, 2002; Field *et al.*, 1993; Geisler *et al.*, 2001; May & Hess, 2007; Yen & Finkel, 1998], whose performance is consistent with human observers' ability to localise contours within noise. Specifically, the finding of a robust effect of context on visual integration reveals the unsuitability of several current models in accounting for these effects. Additionally, the fact that these contextual effects likely involve both *local* and *global* mechanisms highlights the need of new, more articulated models of contour integration (or at least an extension of the current models), which also take into account the role of context. Our proposal of a two-stage process (see the general discussion of Study 2) makes no pretence of being an exhaustive model of the contextual effects on contour-localisation. It is simply meant to be a starting point for a new approach at the study of contour integration, in which also the effect of context is taken into account. The contribution of this thesis-work is not limited to the basic research, but also extends to a more ecological field. It is sufficient to think that outside the laboratory objects rarely appear in isolation to understand the relevance of studying the effect of context on visual perception.

In line with this claim is also the second aspect that could benefit from our results, namely visual rehabilitation. In particular, the two clinical studies presented above clearly indicate a substantial role of poor or abnormal context processing in some visual deficits shown by specific clinical populations. For example, in Study 3 we provided evidence that ageing affects the ability to discard irrelevant contextual information and suppress spurious linkages with irrelevant distracting-elements, thus impairing the localisation of contours in noise. Similarly, in Study 4 we reported that an abnormal processing of context likely contributes to the poor contour detection in schizophrenia. Knowing what likely causes, underlies or contributes to a deficit facilitates the setting-up of more focused rehabilitation programs, thus helping in saving precious time.

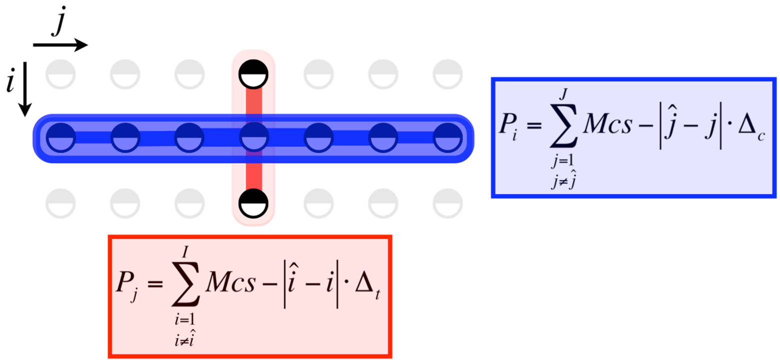
To conclude…



Studying the effects of CONTEXT on visual INTEGRATION is crucial to understand how the visual system turns a patchwork of local inputs into coherent global percepts and what happens when this process goes wrong.

APPENDIX

SNAKE in PARALLEL surround: perceptual salience of global structures



$$P_i = \sum_{\substack{j=1 \\ j \neq \hat{j}}}^{J} Mcs - \left|\hat{j} - j\right| \cdot \Delta_c$$

$$P_j = \sum_{\substack{i=1 \\ i \neq \hat{i}}}^{I} Mcs - \left|\hat{i} - i\right| \cdot \Delta_t$$

Blue global structure (target-snake):

- $\hat{j} = 4$
- Let us hypothesize that $\Delta_c = 0.5$ and $Mcs = 100$

$$\begin{aligned} \Rightarrow P_i\big|_{i=2} &= 2 \cdot \left\{ \left[100 - \left(\left|4-5\right| \cdot 0.5\right)\right] + \left[100 - \left(\left|4-6\right| \cdot 0.5\right)\right] + \left[100 - \left(\left|4-7\right| \cdot 0.5\right)\right] \right\} \\ &= 2 \cdot \left\{ \left[100 - \left(\left|-1\right| \cdot 0.5\right)\right] + \left[100 - \left(\left|-2\right| \cdot 0.5\right)\right] + \left[100 - \left(\left|-3\right| \cdot 0.5\right)\right] \right\} \\ &= 2 \cdot \left\{ \left[100 - 0.5\right] + \left[100 - 1\right] + \left[100 - 1.5\right] \right\} \\ &= 2 \cdot \left\{ 99.5 + 99 + 98.5 \right\} = 2 \cdot 297 = 594 \end{aligned}$$

