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Multiple forms of contour grouping deficits in schizophrenia: What is the role of spatial frequency?

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ABSTRACT

Schizophrenia patients poorly perceive Kanizsa figures and integrate co-aligned contour elements (Gabors). They also poorly process low spatial frequencies (SFs), which presumably reflects dysfunction along the dorsal pathway. Can contour grouping deficits be explained in terms of the spatial frequency content of the display elements? To address the question, we tested patients and matched controls on three contour grouping paradigms in which the SF composition was modulated. In the *Kanizsa task*, subjects discriminated quartets of sectored circles ("pac-men") that either formed or did not form Kanizsa shapes (illusory and fragmented conditions, respectively). In *contour integration*, subjects identified the screen quadrant thought to contain a closed chain of co-circular Gabors. In *collinear facilitation*, subjects attempted to detect a central low-contrast element flanked by collinear or orthogonal high-contrast elements, and facilitation corresponded to the amount by which collinear flankers reduced contrast thresholds. We varied SF by modifying the element features in the Kanizsa task and by scaling the entire stimulus display in the remaining tasks (SFs ranging from 4 to 12 cycles/deg). Irrespective of SF, patients were worse at discriminating illusory, but not fragmented shapes. Contrary to our hypothesis, collinear facilitation and contour integration were abnormal in the clinical group only for the higher SF ($>=10$ c/deg). Grouping performance correlated with clinical variables, such as conceptual disorganization, general symptoms, and levels of functioning. In schizophrenia, three forms of contour grouping impairments prominently arise and cannot be attributed to poor low SF processing. Neurobiological and clinical implications are discussed.

1. Introduction

Schizophrenia is a devastating psychiatric disorder characterized by delusions, hallucinations, disorganized thought, erratic behavior, affective and volitional disturbances, and a decline in functioning. Recent studies from brain imaging and visual psychophysics have revealed a constellation of visual abnormalities that cannot be readily identified from standard clinical interviews. One such abnormality is in what might be generically termed "contour grouping" (CG)[1], which represents smooth, well-formed contours on the basis of the relative positions and orientations of spatially discrete line elements. Contour grouping is of interest not just because it has been repeatedly shown to be abnormal in schizophrenia (for reviews, see Silverstein and Keane, 2011; Uhlhaas and Silverstein, 2005), but also because it is important in its own right, enabling species throughout the animal kingdom to rapidly identify the number and shape of the objects that they visually confront (Mandon and Kreiter, 2005; Nieder, 2002). The underlying neurobiology of contour grouping is also well-explored, involving long-range horizontal connections between orientation-tuned, co-aligned, spatial frequency filters in early visual cortex, and also feedback from higher-order visual areas, such as lateral occipital complex (Grossberg and Mingolla, 1985; Lee and Nguyen, 2001; Seghier and Vuilleumier, 2006; Shpaner

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[1] "Contour grouping" is not an ideal term because—unlike many others sorts of grouping—the visual system does not merely decide which elements belong together, it also *fills-in* and relies upon the regions between the grouped elements. Because there seems to be no better term that subsumes the three phenomena of interest, we somewhat reluctantly continue with the term "contour grouping" here.

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et al., 2013; Wagemans et al., 2012a; Wokke et al., 2013). A major challenge in schizophrenia research is to remove potential confounds of CG deficits so as to clarify the neurophysiological consequences of the disorder.

Here, we test the hypothesis that poor CG in schizophrenia arises not from dysfunctional circuitry for integration, but from poor processing of the lower spatial frequencies (SFs) that compose the elements integrated. We consider this possibility because prior research has shown that when subjects discriminate high-contrast sinusoidal luminance gratings differing slightly in spatial frequency, schizophrenia patients were severely impaired for gratings of low SF (0.5 c/deg, $p=0.001$), less impaired for intermediate SF (4.7 c/deg, $p=0.02$), and marginally impaired even at the highest SF (8.3 c/deg; $p=0.07$) (O'Donnell et al., 2002). Qualitatively the same, but smaller, effects were found for highly-functioning (remitted), unmedicated outpatients (Kiss et al., 2006). Although differing results have been obtained for untreated first episode patients in contrast senstivity studies (Kelemen et al., 2013), we know of no contrary results when multi-episode schizophrenia patients must detect or discriminate high-contrast gratings or Gabors. These effects fit within a broader picture according to which early dorsal stream processing—a primary pathway for low spatial frequency information (Bar, 2003; Bar et al., 2006)—is fundamentally compromised in the disorder (Butler et al., 2007b; Calderone et al., 2013; Foxe et al., 2005). The problem is that the individual elements in clinical CG studies are Gabor patches—that is, oriented sinusoidal luminance gratings multiplied with a circularly symmetric Gaussian kernel—and the carrier frequencies were almost always below 8.3 cycles/deg. In some cases, the SF was 6.7 cycles/deg (Kéri et al., 2009; Kéri et al., 2005a; Kéri et al., 2005b; Must et al., 2004); in other cases, it was 5 cycles/deg (Kozma-Wiebe et al., 2006; Silverstein et al., 2009; Silverstein et al., 2000), and in still other cases, it was less than 4 cycles/deg (Robol et al., 2013; Schallmo et al., 2013). It is thus entirely possible that the reason that patients perform poorly in grouping tasks owes not to an integration deficit per se, but to a problem in detecting or accurately representing the elements integrated. The confound may be especially worth considering since spatial frequency processing impairments may become compounded whenever multiple elements must be detected at once, as would need to happen in CG tasks.

To our knowledge, only one SZ study has behaviorally established a CG deficit with spatially broadband stimuli. Keane et al. (2014) had subjects discriminate quartets of sectored circles that either formed or did not form illusory "Kanizsa" shapes (Kanizsa, 1976; Ringach and Shapley, 1996). It was found that—when the elements were oriented so that they could be organized into a single well-formed shape—performance improved in healthy controls but not in schizophrenia patients. However, even here, low SF processing may be relevant. In EEG studies of healthy humans, stimulus-evoked gamma band amplitude strengthens in response to lower spatial frequency gratings (Frund et al., 2007) and Kanizsa shapes (Csibra et al., 2000; Tallon-Baudry and Bertrand, 1999). At the same time, persons with schizophrenia exhibit gamma oscillations with a reduced frequency during Kanizsa shape detection tasks (Spencer et al., 2003, 2004) and other perceptual organization tasks (Uhlhaas and Singer, 2010). It is thus conceivable that poor low SF processing may lead to inadequate Kanizsa shape perception and abnormal gamma oscillations.

To assess the role of spatial frequency on CG, we had patients and healthy controls perform three tasks previously shown to be difficult for schizophrenia patients. In the contour integration task, a co-circular set of Gabors shape was presented along with varying numbers of randomly oriented and positioned "noise" Gabors, and subjects attempted to identify the quadrant in which the shape appeared (Del Viva et al., 2006; Field et al., 1993). In the collinear facilitation task, subjects aimed to detect the presence of a low-contrast, target Gabor that was laterally flanked by orthogonal or collinear high-contrast Gabors, with the collinear Gabors making the detection easier (Polat and Sagi, 1994a, 1994b). Finally, in the Kanizsa shape completion task (the "fat/thin" task), subjects discriminated quartets of sectored circles that either formed or did not form an illusory shape (illusory and fragmented conditions, respectively) (Ringach and Shapley, 1996). The degree of discriminatory advantage conferred by the Gestalt layout provided an index of how well subjects could organize the pac-men into a high-fidelity shape representation. We modulated SF composition by shrinking/expanding the retinal size of the display in the contour integration and collinear facilitation tasks (Hess and Dakin, 1997; Polat, 2009) and by switching between wire and ordinary pac-men (without scaling) in the Kanizsa task (Davis and Driver, 1994). We selected the lower and upper-bound spatial frequency values in our tasks (4 to 12 cycles/deg) so that they spanned the values typically used in contour integration and collinear facilitation studies (see above) and so that they encompassed the range within which patients transition from abnormal to normal spatial frequency processing (O'Donnell et al., 2002).

Prior research led us to predict overall worse CG in schizophrenia. That is, patients would tolerate less noise when integrating contours (Keane et al., 2012a; Kozma-Wiebe et al., 2006; Silverstein et al., 2000), benefit less from collinear flankers when detecting a central target (Kéri et al., 2009, 2005a, 2005b; Must et al., 2004), and benefit less from Gestalt grouping when discerning the orientations of multiple pac-man elements (Keane et al., 2014). More tenuously, we hypothesized that CG dysfunction would be improved by increasing the peak spatial frequency or reducing the lower spatial frequency amplitude of the integrated elements. This last conjecture, if affirmed, would provide a new interpretation of results stemming from grouping tasks and show that dorsal stream processing may best explain previously reported visual organization impairments. Alternatively, if dysfunctional contour grouping arises independently of SF structure, then this would provide evidence that integrated elements are processed somewhat normally in SZ and that lateral interactions in striate cortex, or poor top-down feedback from other ventral areas, such as the lateral occipital complex, ultimately drive CG deficits in the disorder.

