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Late, not early, stages of Kanizsa shape perception are compromised in schizophrenia

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ABSTRACT

Background: Schizophrenia is a devastating psychiatric disorder characterized by symptoms including delusions, hallucinations, and disorganized thought. Kanizsa shape perception is a basic visual process that builds illusory contour and shape representations from spatially segregated edges. Recent studies have shown that schizophrenia patients exhibit abnormal electrophysiological signatures during Kanizsa shape perception tasks, but it remains unclear how these abnormalities are manifested behaviorally and whether they arise from early or late levels in visual processing.
Method: To address this issue, we had healthy controls and schizophrenia patients discriminate quartets of sectored circles that either formed or did not form illusory shapes (illusory and fragmented conditions, respectively). Half of the trials in each condition incorporated distractor lines, which are known to disrupt illusory contour formation and thereby worsen illusory shape discrimination.
Results: Relative to their respective fragmented conditions, patients performed worse than controls in the illusory discrimination. Conceptually disorganized patients—characterized by their incoherent manner of speaking—were primarily driving the effect. Regardless of patient status or disorganization levels, distractor lines worsened discrimination more in the illusory than the fragmented condition, indicating that all groups could form illusory contours.
Conclusion: People with schizophrenia form illusory contours but are less able to utilize those contours to discern global shape. The impairment is especially related to the ability to think and speak coherently. These results suggest that Kanizsa shape perception incorporates an early illusory contour formation stage and a later, conceptually-mediated shape integration stage, with the latter being compromised in schizophrenia.

1. Introduction

Schizophrenia is a devastating psychiatric disorder characterized by delusions, hallucinations, disorganized thought, bizarre behavior, flat affect, and declines in social, academic, and vocational functioning. Recent studies from brain imaging and visual psychophysics have revealed a constellation of visual abnormalities that are not immediately apparent from the clinician's armchair, ranging from reduced contrast sensitivity (Slaghuis, 1998) to weaker three-dimensional depth illusions (Emrich, 1989; Keane, Silverstein, Wang, & Papathomas, 2013). In the last 30 years, and especially in the last 10 years (Silverstein & Keane, 2011; Uhlhaas & Silverstein, 2005), it has become increasingly apparent that schizophrenia impairs *perceptual organization*—the process whereby coherent and persisting object representations are derived from spatiotemporally fragmented retinal images. As examples, when faces or line drawings are shown in degraded fashion, persons with schizophrenia are worse than healthy controls at identifying those stimuli (Doniger, Foxe, Murray, Higgins, & Javitt, 2002); and when presented with a scattered array of oriented elements (Gabors), patients are less adroit at representing a subset of those Gabors as forming a single contour (Silverstein et al., 2009, 2012; Silverstein, Kovács, Corry, & Valone, 2000). The deficit can also lead to a paradoxical performance *advantage* whenever perceptual organization renders the task more difficult, as with size contrast illusions (Silverstein et al., 2013; Tibber et al., 2013; Uhlhaas, Phillips, Mitchell, & Silverstein, 2006).

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An unresolved issue is why perceptual organization impairment arises in schizophrenia. Does it occur as a result of a dysfunction of lateral connectivity in early visual cortex, as some have maintained (Kéri, Kelemen, Janka, & Benedek, 2005; Robol et al., 2013; Dakin et al., 2005)? Or does it instead arise from higher order circuits, perhaps from faulty feedback from frontal and parietal regions (Keane, Silverstein et al., 2012)? We investigated this question with a classic "Kanizsa" square stimulus, in which four white sectored circles form a darkened surface bounded by illusory contours. Kanizsa shapes make for nearly ideal test stimuli: the eliciting conditions have been extensively documented since the 1950s (Geisler, Perry, Super, & Gallogly, 2001; Kanizsa, 1955; Kellman & Shipley, 1991; Lesher & Mingolla, 1993) and the neural underpinnings of the process have been investigated non-clinically with a variety of techniques including EEG, fMRI, single-cell recording, and TMS (Lee & Nguyen, 2001; Maertens, Pollmann, Hanke, Mildner, & Moller, 2008; Murray et al., 2002; Wokke, Vandenbroucke, Scholte, & Lamme, 2013), revealing a critical role of feedback from LOC and long-range horizontal connections in V1/V2 (Seghier & Vuilleumier, 2006). Moreover, a key component process of illusory shape perception—contour completion (or contour interpolation)—is important in its own right, allowing species throughout the animal kingdom to extract object shape and number (Nieder, 2002).