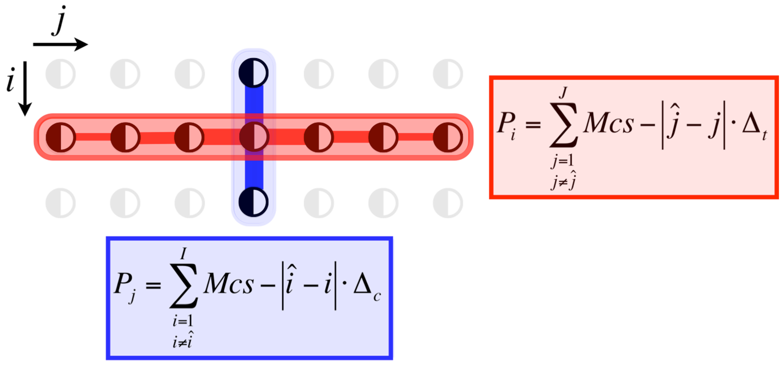
Red global structure (*false match* between contour- and surrounding-elements):

- $\hat{i} = 2$
- Let us hypothesize that $\Delta_t = 0.9$ and $Mcs = 100$

$$\begin{aligned} \Rightarrow P_j\big|_{j=4} &= 2 \cdot \left[100 - \left(\left|2-3\right| \cdot 0.9\right)\right] \\ &= 2 \cdot \left[100 - \left(\left|-1\right| \cdot 0.9\right)\right] \\ &= 2 \cdot \left[100 - 0.9\right] = 2 \cdot 99.1 = 198.2 \end{aligned}$$

$\Rightarrow$ the *Blue* structure (target-snake) is perceptually more salient than the *Red* structure (false match between contour- and surrounding-elements).

LADDER in PARALLEL surround: perceptual salience of global structures



Blue global structure (*false match* between contour- and surrounding-elements):

- $\hat{i} = 2$
- Let us hypothesize that $\Delta_c = 0.5$ and $Mcs = 100$

$$
\begin{aligned}
\Rightarrow \; P_j\big|_{j=4} &= 2 \cdot \left[100 - \left(|2-3| \cdot 0.5\right)\right] \\
&= 2 \cdot \left[100 - \left(|-1| \cdot 0.5\right)\right] \\
&= 2 \cdot \left[100 - 0.5\right] = 2 \cdot 99.5 = 199
\end{aligned}
$$

Red global structure (target-ladder):

- $\hat{j} = 4$
- Let us hypothesize that $\Delta_t = 0.9$ and $Mcs = 100$

$$
\begin{aligned}
\Rightarrow \; P_i\big|_{i=2} &= 2 \cdot \left\{\left[100 - \left(|4-5| \cdot 0.9\right)\right] + \left[100 - \left(|4-6| \cdot 0.9\right)\right] + \left[100 - \left(|4-7| \cdot 0.9\right)\right]\right\} \\
&= 2 \cdot \left\{\left[100 - \left(|-1| \cdot 0.9\right)\right] + \left[100 - \left(|-2| \cdot 0.9\right)\right] + \left[100 - \left(|-3| \cdot 0.9\right)\right]\right\} \\
&= 2 \cdot \left\{\left[100 - 0.9\right] + \left[100 - 1.8\right] + \left[100 - 2.7\right]\right\} \\
&= 2 \cdot \left\{99.1 + 98.2 + 97.3\right\} = 2 \cdot 294.6 = 589.2
\end{aligned}
$$

$\Rightarrow$ the *Red* structure (target-ladder) is perceptually more salient than the *Blue* structure (false match between contour- and surrounding-elements).

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