2. Methods

2.1. Subjects

The study consisted of 25 persons with schizophrenia ($N=15$) or schizoaffective disorder, and 25 healthy controls. For all subjects, inclusion/exclusion criteria were (1) age 18–65; (2) no electroconvulsive therapy in the past 8 weeks; (3) no neurological or pervasive developmental disorders; (4) no drug dependence in the last six months as assessed with the Mini International Neuropsychiatric Interview 6.0 (MINI; Sheehan et al., 1998); (5) no head injury due to accident or illness (e.g., stroke or brain tumor); (6) no amblyopia (as assessed by informal observation and self-report) and (7) the ability to understand English and to provide written informed consent. Additional criteria for patients were: currently taking medication for schizophrenia and DSM IV-TR diagnosis of schizophrenia or schizoaffective disorder (APA, 2000). Intellectual functioning of all subjects was assessed with a ten minute vocabulary test that correlates highly (≥ 0.8) with WAIS-III verbal and full-scale IQ scores (Shipley et al., 2009) and that provides a reasonable measure of premorbid IQ in patients. All subjects accepted payment for their time.

In the eligible patient sample, diagnoses were established with the Structured Clinical Interview for DSM-IV Diagnosis for patients (First et al., 2002b) and, when necessary, electronic medical records. We included subjects with schizoaffective disorder because previous contour integration and Kanizsa shape perception studies found that the schizophrenia/schizoaffective diagnosis had no bearing on the results (Keane et al., 2014; Owoso et al., 2013). We assessed whether or not there were medication effects by first converting antipsychotic dosages to chlorpromazine equivalents based on published standards (Andreasen et al., 2010) and then correlating those values with task performance.

Table 1
Demographic and clinical characteristics of participants.

	Schizophrenia ($N=25$)		Controls ($N=25$)		Group comparison
Variable	*Mean*	*SD*	*Mean*	*SD*	*P value*
Age (years)	46.5	10.9	41.4	12.5	0.42
Education, father (years)	13.4	4.4	13.3	3.6	0.76
Education, mother (years)	13.0	2.4	13.3	2.7	0.45
Education, self (years)	13.1	2.4	14.2	2.7	0.57
Ethnicity (% Caucasian)	48		28		0.11
FSIQ (Shipley)	89.8	16.6	97.6	16.9	0.72
Gender (% male)	60		48		0.40
Handedness (% right)	88		96		0.30
Visual Acuity (LogMAR)	0.01	0.10	−0.02	0.10	0.83
Antipsychotics: typical/atypical/both (%)	17/79/4				
Chlorpromazine equiv. (mg/day)	430.4	299.4			
MSIF Global Role Functioning	3.9	1.0			
PANSS, positive	11.7	4.7			
PANSS, negative	14.4	4.5			
PANSS, general	31.6	8.0			
Premorbid adjustment (Overall)	2.5	0.8			
Outpatient/Extended/Acute (%)	40/32/28				
SZ/SA (% SZ)	60				

Note. Values correspond to means unless noted. FSIQ, Full-Scale IQ as estimated with the Shipley-2 (Shipley et al., 2009). The Multidimensional Scale of Independent Functioning measured overall current level of functioning (Jaeger et al., 2003). Premorbid Adjustment Scale (PAS) measured premorbid social functioning (Cannon-Spoor et al., 1982). The outpatient/extended/acute variable gives percentages of patients in either the outpatient, extended partial hospital, or acute partial hospital program.

Positive, negative, and general symptoms were assessed with the Positive and Negative Syndrome Scale (PANSS; Kay et al., 1987). We specifically probed the relationship between conceptual disorganization (PANSS item P2) and perceptual organization, since many prior studies have uncovered relations between the two (Keane et al., 2014; Silverstein et al., 2013; Spencer et al., 2004; Uhlhaas et al., 2006). The Premorbid Adjustment Scale (PAS; Cannon-Spoor et al., 1982) was administered to assess social isolation, peer relationships, scholastic performance, school adaptation, and social-sexual aspects of life prior to illness onset. The multidimensional scale of independent functioning (MSIF; Jaeger et al., 2003) evaluated how patients performed in three domains—work, education, and home life (in decreasing order of emphasis)—within the month prior to the interview. Of particular interest was the composite score expressing overall role functioning (across vocational, educational, and residential domains), which reflects the nature of expected roles, how well they are performed, and how much support is required in each role. The MSIF and PAS were included because prior data suggest that schizophrenia patients with more impaired perceptual organization also tend to be more severely disabled (e.g., require more than an outpatient level of care) (Keane et al., in press) and have poorer social functioning prior to illness onset (Knight and Silverstein, 1998; Silverstein and Keane, 2011; Uhlhaas and Silverstein, 2005).

The control group comprised psychologically healthy individuals, as determined with the Structured Clinical Interview for DSM-IV Diagnosis for non-patients (SCID-NP; First et al., 2002a). In an effort to match on IQ and education, we preferentially recruited healthy individuals without four-year college degrees. The resulting groups were equated on a number of variables including education, IQ, sex, and age, among others (See Table 1 for demographic and clinical characteristics).

Special effort was made to match groups on visual acuity, which is important because even small differences within the 20/20 ("normal") range alter contour element detection or integration (Keane et al., in press). For all subjects, visual acuity was established binocularly with a logarithmic visual acuity chart (PrecisionVision, LaSalle, Illinois) presented under fluorescent overhead lighting. The lower testing limit of the chart was 20/10 (logMAR $=-0.3$). Visual acuity estimates were obtained at a viewing distance of 2 m and therefore were expected to apply to the distances in our study (0.88 m and 1.82 m) (Heron et al., 1995, p. 25). An in-house visual acuity correction kit was used for individuals without appropriate glasses or contacts. Each group had an average binocular acuity of almost exactly ~20/20 (see Table 1) and no subject had worse than 20/32 binocular acuity, a cut-off similar to previous studies (Butler et al., 2007b; Martinez et al., 2008; Schechter et al., 2005).

All subjects completed the three psychometric tasks described below. One control did not finish the Kanizsa shape discrimination task, one patient finished neither the contour integration nor the Kanizsa task, and one other patient did not finish the collinear facilitation task. Data for these subjects were missing because of computer malfunction or unwillingness to proceed. The research followed the tenets of the Declaration of Helsinki and subjects provided informed written consent upon being apprised of the nature and possible consequences of the study. The research was approved by the Rutgers University Institutional Review Board.

2.2. Apparatus

Subjects viewed stimuli on a 21″ cathode ray tube monitor in a darkened room with their heads stabilized by a chinrest. The screen had a resolution of 1024×768, a frame rate of 100 Hz non-interlaced, and a mean background luminance of 30 cd/m^2. Lookup table values for the monitor were linearized with psychophysics toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) and calibrated with a Konica-Minolta CS-100 photometer. The viewing distance was 181.5 cm, except for the lower spatial frequency condition of the contour integration task, which had a viewing distance of 87.6 cm. Modulating spatial frequency via viewing distance does not affect contour integration performance in healthy human adults for spatial frequencies ranging from 3 to 24 cycles/deg (Hess and Dakin, 1997).

2.3. Stimulus and procedure: Collinear facilitation

The stimulus and procedure were either identical (contour integration and collinear facilitation; Keane et al., in press) or nearly identical (Kanizsa shape perception; Keane et al., 2014) to what has been described elsewhere. In all tasks, the experimenter entered a response on behalf of the subjects to minimize the chance of group differences in key press errors (mismatching a key press with a response). Other details of the tasks are reproduced below.

Stimuli consisted of Gabor patches, which are oriented sinusoids multiplied by a circular Gaussian:

$$G(x,y,\theta)=c\sin(2\pi f(x\sin\theta+\cos\theta))\exp\left(-\frac{x^2+y^2}{2\sigma^2}\right)$$

where (x,y) denotes the distance in degrees from the center of the element, θ is the element's orientation (in deg), f is the peak spatial frequency of the element, and c is the contrast. The Gabors had a sine phase (to create a balanced luminance profile), a peak spatial frequency of 4 cycles/deg, and a Gaussian envelope SD of 10.6 arcmin. The central Gabor was vertically oriented and separated from the flankers by 4 lambda (wavelength) center-to-center (Fig. 1). One half of the collinear facilitation experiment consisted of lower spatial frequency (LSF) stimuli and the other half consisted of high spatial frequency (HSF) stimuli. The two block types were counterbalanced across observers. In the LSF trials, there were three vertically aligned Gabor elements centered on a mean gray background (45 cd/m^2). Stimuli in the HSF trials were similar to the LSF trials, except that the entire stimulus was scaled to 40% of the retinal size (i.e., Gabors had a peak SF of 10 c/d). Similar to an earlier study (Polat, 2009), we increased the flanker contrast from 64% in the LSF block to 94% in the HSF block so that the latter would be easier to see. Flanker contrast differences within this range do not alter facilitation for lower SF stimuli (Polat, 2009; see also, Zenger and Sagi, 1996).