1.1. EEG studies of Kanizsa shape perception in schizophrenia

The neurobiological substrate and time course of Kanizsa shape perception in schizophrenia have been studied with the scalp-recorded electroencephalogram (EEG), but the results have not always been consistent. Spencer et al. (2003) had observers discriminate Kanizsa shapes from featurally similar fragmented configurations, and measured stimulus-locked phase locking, which records EEG phase variance at a fixed duration after stimulus onset. Healthy controls, but not patients, evinced an early evoked gamma band response (72–98 ms) over occipital electrodes when responding to illusory vs. fragmented shapes. In a follow-up study, "response-locked phase locking"—measured backward in time from a subject's button press—was greater for the illusory than the fragmented stimulus for both groups. However, the difference arose at a higher frequency for controls than patients (31–44 Hz vs. 22–24 Hz) (Spencer et al., 2004). The reduced oscillation frequency was considered to reflect disrupted early "feature-binding" (though see below).

Foxe, Murray, and Javitt (2005) applied a virtually identical behavioral paradigm as above, but analyzed high density visual evoked potentials (VEPs) rather than oscillations. They found that the N1 component (106–194 ms) was enhanced for the illusory relative to the fragmented stimulus for patients and controls. It was thereby argued that illusory contour formation is intact in schizophrenia. The interpretation is plausible given that: (i) the N1 component reflects ventral stream processing, especially in the lateral occipital complex, a primary locus for illusory contour formation (Doniger et al., 2002; Halgren, Mendola, Chong, & Dale, 2003; Mendola, Dale, Fischl, Liu, & Tootell, 1999; Murray, Foxe, Javitt, & Foxe, 2004; Murray et al., 2002); and (ii) the N1 time frame corresponds to the period in which illusory contours form in behavioral and neurophysiological studies (Gold & Shubel, 2006; Guttman & Kellman, 2004; Keane, Lu, & Kellman, 2007; Lee & Nguyen, 2001; Ringach & Shapley, 1996).

Importantly, both sets of studies left open the possibility of abnormal high-level contributions to Kanizsa shape perception. Foxe et al. (2005) unexpectedly found greater right inferior frontal activation among patients in the time period of the so-called N_{Cl} waveform (240–400 ms), an established signature of perceptual closure (Butler et al., 2013). Spencer et al. (2004) discovered that the two strongest clinical correlates of reduced response-locked phase locking were global thought disorder ($r=.61$) and one of its components, conceptual disorganization ($r=.58$). These symptom correlates were estimated on the basis of how clearly a patient communicated during a clinical interview (see below) and suggest that Kanizsa shape perception is at least associated with higher order cognition (Silverstein et al., 2013; Uhlhaas et al., 2006). Spencer and colleagues also acknowledge that reduced synchrony over occipital electrodes could be ascribed to an aberrant high-level template matching process in which a configuration is recognized as a target.

Importantly, behavioral results from the above EEG studies could not settle whether perceptual differences exist in schizophrenia. Lower patient accuracy in the discrimination task (as in Spencer et al., 2003, 2004) could be blamed on generalized deficits—that is, reduced attention or motivation. Normal patient accuracy (as in Foxe et al., 2005) could be explained by ceiling effects, since the task was extremely straightforward and the stimuli so distinct. Therefore, considered jointly, the above EEG studies have not made it clear whether Kanizsa shape perception deficits exist in schizophrenia, let alone the level at which such deficits arise. What is needed, and what we provide here, are the first psychophysical data that directly address this issue.