Each trial began with a white fixation cross centered on a gray background. Upon initiating a trial, the observer saw a blank screen (400 ms), a three Gabor array (90 ms), and then another gray screen until a response was provided (present or absent). We opted to present the stimulus on every trial rather than use a two-interval forced choice since qualitatively the same results arise in the two cases (Kéri et al., 2005a), and since the former allows for a shorter experiment. A 1-up, 3-down staircase determined the threshold, the amount of contrast needed to detect the stimulus with 79.4% accuracy (Kéri et al., 2009; Kéri et al., 2005a; Kéri et al., 2005b; Must et al., 2004). Specifically, in the event of one incorrect response (miss), the contrast between the background and the central Gabor increased by 0.1 log units (26%) and in the event of three consecutive correct responses (hit), the contrast decreased by the same amount. A decrease or increase of contrast

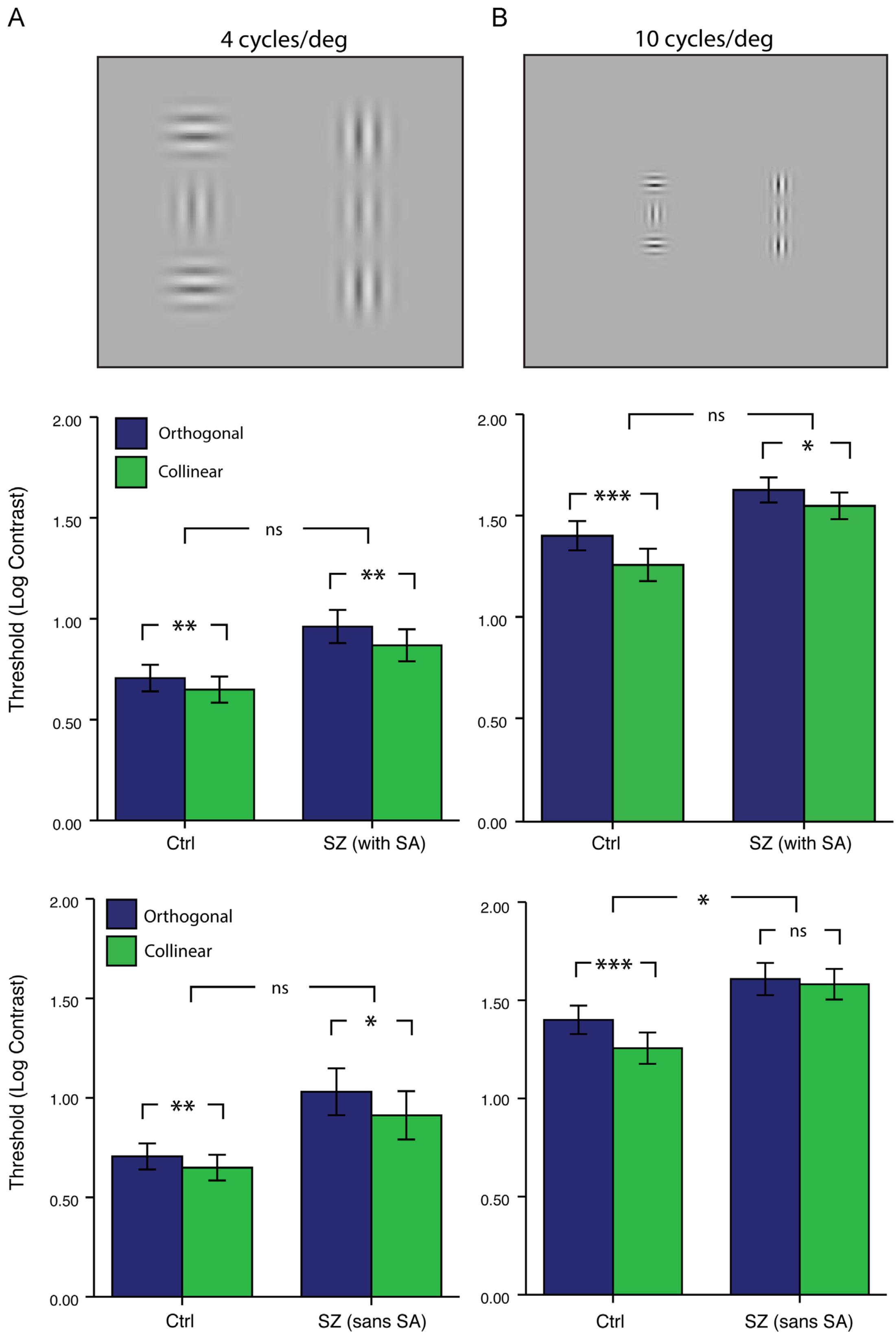

Fig. 1. *Collinear facilitation stimuli and results.* Subjects attempted to detect the presence of a central target element flanked by orthogonal or collinear high contrast elements. The target contrast varied from trial to trial, and threshold corresponded to the amount of contrast needed to reliably detect the target. Collinear facilitation is the phenomenon in which contrast detection thresholds become reduced in the presence of collinear flankers. (A, left panels) For the lower SF conditions, collinear facilitation was similar between groups regardless of whether the schizoaffective (SA) subjects were included. (B, right panels) For the high SF, the control group demonstrated more facilitation than the clinical groups, but only when the SA subjects were removed; $^{*}p<.05$, $^{**}p<.01$, $^{***}p<.001$.

preceded by a contrast change in the opposite direction was labeled a "reversal", and a block of trials terminated after seven reversals. Threshold for a condition was computed as the average contrast (in log units) for all the trials following the 4th reversal. (Averaging contrasts over all trials rather than just the reversal values improves threshold estimates (Klein, 2001, p. 1449)).

In each half of the experiment, there were two blocks corresponding to whether the flankers were orthogonal or collinear to the central target. The two blocks were counterbalanced across observers and so too was the SF ordering. Collinear facilitation was measured as the difference in thresholds between the orthogonal minus the collinear conditions, with larger (more positive) differences reflecting greater facilitation. Subjects began each half of the experiment with 25 practice trials without flankers.

2.4. Stimulus and procedure: contour integration

The contour integration experiment comprised a lower spatial frequency (LSF) and a high spatial frequency (HSF) block of trials, which were counterbalanced across observers (Fig. 2). In the LSF block, Gabors were drawn using the same formula as above, but had 95% Michelson contrast, a peak spatial frequency of 4 cycles/deg, and a Gaussian envelope SD (space constant) of 7.3 arcmin. The stimulus area in which Gabors could appear subtended 19.8° on a side. The circular target (diameter = 7.37°) consisted of twelve equally spaced Gabors (inter-element spacing = 1.93°) and was positioned at a quadrant center with randomly added jitter (± 0.5° along each dimension). The target quadrant was randomly assigned on each trial and contained the same number of Gabors as at least two neighboring quadrants. Noise Gabors never overlapped with each other or with the target Gabors, and ranged in number from 36 to 464 depending on the staircase recommendation (see below). Stimuli in the HSF block were the same as the LSF block, except that the entire stimulus was scaled to one-third the retinal size (e.g., so that Gabors had a peak SF of 12 c/d). Scaling was achieved by shrinking the stimulus display and increasing the viewing distance from 87.6 cm to 181.5 cm.

On each trial, an array of oriented Gabors appeared for 1000 ms after which subjects saw a homogeneous gray screen with numbers 1 through 4 centered in each quadrant (see Fig. 2). Subjects were given an unlimited amount of time to identify the target quadrant number and did not receive feedback on response accuracy.

Within a block, there were three randomly interleaved Bayesian ("QUEST") adaptive staircases—30 trials per staircase—and each determined the number of noise patches needed to yield 75% accuracy (Watson and Pelli, 1983). The three threshold estimates were averaged to produce one value per SF per subject. Fifteen catch trials (without noise) also appeared randomly in each block to ensure that all subjects were on task. Prior to the CI experiment, subjects received 20 practice trials that were of the same SF as the subsequent non-practice trials.

2.5. Stimulus and procedure: Kanizsa shape perception ("fat/thin" task)

In the traditional condition, stimuli consisted of four, white, sectored circles (diameter = 1.5°) centered at the vertices of an invisible square (side = 4.5°), which itself was centered on the screen (Fig. 3). Whether the pac-men formed illusory contours depended on the geometric property of "relatability" (Kellman and Shipley, 1991): when the elements were aligned ("relatable") they formed illusory contours (the "illusory condition"); when they were misaligned ("unrelatable") they produced no such contours ("fragmented condition"). The support ratio (luminance-defined edge length/total edge length) of the relatable square was equal to one-third (Shipley and Kellman, 1992). Stimuli in the wire condition were exactly the same as the traditional condition except that the sectors were replaced with line segments (width = 0.05°; see Fig. 3). Anti-aliasing (edge artifact removal) was applied by projecting the stimuli from a matrix that was four times larger than the screen stimulus. A fixation point appeared at the screen center on each trial.

We did not manipulate spatial frequency via blurring or applying a filter in the Fourier domain since doing so would essentially destroy the illusory nature of the contours and thereby remove an essential distinguishing feature of this experiment. Others have also reduced the low spatial frequency content of Kanizsa figures by switching to wire shapes (Davis and Driver, 1994). However, to confirm that our stimuli differed in the expected way, we decomposed the spatial frequency structure of the wire and traditional elements via a discrete Fourier transform. The analysis revealed that—for the wire stimulus—the wave amplitude averaged across all orientations was diminished from 1 to 4 cycles/deg and enhanced from 5 to 15 cycles/deg (see Fig. 3C,D).

The trial presentation sequence was similar to earlier studies (Keane et al. 2012b; Ringach and Shapley, 1996; Zhou et al., 2008) and consisted of a 1000 ms black (dark gray) screen, a 200 ms target presentation, a 50 ms uniform black screen, a 300 ms mask (to cap stimulus processing time), and another black screen that lingered until a response. An auditory beep sounded for each correct answer.

One half of the experiment consisted of the illusory condition, and the other half, the fragmented condition. The ordering of the two conditions was counterbalanced across subjects. In the illusory trials, the sectored circles were individually rotated clockwise or counter-clockwise to form fat or thin shapes (e.g., the top right and bottom left were rotated clockwise and the other elements were rotated counter-clockwise to produce a fat shape). In the fragmented trials, the elements were oriented downward (to block the formation of illusory contours) and were individually rotated right or left. A left/right task was chosen because it forced subjects to make judgments on the lateral properties of the stimulus—similar to the illusory condition—and because the task was easier to explain than alternative control conditions, such as clockwise vs. counterclockwise. Each half of the experiment began with 64 practice trials, which were needed to allow the subjects to become acclimated to the fast presentation times and slight orientation differences. Other studies have employed 75–100 practice trials to familiarize participants with the task (Keane et al. 2012b; Zhou et al., 2008). Following practice, there were 84 (non-practice) trials, one half of which were traditional and the other half, wire. The ordering between the two was counterbalanced across observers. The practice trials were of the same trial type (traditional/wire) as the subsequent non-practice trials. Half way through the non-practice trials of a block, subjects received a brief break to rest their eyes. The first non-practice trial of each of the four blocks was thrown out for the purposes of threshold estimation (since such trials were more often missed by observers).

Task difficulty depended on rotational magnitude, with larger rotations making the alternatives easier to distinguish. The slope and threshold of psychometric functions were measured with the Bayesian adaptive "Psi" method (Kontsevich and Tyler, 1999), which recommended on each trial a rotational magnitude that would minimize entropy (uncertainty) of the threshold and slope of the psychometric function. Rotational magnitude was expressed in log units given the decelerating function relating this quantity to proportion correct (Keane et al. 2012b; Zhou et al., 2008). The staircase assumed a log-Weibull (Gumbel) function and a non-zero (3%) attentional lapse rate (Prins and Kingdom, 2009). An advantage of the Psi method is that it makes no assumption about slope—which can change from condition to condition—and provides an efficient means for simultaneously estimating two parameters of psychometric functions (Klein, 2001).

Instructions were shown immediately before and after the practice trials on each half of the experiment. We strove to make the illusory condition as clear as possible to all subjects. On one screen, luminance-defined lines were drawn on the borders of the illusory shape, so that subjects could see clearly what was meant by "fat" or "thin". On subsequent screens, starkly different fat/thin shapes (rotation = 10°) were shown individually, side-by-side, and then in temporal succession (period = 2 s). In the practice trials, the target presentation time and rotational magnitude decreased incrementally (3200 ms, 1600 ms, 800 ms, 400 ms, and 200 ms; 10°, 8°, 6°, and 4°) so that observers could gradually become acclimated to the subtle shape differences and brief stimulus presentation.

2.6. Analysis

For the CF task, we compared thresholds (log contrast values) with a 2 (SF) by 2 (facilitation: orthogonal, collinear) by 2 (group) mixed model analysis of variance (ANOVA). For the CI task, we analyzed the data with a two 2 (SF: lower, high) by 2 (group) mixed model ANOVA—once for the catch trials (percent correct) and once for the non-catch trials (number of noise Gabors needed for 75% accuracy). In the Kanizsa ("fat/thin") task, we evaluated thresholds (log deg of rotation) and conducted a 2 (relatability: illusory, fragmented) by 2 (SF: traditional, wire) by 2 (group) mixed model ANOVA. Better contour grouping corresponded to: a greater threshold in the orthogonal vs. collinear condition in the CF experiment, a higher threshold in the contour integration experiment, and greater threshold in the fragmented relative to illusory condition in the Kanizsa experiment. Relationships between symptoms and CG performance were evaluated using Spearman rho correlations. *T*-tests were two-tailed and equal variances were assumed, unless otherwise noted.

3. Results

3.1. Collinear facilitation

Results from the collinear facilitation experiment are shown in Fig. 1. One control had an extreme negative collinear facilitation value at the lower SF (> 3 SD) and one SZ subject had an extreme positive collinear facilitation value at the high SF (> 3 SD); both were excluded from further analysis. There was a main effect of SF such that targets were less detectable (log contrast thresholds were higher) for the scaled-down (HSF) stimulus than for the large (LSF) display ($F(1,45) = 248.76$, $p < 0.000001$, $\eta_p^2 = 0.847$). There was an effect of group such that the patients required overall more contrast to see the targets than controls ($F(1,45) = 7.52$, $p = 0.009$, $\eta_p^2 = 0.143$). Group differences in overall contrast sensitivity did not depend on SF ($F(1,45) = 0.065$, $p = 0.80$, $\eta_p^2 = 0.001$). There was an

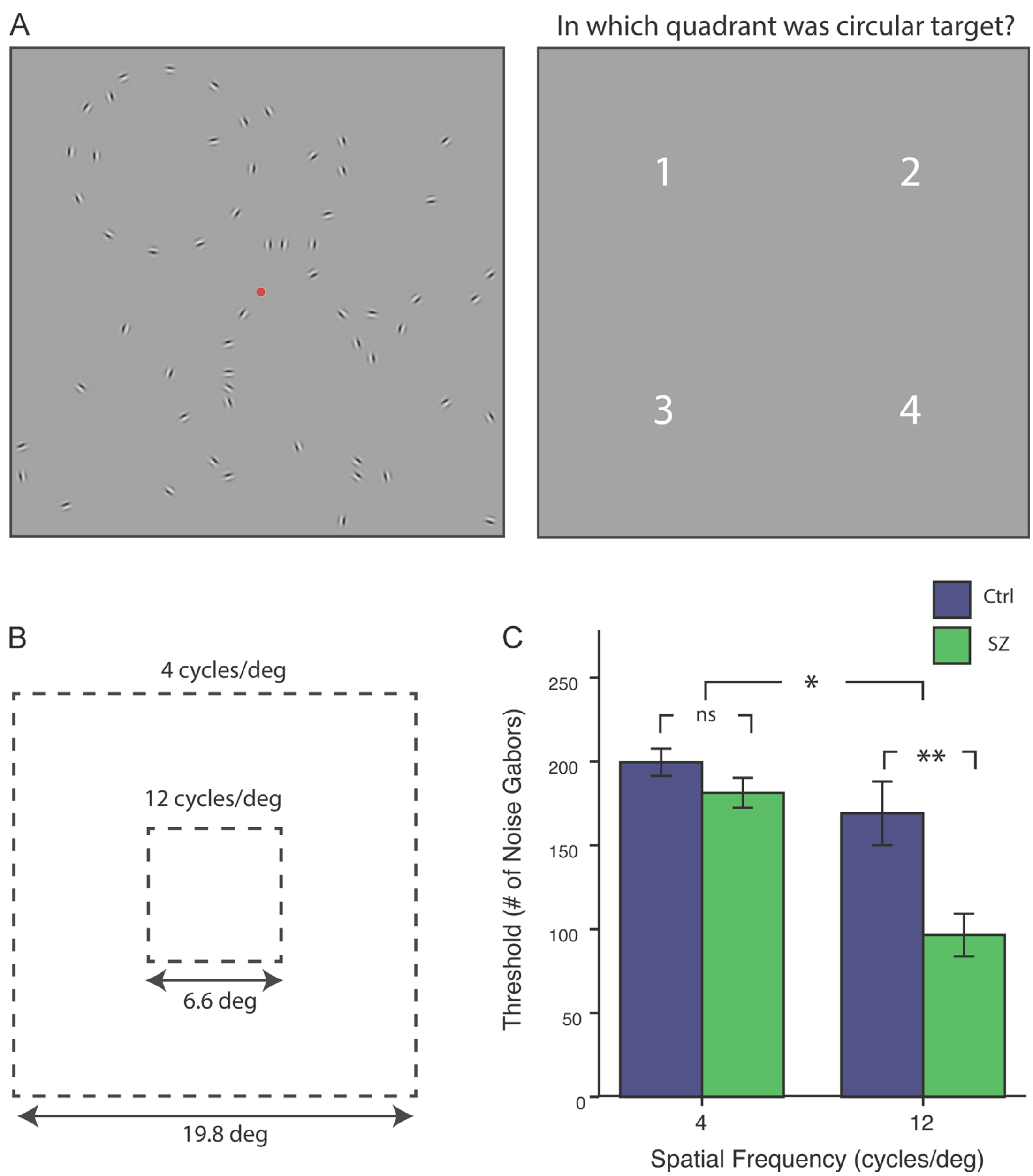

Fig. 2. *Contour integration stimuli and results.* (A) Subjects observed a briefly presented array of oriented elements (Gabors) and identified the quadrant thought to contain a circular target. Task difficulty depended on the number of noise Gabors co-presented with the target. (B) The display was scaled in size to produce two SF conditions (4 and 12 cycles/deg) (C) Patients performed worse only at 12 cycles/deg; *$p<.05$, **$p<.01$.