1.2. Establishing and understanding illusory shape perception deficits in SZ

We probed Kanizsa shape perception with a variation of Ringach and Shapley's (1996) "fat/thin" shape discrimination task, which has been extensively employed to understand perceptual development (Hadad, Maurer, & Lewis, 2010), modal and amodal completion (Kellman, Garrigan, Shipley, & Keane, 2007), completion speed (Guttman & Kellman, 2004) and autism (Milne & Scope, 2008), among other issues. On each trial of our experiment, subjects discriminated the orientations of four sectored circles or pac-men (Gold, Murray, Bennett, & Sekuler, 2000; Gold & Shubel, 2006; Guttman & Kellman, 2004; Keane et al., 2007; Murray, Sekuler, & Bennett, 2001; Pillow & Rubin, 2002; Ringach & Shapley, 1996; Zhou, Tjan, Zhou, & Liu, 2008). In the illusory condition, the sectored circles jointly formed a Kanizsa square, and subjects decided whether the elements formed a fat or thin shape (see Fig. 1A). In a control ("fragmented") condition, the sectored circles faced downward to prevent illusory contours, and the task was to discern whether the elements were each rotated left or right. These two conditions have sometimes been described as differing by a geometric property, "relatability", which governs when elements can and cannot connect via interpolation (Kellman & Shipley, 1991). Half of the trials involved distractor lines, which disrupt illusory contour formation and worsen illusory shape discrimination (Dillenburger & Roe, 2010; Keane, Lu, Papathomas, Silverstein, & Kellman, 2012, 2013; Ringach & Shapley, 1996; Zhou et al., 2008). Task difficulty depended on pac-man rotational magnitude, with larger rotations making the alternatives easier to distinguish. An adaptive staircase determined the difficulty for a trial and estimated the amount of rotation needed to achieve threshold accuracy (79.7%).

Two metrics were of interest. One is *global shape integration*, which corresponds to how well subjects distinguish Kanizsa shapes relative to featurally similar fragmented shapes (without distractors). A lower relative threshold in the illusory condition demonstrates an enhanced capacity to take advantage of the Gestalt layout of the stimulus. Also of interest was how well subjects *fill-in* illusory contours. Filling-in was gauged by how much subjects responded to seemingly irrelevant information (distractor lines) placed near the filled-in paths. The underlying assumption was that the more that subjects fill-in illusory