overall large effect of facilitation: contrast thresholds were lower for collinear than orthogonal flankers ($F(1,45)=41.63$, $p<0.000001$, $\eta_p^2=0.481$). This collinear facilitation effect was not modulated by spatial frequency ($F(1,45)=1.70$, $p=0.198$, $\eta_p^2=0.036$) and more crucially it did not depend at all on subject group ($F(1,45)=0.253$, $p=0.618$, $\eta_p^2=0.006$). There was, however, a marginal, three-way interaction ($F(1,45)=3.40$, $p=0.072$, $\eta_p^2=0.070$). Follow-up comparisons revealed that the collinear facilitation effect in patients was non-significantly larger than that of controls at 4 cycles/deg ($F(1,45)=1.13$, $p=0.293$, $\eta_p^2=0.025$) and non-significantly smaller than that of controls at 10 cycles/deg ($F(1,45)=2.14$, $p=0.15$, $\eta_p^2=0.045$). To put these results another way, the control group exhibited a classic collinear facilitation effect ($F(1,23)=31.37$, $p=0.00001$, $\eta_p^2=0.577$) that strengthened with higher SF ($F(1,23)=6.49$, $p=0.018$, $\eta_p^2=0.220$), consistent with prior studies (Polat, 2009; Woods et al., 2002). The schizophrenia group, by contrast, demonstrated a collinear facilitation effect ($F(1,22)=14.185$, $p=0.001$, $\eta_p^2=0.392$) that remained constant across SF ($F(1,22)=0.116$, $p=0.737$, $\eta_p^2=0.005$).

Because prior collinear facilitation studies in schizophrenia did not include subjects with a schizoaffective diagnosis (Kéri et al., 2009; Kéri et al., 2005a; Kéri et al., 2005b; Must et al., 2004), we re-ran the same analyses without this subgroup of patients. On this analysis, we found a facilitation effect ($F(1,36)=28.06$, $p<0.001$, $\eta_p^2=0.438$) that did not depend on group ($F(1,36)=0.73$, $p=0.398$, $\eta_p^2=0.002$, respectively), as before. Critically, there was now a three-way interaction ($F(1,36)=9.02$, $p=0.005$, $\eta_p^2=0.200$). Follow-up comparisons revealed that the schizophrenia group (without SA patients) exhibited a similar (and indeed a non-significantly stronger) facilitation effect than controls at the lower SF ($F(1,36)=2.54$, $p=0.12$, $\eta_p^2=0.066$) and a significantly weaker effect at the high SF ($F(1,36)=5.75$, $p=0.02$, $\eta_p^2=0.138$). To

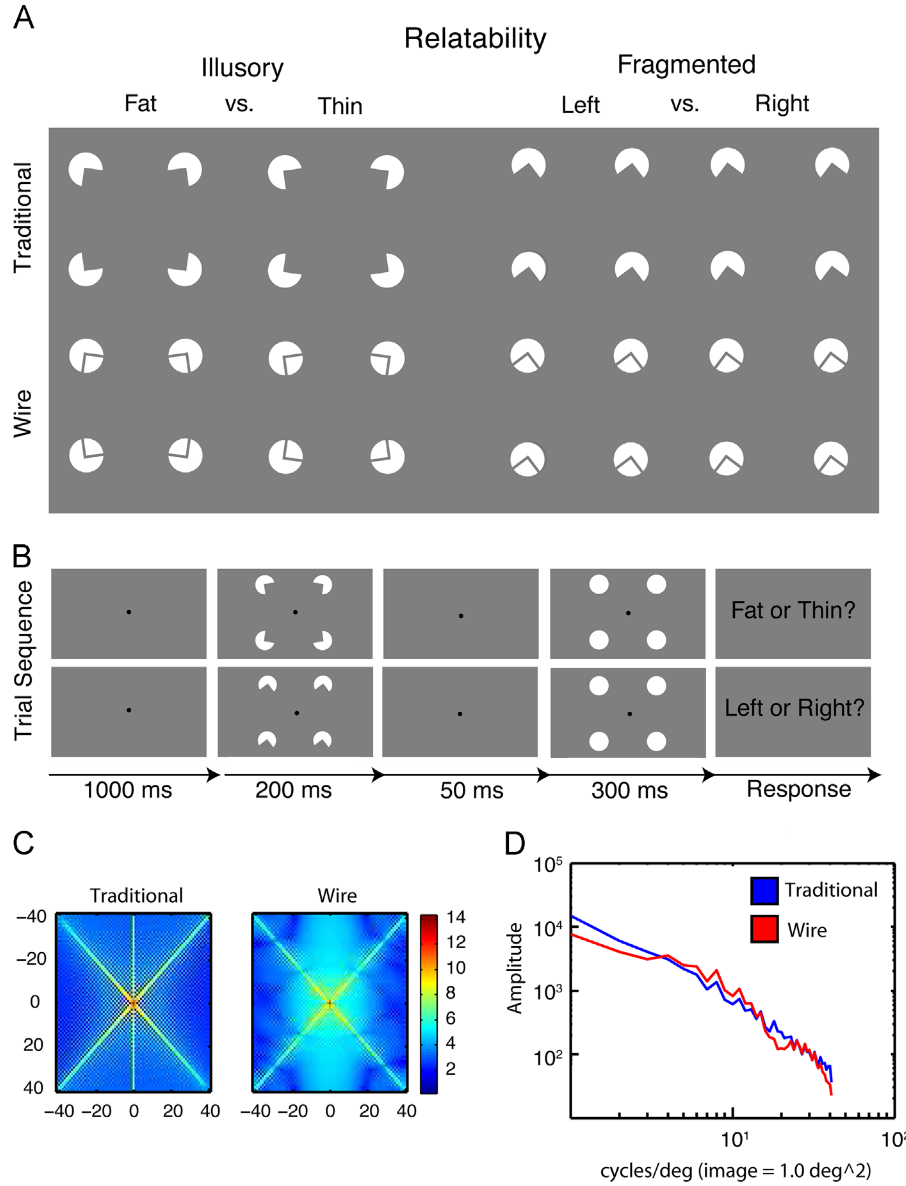

Fig. 3. *Stimuli, procedure, and spatial frequency spectra for the Kanizsa discrimination experiment.* (A) Sectored circles (pac-men) were oriented inward to form fat/thin Kanizsa shapes (illusory condition) or downward to generate uniformly-rotated left/right configurations that lacked illusory contours (fragmented condition). (B) The task was to say whether the target was fat or thin or rotated left or right. Task difficulty depended on the amount by which the pac-men were individually rotated to create the response alternatives. (C) Amplitude spectra (log units) are shown for the traditional and wire pac-men for a square region inscribed within the circular pac-man elements (1.0 deg square). (D) When the amplitudes were averaged across all orientations, the wire pac-men had reduced amplitude in the lower SF bands (1–4 cycles/deg) and enhanced amplitude in the mid-upper SF bands (5–15 cycles/deg). On a log-log coordinate system, both spectra fall off roughly as a power of 1/*f* (slope of −1).

further consider the results, we re-ran the ANOVA with only patients and used diagnosis type (SZ vs. SA) as the between subjects variable. Once again, there was strong main effect of facilitation ($F(1,21)=14.4$, $p=0.001$, $\eta_p^2=0.407$), no two-way interaction with diagnosis type ($F(1,21)=0.526$, $p=0.476$, $\eta_p^2=0.024$), but a significant three-way interaction with diagnosis ($F(1,21)=5.836$, $p=0.025$, $\eta_p^2=0.217$). Thus it seems that collinear facilitation arises regardless of schizophrenia/schizoaffective diagnosis at 4 cycles/deg and becomes greatly reduced at 10 cycles/deg for patients without significant mood symptoms.