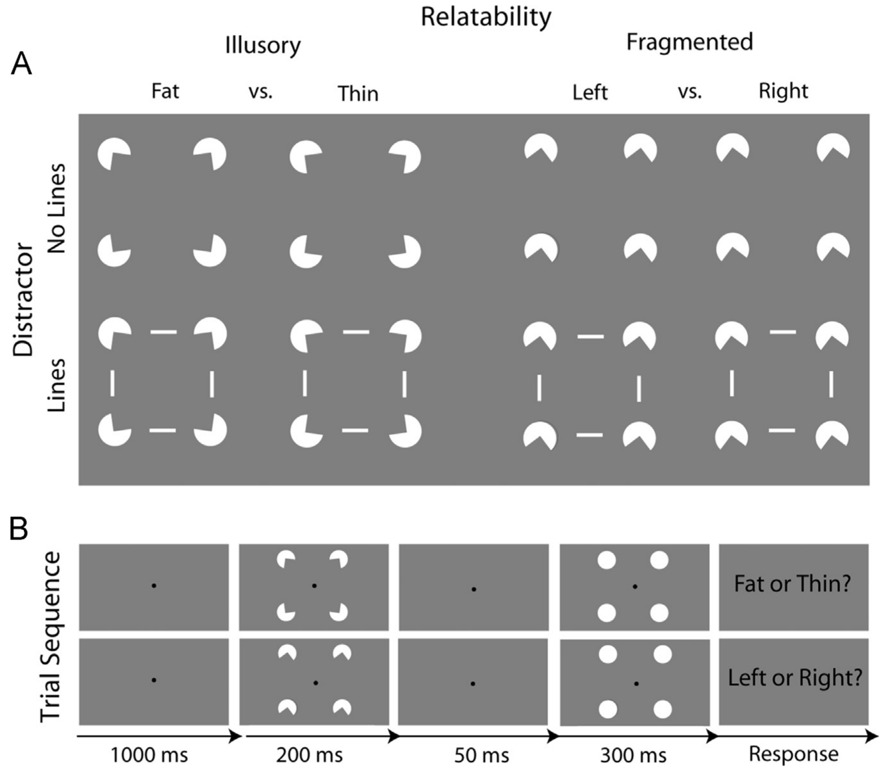

Fig. 1. *Stimuli and trial sequence*: (A) subjects discriminated illusory or fragmented squares, which were accompanied by distractor lines for half of the trials. (B) The task was to say "fat"/"thin" for the illusory condition or "left"/"right" for the fragmented condition.

contours, the more that distractors would impair discrimination in the illusory relative to the fragmented condition. This second metric was chosen because others have shown that distractor lines near the edges of Kanizsa shapes worsen illusory shape perception, but exercise little, if any effect when illusory contours are absent (Keane, Lu et al., 2012, 2013; Ringach & Shapley, 1996; Zhou et al., 2008). Reverse correlation and other studies have also revealed filling-in by examining behavioral or neural responses to line segments or luminance noise placed near filled-in boundaries (Dillenburger & Roe, 2010; Dresp & Bonnet, 1991; Dresp & Grossberg, 1997, 1999; Gold et al., 2000; Gold & Shubel, 2006; Keane et al., 2007; Keane, Lu et al., 2013). Certain displays also show phenomenologically that background texture increases contour salience when aligned with the pac-men and degrades contour salience otherwise (Ramachandran, Ruskin, Cobb, Rogers-Ramachandran, & Tyler, 1994).

Our two metrics—global shape integration and filling-in—may seem like they are measuring the same thing, but prior studies suggest otherwise. Murray, Imber, Javitt, and Foxe (2006) employed a fat/thin discrimination task and showed that—within 124–186 ms post-stimulus onset—the response magnitude and scalp topography of the VEP was strongly modulated by the presence of illusory contours but not the accuracy of response. By contrast, a later VEP time period (330–406 ms) depended on response accuracy for illusory configurations. These results were taken to show that boundary completion is automatic and dissociable from shape discrimination. Keane, Lu et al. (2013) utilized a behavioral fat/thin task and reached virtually identical conclusions. Subjects in that study were biased to conceptualize each discriminated stimulus as a single partly visible shape or as a disconnected set of edge elements (group and ungroup strategy, respectively). The elements of the stimulus were geometrically arranged to either allow or prevent illusory contours (relatable and non-relatable conditions, respectively). The "group" strategy enhanced the discrimination of relatable stimuli but not non-relatable stimuli. This provides evidence that how a subject cognitively regards a Kanizsa stimulus can play an important role in how well it is discriminated. At the same time, distractor line effects obtained regardless of strategy, indicating that illusory contours were filled in automatically and independently of cognitive expectation.

We investigated illusory contour and shape completion in the context of a key symptom of schizophrenia, *conceptual disorganization*, which was evaluated by how a participant communicated during the clinical interview. A conceptually disorganized person's speech tends to be long-winded and rambling, with no obvious final objective; it contains logical errors, non-sequiturs and loose associations, so that one topic does not clearly relate to the next; and it is often interrupted with extended pauses, where the individual might completely lose his/her train of thought. In its most severe forms, disorganized speech may be almost completely incomprehensible, producing a veritable "word salad." There are good reasons to focus on conceptual disorganization. Spencer and colleagues found that it strongly correlated with stimulus- and response-locked phase locking in Kanizsa detection tasks ($rs > .57$) (2003, 2004). Cross-sectional and longitudinal studies have linked conceptual disorganization with reduced size contrast (Ebbinghaus) illusions and impaired contour integration (Silverstein et al., 2013; Uhlhaas et al., 2006). More generally, thought disorder, a symptom which encompasses conceptual disorganization, has been touted as the "primary defining feature" of schizophrenia in that it unifies an otherwise extremely heterogeneous illness (Andreasen, 1999). Indeed, a disturbance in associative processes was seen as the hallmark of schizophrenia in one of the original formulations of the disorder (Bleuler, 1911/1950).

To summarize, we examined the pac-man rotational magnitude (threshold) needed to reach ~80% accuracy for four different conditions, corresponding to whether or not there were illusory contours (relatability) and whether or not there were distractor lines. Illusory contour formation was assessed by gauging how much distractors increased threshold in the illusory vs. the fragmented conditions; global shape integration was assessed by comparing thresholds for the illusory and fragmented conditions without distractors. If distractor lines increase threshold in the illusory condition with little effect in the fragmented, and if only global shape integration is impaired in the illness, then primarily late integration processing stages would be implicated in schizophrenia. By contrast, if patients are less susceptible to distractor lines *and* they more poorly distinguish Kanizsa shapes, then early and perhaps also late stages could be impaired. A high-level integration deficit further implies worse global shape integration among conceptually disorganized individuals.

2. Methods

2.1. Observers

For all subjects, inclusion/exclusion criteria were: (1) age 18–65; (2) no history of electroconvulsive therapy; (3) absence of neurological, pervasive developmental, or affective disorders; (4) no drug dependence in the last 6 months (as assessed with the Mini International Neuropsychiatric Interview 6.0 (Sheehan et al., 1998); (5) Full Scale IQ ≥ 75, as estimated with a vocabulary test (Zachary, 1991) (cut-off similar to Spencer et al. (2003, 2004); (6) no brain injury due to accident or illness (e.g., stroke); and (7) the ability to provide written informed consent. All subjects accepted payment for their time.

The eligible patient sample consisted of 78 paid persons who met DSM IV-TR (APA, 2000) criteria for schizophrenia or schizoaffective disorder, according to the Diagnostic Interview for Genetic Studies (DIGS) (Nurnberger et al., 1994) and electronic medical records. Three patients (3.9% of the sample) could not reach threshold at the lowest difficulty level (maximum rotation) on the fragmented condition and were removed from the study. The Premorbid Adjustment Scale (PAS) was administered to assess social isolation, peer relationships, scholastic performance, school adaptation, and social-sexual aspects of life prior to illness onset (Cannon-Spoor, Potkin, & Wyatt, 1982). All patients except one were taking atypical and/or typical antipsychotic medications at the time of testing. We assessed whether or not there was any correlation between medication and task performance after converting total daily antipsychotic medication dosages to chlorpromazine equivalents (Andreasen, Pressler, Nopoulos, Miller, & Ho, 2010).

The control group comprised 18 psychologically healthy individuals, as determined with the Structured Clinical Interview for DSM-IV Diagnosis for non-patients (SCID-NP; Spitzer, Williams, Gibbon, & First, 1992). In an effort to match on IQ and education, healthy individuals without 4-year college degrees were preferentially recruited. Demographic and clinical variables for the final samples are shown in Table 1.

Symptoms of the illness were assessed with the Positive and Negative Syndrome Scale (PANSS; Kay, Fiszbein, & Opler, 1987). As in prior studies (Silverstein et al., 2013; Uhlhaas et al., 2006), we categorized members of our clinical sample as "disorganized" if they exhibited moderate to severe levels of conceptual disorganization (viz., scoring >3 on item P2 of the PANSS) and as "non-disorganized", otherwise (see Table 2). One of the 75 subjects did not complete the PANSS assessment and so could not be categorized into these two groups.