For clinical correlations, we found that, at the lower SF, poorer collinear facilitation was associated with increased conceptual disorganization (PANSS; $rho=-0.431$, $p=0.04$) and, at the high SF, there were no correlations. There were no significant correlations at either SF when subjects with a schizoaffective diagnosis were removed.

3.2. Contour integration

One SZ subject guessed throughout (overall catch accuracy=20%; chance =25%) and was excluded from the remaining analyses. Average catch trial accuracy for each group and SF condition was ≥89%, meaning that the two groups were performing the task adequately. There was a marginally significant group difference (3.9%) on overall catch trial performance ($F(1,47)=3.45$, $p=0.07$, $\eta_p^2=0.068$; M=93.1% vs. 96.9%) with patients performing slightly worse. The group effect would remain non-significant if non-parametric (bootstrapped) *t*-tests were used for the lower SF, high SF, or values averaged across SF ($ps>0.09$). There was a main effect of SF in that, even for noise-free displays, the smaller Gabor targets were harder to see than the larger ones ($F(1,47)=10.57$, $p=0.002$, $\eta_p^2=0.184$). This SF effect was similar between groups ($F(1,47)=1.11$, $p=0.297$, $\eta_p^2=0.023$).

For the threshold data, as shown in Fig. 2, the lower SF displays were easier to integrate than the high SF displays ($F(1,47)=24.15$, $p=0.00001$, $\eta_p^2=0.339$) and the SZ group had lower thresholds than the controls ($F(1,47)=10.31$, $p=0.002$, $\eta_p^2=0.180$). The two main effects interacted ($F(1,47)=5.38$, $p=0.025$, $\eta_p^2=0.103$). Follow-up comparisons uncovered superior thresholds for the control group at the high SF ($t(47)=3.15$, $p=0.003$, Cohen's $d=0.91$) and no significant difference at the lower SF ($t(47)=1.50$, $p=0.138$, Cohen's $d=0.43$), which was opposite to what we predicted.

Here, it should be noted that the main effect of SF in the catch and threshold data can be explained in terms of visual acuity: Whereas healthy people with better-than-20/20 vision actually perform the same on the small and large element displays (consistent with Hess and Dakin, 1997), healthy people *with* 20/20 vision perform worse on the HSF displays because of reduced element visibility (Keane et al., in press). In agreement with this result, we found that—across subjects—larger (worse) logMAR values correlated with a larger performance difference between the SF conditions ($rhos>0.48$, $ps<0.0005$). That is, seeing (and hence integrating) elements at 4 cycles/deg became easier than at 12 cycles/deg as acuity worsened from 20/12.5 to 20/32.

Clinical correlates were next considered. Thresholds did not depend on schizoaffective diagnosis at the lower or high SF ($ps>0.5$), which fits with prior contour integration studies (Owoso et al., 2013). For the lower SF, elevated thresholds were associated with decreased overall independent functioning, as measured by the MSIF ($rho=-0.587$, $p=0.003$). For the high SF, increased thresholds were correlated with increased negative symptoms ($rho=0.43$, $p=0.035$). The negative symptom correlate was opposite to the predicted direction, just met the cut-off for significance, and therefore will need to be replicated in future studies. More interestingly, however, the score for overall independent functioning—which refers to how much responsibility the patient can handle at work, school, and home—was strong and in the predicted direction and in accord with prior studies (Uhlhaas and Silverstein, 2005). For comparison, catch trial performance at the lower SF did not correlate with the MSIF score ($p=0.9$), indicating that the correlation does not arise simply from the lower functioning patients exerting less effort during the task.

3.3. Kanizsa shape perception

Results are shown in Fig. 4. There were main effects of SF and group ($F(1,46)=5.93$, $p=0.019$, $\eta_p^2=0.114$; $F(1,46)=14.79$, $p<0.001$, $\eta_p^2=0.243$). In agreement with a prior study (Keane et al., 2014), the difference between groups depended on whether the pac-men contours could be interpolated to form illusory figures ($F(1,46)=12.31$, $p=0.001$, $\eta_p^2=0.211$). Follow-up tests showed that whereas patients were not compromised in discriminating left/right elements ($F(1,47)=2.19$, $p=0.145$, $\eta_p^2=0.045$), they were poor at discriminating illusory shapes ($F(1,47)=23.15$, $p=0.00002$, $\eta_p^2=0.33$). A somewhat unexpected result was the interaction between relatability and SF ($F(1,46)=22.76$, $p=0.00002$, $\eta_p^2=0.331$): the wire stimuli were easier to discriminate than the traditional variants when forming illusory contours ($F(1,47)=19.51$, $p=0.00006$, $\eta_p^2=0.293$), but the opposite held true when illusory contours were absent ($F(1,47)=4.31$, $p=0.043$, $\eta_p^2=0.084$). Intriguingly, this "illusory wire advantage" interaction effect arose regardless of clinical status ($F(1,46)=0.559$, $p=0.459$, $\eta_p^2=0.012$; see Fig. 4C), so it was not only the controls who availed themselves of the visually completed wire stimulus structure.

Others have argued for broad orientation tuning in schizophrenia and that this might underlie at least some forms of contour grouping deficits in schizophrenia (Robol et al., 2013; Schallmo et al., 2013). We found no difference in orientation discrimination in our fragmented task. To be sure that the variable was not playing a role, we included only those patients whose average fragmented threshold was *better* (lower) than the control mean ($M=0.54$; $N=9$). On this highly conservative analysis, qualitatively the same results emerged, with the clinical group still performing worse on the illusory discrimination ($F(1,31)=6.27$, $p=0.018$, $\eta_p^2=0.168$).

For the traditional pac-men stimuli, shape integration impairments (measured as the difference between the illusory and fragmented thresholds) were more severe for those with increased levels of conceptual disorganization ($rho=-0.45$, $p=0.027$), increased general PANSS symptoms ($rho=-0.55$, $p=0.005$), and reduced overall (MSIF) functioning ($rho=-0.544$, $p=0.007$). For the wire variant, integration impairments worsened with increased general symptoms ($rho=-0.405$, $p=0.049$). All symptom effects were in the expected direction.

3.4. Between-task correlations

To assess the extent to which the different tasks were tapping into shared processing mechanisms, we examined correlations between the three CG metrics. Collapsing across SF, we found no significant (or marginally significant) correlations for any pairing of tasks for the control group. For the patients, only the Kanizsa and contour integration tasks were positively correlated (worse grouping on one predicted worse grouping on the other; $rho=0.45$, $p=0.027$). When we broke down tasks by spatial frequency condition and looked at all possible between-task pairings, again there were no CG correlations for either group. (One dubious exception is that controls who were better at contour integration at 4 cycles/deg were also worse at CG in the Kanizsa wire task, $rho=-0.41$, $p=0.046$, but this correlation would obviously disappear with a correction for multiple comparisons).

4. Discussion

In this study, we sought to replicate past findings of contour grouping deficits in schizophrenia and examine whether modulating element spatial frequency structure can improve CG performance. It was found that patients did not demonstrate collinear facilitation (in the high SF condition only, with schizoaffective subjects removed), could not tolerate as much noise during contour integration, and were less able to make use of Gestalt properties when discriminating configurations of sectored circles. Contrary to our hypothesis, increasing the peak spatial frequency or decreasing the amplitude of lower SF bands of the individual elements did not ameliorate the impairments: in the Kanizsa task, illusory shape discrimination was worse regardless of SF structure; in the collinear facilitation and contour integration experiments, patients went from not having any CG deficits at 4 cycles/deg to being significantly impaired at 10 or 12 cycles/deg. CG dysfunction at times correlated with conceptual disorganization, level of functioning, and general symptoms. The between-group differences could not be ascribed to generalized deficits since lower SF (and catch trial) performance was similar between groups in the contour integration task and since CG was measured as a within-subject difference in the other two tasks (orthogonal vs. collinear; fragmented vs. illusory). The effects also cannot be blamed on differences in visual acuity or orientation tuning. Below, we consider alternative explanations for some of these findings and discuss implications for both schizophrenia and normal vision.