Table 1
Demographic and clinical characteristics of study participants.

Demographic/clinical factor	Schizophrenia ($N=75$)		Controls ($N=18$)		Group comparison
	Mean	*SD*	*Mean*	*SD*	
Age	46.0	11.2	41.1	9.9	$p=.097$
Education, father (years)	13.4	3.0	12.6	3.5	$p=.319$
Education, mother (years)	12.5	2.6	12.2	2.8	$p=.701$
Education, self (years)	13.1	2.2	13.4	2.0	$p=.531$
Ethnicity (% Caucasian)	60.0	NA	38.9	NA	$p=.120$
FSIQ (Shipley)	93.9	10.5	94.7	7.4	$p=.771$
Gender (% male)	62.7	NA	50.0	NA	$p=.422$
Handedness (% right)	90.7	NA	83.3	NA	$p=.596$
Neuroleptics: typical/atypical/both	6/55/8	NA	NA	NA	NA
PANSS, positive	20.1	4.6	NA	NA	NA
PANSS, negative	18.2	4.6	NA	NA	NA
PANSS, general	39.6	7.2	NA	NA	NA
PANSS, total	77.9	13.7	NA	NA	NA
Schizophrenia/schizoaffective disorder	46/29	NA	NA	NA	NA

Note: FSIQ, Full Scale IQ, as estimated with the Shipley Institute of Living Scale (Zachary, 1991)

2.2. Apparatus

Experimental stimuli were shown on LED monitors (60 Hz) at one of three testing sites and the viewing distance was varied (between 620 and 650 mm) so that individual pixels subtended .025° of visual angle square. Stimuli were displayed at (achromatic) intensities of 59 cd/m^2 (black) or 76 cd/m^2 (white), as verified with a Konica Minolta LS-100 luminance meter. The experiment was coded in Matlab with Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997) and Palamedes Toolbox extensions (Prins & Kingdom, 2009).

2.3. Stimulus

Stimuli consisted of four white sectored circles (diameter$=3.0°$; wedge angle $=90°$) centered at the vertices of an invisible square (side$=9.0°$), which itself was

Table 2
Demographic and clinical characteristics of patient subgroups.

Demographic/clinical factor	Disorganized ($N=15$)		Non-disorganized ($N=59$)		Group comparison
	Mean	*SD*	*Mean*	*SD*	
Age (years)	45.3	12.7	46.1	11.0	$p=.797$
Age of psychosis onset	21.5	7.1	22.9	7.5	$p=.534$
Chlorpromazine equiv. (mg/day)	828	527	462	329	$p=.02$*
Education, father (years)	13.8	2.6	13.4	3.1	$p=.664$
Education, mother (years)	13.2	2.8	12.3	2.6	$p=.292$
Education, self (years)	13.6	2.2	12.9	2.3	$p=.346$
Ethnicity (% Caucasian)	53.3	NA	61.0	NA	$p=.769$
FSIQ (Shipley)	93.9	10.7	93.8	10.6	$p=.965$
Gender (% male)	66.7	NA	61.0	NA	$p=.772$
Handedness (% right)	93.3	NA	89.8	NA	$p=1.000$
Hospitalizations (#)	11.8	8.3	8.2	7.3	$p=.115$
Neuroleptics: typical/atypical/both	3/10/2	NA	3/44/6	NA	$p=.206$
Outpatient (%)	33.3	NA	66.7	NA	$p=.037$*
PANSS, positive	25.1	4.9	18.9	3.5	$p<.001$***
PANSS, negative	19.9	4.0	17.8	4.7	$p=.107$
PANSS, general	44.8	7.3	38.3	6.5	$p=.001$**
PANSS, total	89.9	13.1	74.9	12.1	$p<.001$***
Premorbid adjustment (overall)	2.5	.9	2.5	.7	$p=.863$
Premorbid adjustment (social sexual functioning)	6.86	5.10	4.34	2.79	$p=.095$

* $p<.05$.
** $p<.01$.
*** $p<.001$.