4.1. Contour grouping deficits in schizophrenia: Why do they occur?

Impaired contour integration in schizophrenia was expected on the basis of many prior studies (Keane et al., 2012a; Kozma-Wiebe

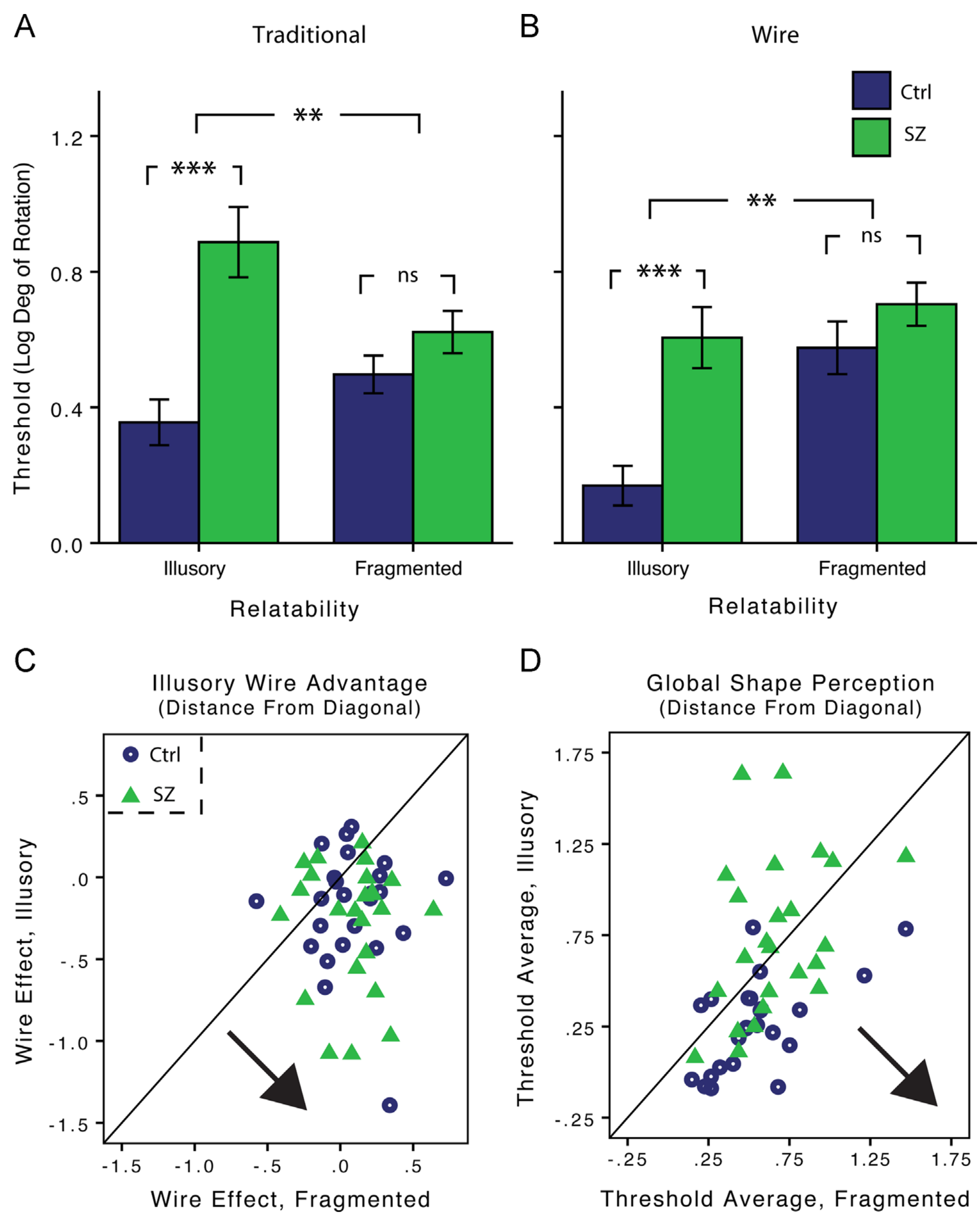

Fig. 4. *Kanizsa shape discrimination results.* (A,B) Regardless of the element type, patients did worse than controls (thresholds were higher) for the illusory condition and about the same as controls in the fragmented condition; $^{*}p<.05$, $^{**}p<.01$, $^{***}p<.001$. (C) The wire effect corresponded to how much thresholds changed as a result of swapping traditional for wire pac-men (wire – traditional). For both groups, the swap improved performance in the illusory condition and worsened it in the fragmented. Values farther from the diagonal (in the direction of the arrow) are those that displayed more of this *illusory wire advantage.* (D) Thresholds were lower in the illusory than the fragmented condition for the control group (falling below the diagonal, in the direction of the arrow), but not for the clinical group, indicating dysfunctional illusory shape perception in schizophrenia.

et al., 2006; Silverstein et al., 2009, 2000), but we were surprised that patient performance deteriorated as SF increased. It is unlikely that the smaller elements were harder for patients to see given that: (1) the two groups were matched almost perfectly on visual acuity, as noted; (2) between-group threshold differences in the orthogonal CF condition were constant from 4 to 10 cycles/deg ($p>0.7$), consistent with prior studies (Martinez et al., 2008; Skottun & Skoyles, 2007; Slaghuis, 1998) (though see, Butler et al., 2005); (3) the between-group catch trial performance did not depend on scaling and did not differ at the high SF; and (4) patients in others studies were better, not worse, at distinguishing high vs. lower spatial frequency high-contrast luminance gratings (Kiss et al., 2006; O'Donnell et al., 2002). The most straightforward inference is that contour integration (though not element detection) is especially compromised for small, finely, detailed displays. Area V1 contains a rich plexus of long-range axonal connections that stretch up to 7 mm horizontal to the cortical surface; such connections are important for contour integration, especially when the receptive fields are less distantly spaced (Stettler et al., 2002). Therefore, the amplification of the patients' contour integration dysfunction at smaller (rather than larger) inter-element distance implicates these connections. Inadequate feedback from extrastriate areas such as V4 may also be responsible. During contour integration, V4 evinces a reduced BOLD response in schizophrenia patients (Silverstein et al., 2009) and could modulate V1 so as to suppress noise and enhance the global contour (Chen et al., 2014).

Another surprise was that contour integration was somewhat normal for the lower SF condition. We conjecture that our lower SF may not have been low enough. A lower bound of 4 cycles/deg was originally chosen because O'Donnell et al. (2002) uncovered an effect at just above this SF (4.7 cycles/deg) and because we aimed to use elements that were similar to those of prior contour integration studies (typically around 5 cycle/deg). But perhaps our sample was more like that of Kiss et al. (2006), in which case an SF of 0.5 cycles/deg may have been necessary (see also, Martinez et al., 2008). If so, there may be a trade-off between how easy it is for patients to integrate elements in a display (which apparently worsens with higher SF) and the ability to see the elements (which presumably improves with higher SF). On this view, there may be a contour integration “sweet-spot” with both very low and very high SF displays (0.5 and 12 cycles/deg) producing extremely compromised contour integration behavior and with intermediate spatial frequencies yielding only small-to-medium group effects. This speculation will need to be further investigated.

Previous studies have shown that abnormal collinear facilitation in schizophrenia occurs in medication-free patients (washout periods ranging from 2 to 12 weeks), cannot be explained in terms of poor attention (as evidenced by intact Vernier acuity and CPT task performance), does not require active symptoms, and does not arise in persons with bipolar disorder (Kéri et al., 2005a; Must et al., 2004; Kéri et al., 2005b, 2009). We partially replicated the basic result provided that subjects did not have schizoaffective disorder and that stimulus elements were presented at 10 cycles/deg. This result is not best attributed to unusual sampling or inaccurate diagnoses since the two patient subgroups differed in expected ways: People with schizoaffective disorder had better overall premorbid functioning ($t(20)=2.94$, $p=0.008$, Cohen's $d=1.31$), a higher IQ ($t(23)=-2.117$, $p=0.045$, Cohen's $d=0.89$), and more years of education ($t(23)=-2.25$, $p=0.035$, Cohen's $d=0.86$), all of which have been documented before (Cheniaux et al., 2008)

While electrophysiological studies must still be conducted, our results along with others suggest that inadequate feedback from high-order visual areas does not best explain abnormal facilitation. First, practice/expertise effects become less relevant for higher SF displays (Polat, 2009). Second, SZ subjects in prior collinear facilitation studies performed normally on secondary tasks that required intact attention (Kéri et al., 2009; Kéri et al., 2005a). Furthermore, conceptual disorganization—a symptom that is almost by definition high-level—was associated with performance only for the lower SF condition. Others have argued extensively on the basis of single-unit, EEG, optical imaging, and psychophysical data that collinear facilitation is primarily executed via long-range excitatory connections between iso-oriented columns in striate cortex (Cass and Spehar, 2005; Polat et al., 1998; Stettler et al., 2002). Therefore, our data provide some evidence for dysfunction at this level in the cortical hierarchy in schizophrenia.

Might group differences in facilitation be ascribed to differences or non-linearities in conduction velocity along long-range horizontal striate connections? If inadequate time is provided for the signals to reach the target (as a result of short presentation times or large inter-element distances), then facilitation will disappear (Cass and Spehar, 2005). We consider the scenario unlikely. It would require the post-hoc supposition of uneven conduction speeds in patients (the signal would have to arrive too late to be useful in the high SF condition and on time in the lower SF condition). Also, facilitation in schizophrenia has been shown to be abnormal for a variety of target-to-flanker distances ranging from 2 to 12 lambda (0.3 to 1.8 deg of separation) (Kéri et al., 2005a) suggesting that regardless of the retinotopic distance for signal transmission, facilitation does not arise.

The discussion so far has argued for short-range, low-level integration deficits in our moderately symptomatic sample. But our data also indicate that higher order cortical areas may contribute to certain types of contour grouping deficits. As described further below, Kanizsa shape discrimination can be modulated by cognitive grouping strategy and levels of conceptual disorganization, and is dissociable from an earlier automatic boundary formation stage (Keane et al., 2014, Keane et al., 2012b; Murray et al., 2006). Orbitofrontal cortex is specifically considered important for this perceptual task because it is activated during Kanizsa shape perception in healthy adults (Halgren et al., 2003) and it exhibits gray matter reduction in schizophrenia, especially among those with conceptual disorganization. The right inferior frontal cortex may also be important since it exhibits increased activation as schizophrenia patients attempted to detect Kanizsa shapes (Foxe et al., 2005). Poor top-down feedback from frontal cortex (e.g., OFC) to areas such as lateral occipital complex (LOC) may contribute towards worsened fine-grained shape discrimination (Plomp et al., 2013; Sehatpour et al., 2010).

4.2. Magnocellular vs. parvocellular processing in schizophrenia

There has been ongoing debate as to whether poor magnocellular processing can explain various perceptual and attentional deficits not only in schizophrenia (Butler et al., 2007a; Kéri, 2008; Skottun and Skoyles, 2007), but also in other disorders such as autism and dyslexia (Milne et al., 2002; Skottun, 2000; Stein, 2001). Can high-contrast stimuli—such as those that we employed here—distinguish the pathways? In one study on macaque monkeys, high-contrast (70–100%) sinusoidal luminance gratings produced differential responses in layers 4Ca and 4Cb of striate cortex, which respectively receive input from magnocellular and parvocellular LGN layers (Tootell et al., 1988). Specifically, an examination of the uptake of C-2-deoxy-D-glucose (DG) revealed higher uptake in 4Cb than in 4Ca for high spatial frequency gratings, but the opposite was observed for LSF gratings. However, others have since argued that, when eccentricity is held constant, the two subcortical streams cannot be reliably differentiated via high-contrast luminance gratings (Merigan and Maunsell, 1993; Skottun and Skoyles, 2008). It seems that high contrast Gabor or pac-men stimuli, as we have used, do not best address the debate.

Contrast thresholds in the collinear facilitation task provide more relevant data. Here, we found a relatively constant contrast threshold elevation from 4 to 10 cycles/deg, consistent with some studies (Martinez et al., 2008; Skottun and Skoyles, 2007; Slaghuis, 1998). However, because our lower-bound SF may have been too high to distinguish the subcortical channels (some have suggested using SFs <1.5 cycles/deg; Skottun and Skoyles, 2007), our data again do not decisively address the controversy.

4.3. Implications for normal vision

Casual inspection of Fig. 3A suggests that the wire pac-men should be easier to discriminate when forming a shape but harder to discriminate otherwise, and the data confirm this observation (Fig. 4). This “illusory wire advantage”, as we call it, was large in magnitude and rivaled other methods for improving interpolation strength, such as increasing support ratio (Feltner and Kiorpes, 2010; Shipley and Kellman, 1992) or distributing visible edge material along the completed path (Maertens and Shapley, 2008). The reason for the illusory wire advantage is not well understood. It could owe to lightness induction—containing the spread of achromatic surface color (which only happens in the traditional Kanizsa shape) may add position uncertainty to a contour boundary. Or it could be because the accidental alignment of wire segments—consisting of two luminance discontinuities—might be more unlikely than the alignment of traditional pac-man edges, which have a single step-edge gradient. That is, the visual system may internalize the natural scene statistics that govern contour completion (Geisler et al., 2001) and more strongly bind elements that less frequently align by coincidence (Rock, 1983;

Wagemans et al., 2012b), as could be the case for pairs of wire segments.

Our data provide additional support for a multistage model of illusory shape discrimination, according to which observers first automatically interpolate between locally aligned (relatable) edges (Erlikhman et al., 2013; Keane et al., 2013, 2011) and then build high-fidelity shape representations that are categorized into one of the response alternatives. The normal illusory wire advantage among patients suggests that these individuals were responsive to the interpolated contours. At the same time, overall worse performance in the illusory task implies that patients were not as skilled at using such contours to perceive fine differences in illusory global shape. As further support for a multistage model, Murray et al., (2006) found that, while response magnitude and scalp topography of the VEP automatically depended on the presence of illusory contours at earlier time epochs (124–186 ms; N1 component), electrophysiological correlates strongly depended on response accuracy at later time epochs (330–406 ms; N_{CL} component). Similar conclusions were reached with a psychophysical study that manipulated cognitive strategy (Keane et al., 2012b). Healthy adults were instructed to conceptualize four physically visible inducer elements as either belonging to a single object or as being distinct (group or ungroup strategy, respectively). Distractor lines—known to disrupt illusory contour formation—were placed between the pac-man elements on certain trials. It was found that the ungroup strategy did not change performance on the fragmented condition (which lacked illusory contours) and did not alter the adverse effect of distractors placed near the illusory contours (which was taken to show intact contour interpolation), but did worsen performance in the illusory condition. In a methodologically similar study, conceptually disorganized schizophrenia patients performed as if they had adopted an ungroup strategy: they performed normally (in comparison to controls) on the fragmented task, normally in response to the distractor lines, but poorly overall in the illusory shape discrimination (Keane et al., 2014). A two-stage schema of shape completion has also been championed in the context of visual agnosia (Giersch et al., 2000). Collectively, these studies show that it is possible for either conceptual strategy or schizophrenia symptoms to seriously disrupt shape completion without imposing adverse effects on the completion of illusory contours, and that these stages can be reliably distinguished via scalp-recorded electroencephalogram. Thus, although it seems as if we perceive Kanizsa shape differences in one instant, at least two stages are required for the percept, with the latter being effortful and conceptually mediated.

4.4. Clinical implications

It has been argued elsewhere that there exists a subtype of schizophrenia characterized by conceptual and perceptual disorganization, earlier illness onset, poor premorbid social functioning, and a greater need for treatment (Uhlhaas and Silverstein, 2005; Silverstein and Keane, 2011; Keane et al., 2014). We confirm most of these features in our sample. Those individuals who had higher levels of disability (assessed with MSIF) were worse at contour integration (4 cycles/deg), worse at Kanizsa shape discrimination (traditional), and had higher levels of conceptual disorganization ($rho = 0.548$, $p = 0.006$). Increased conceptual disorganization was itself associated with worse discrimination of traditional fat/thin illusory shapes (relative to fragmented), less collinear facilitation at 4 cycles/deg, and increased PANSS positive and general symptoms ($rho = 0.459$, $p = 0.024$; $rho = 0.723$, $p < 0.0001$). (Others have linked increased positive and general symptoms with conceptual disorganization, a greater need for treatment, and a reduced closure negativity (N_{CL}) waveform, a critical marker of visual shape completion (Keane et al., 2014, p. 305; Sehatpour et al., 2010)). Note that it is unclear why several of the clinical correlations (MSIF, conceptual disorganization) arose only with the lower SF stimuli. We surmise that integration of elements distributed across larger regions of space will require frontal lobe integrity (Ciaramelli et al., 2007), which itself may be lacking in those with reduced levels of functioning or conceptual disorganization (Nakamura et al., 2008).

As an exploratory analysis, we also considered the specific PANSS items that correlated with conceptual disorganization. Reporting only rho values greater than 0.5, we found significant correlations with: somatic concerns ($rho = 0.652$, $p < 0.001$), suspiciousness ($rho = 0.561$, $p = 0.004$), poor attention ($rho = 0.652$, $p < 0.001$), stereotyped thinking ($rho = 0.676$, $p < 0.001$), unusual thought content ($rho = 0.809$, $p < 0.00001$), and preoccupation ($rho = 0.744$, $p < 0.0001$). An important exception is that neither conceptual disorganization nor any of the tasks (at either SF) correlated with overall premorbid functioning on the PAS. They also did not correlate with the individual PAS subscales. This could be because we relied primarily on patient self-report, which is inevitably prone to biases and inaccuracies, or because poor premorbid functioning is not a defining feature of the disorganized subtype after all. In either case, conceptual disorganization appears to be a unifying thread that binds an otherwise heterogeneous patchwork of symptoms and characteristics that help define a schizophrenia phenotype.

4.5. Final remarks

By comparing schizophrenia patients and well-matched controls, we have shown that contour grouping deficits exist in some fashion for collinear facilitation, contour integration, and Kanizsa shape perception. The deficits either remained constant across SF conditions or became detectable at the higher peak SF, making it unlikely that poor lower spatial frequency processing best explain previously documented results. Standing on the shoulders of past neurobiological studies, we tentatively propose that—when subjects are moderately disabled and symptomatic—there exist multiple loci of contour grouping deficits, originating as early as V1/V2 when integration is fast and short range (collinear facilitation) and as late as frontal cortex when global shape must be derived from elements dispersed across large regions of visual space (Kanizsa shape perception). Because CG deficits were relevant to symptoms and level of functioning, psychophysical performance on our three paradigms could potentially serve as a biomarker for the presence or state of the illness.

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