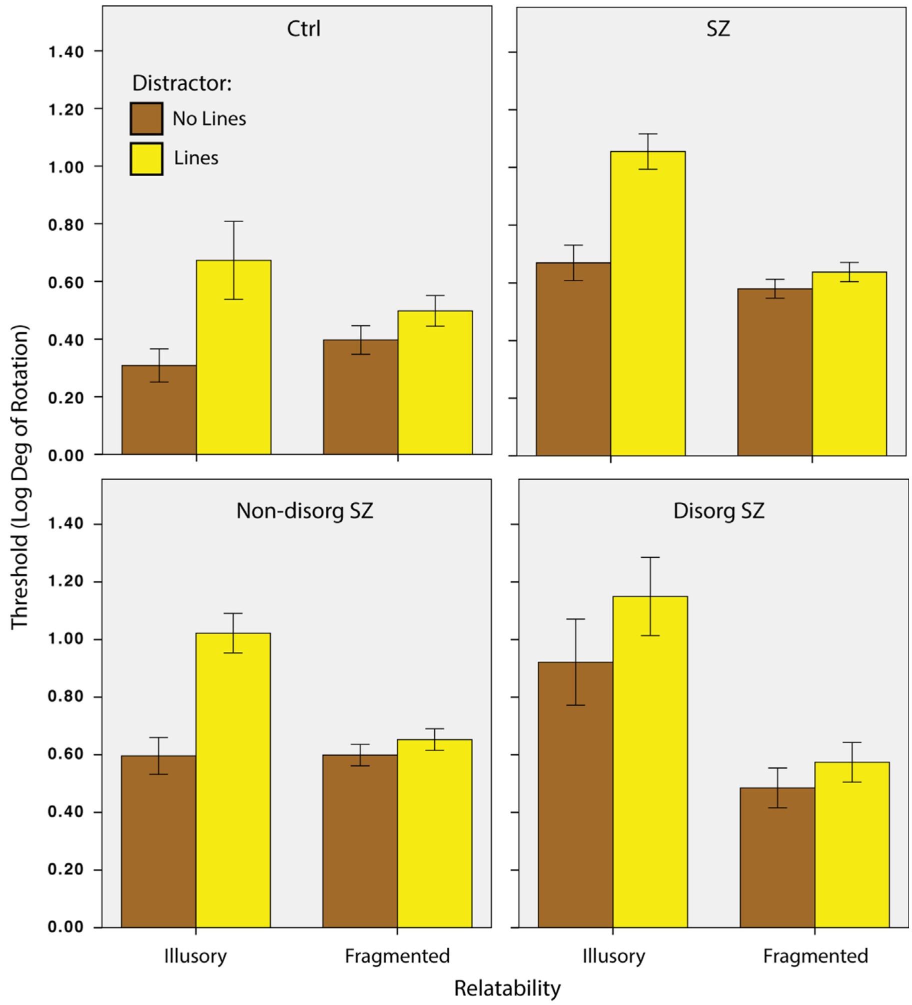

Fig. 2. *Results from the computerized experiment*: Thresholds for trials with and without distractor lines (light yellow and dark orange, respectively) are shown for the healthy control and schizophrenia groups (top) and for the two patient subgroups (bottom). Higher thresholds signify worse performance. Errors = ± SEM.

centered on the screen (Fig. 1A). The total edge length of the mouths of the four pac-men divided by the perimeter of the invisible square on which they were centered was equal to one-third. To put it another way, the unrotated pac-men in the illusory condition formed a square, one-third of which was physically specified (support ratio = .33; Shipley & Kellman, 1992). Certain trials contained distractor lines (dimensions = 4.0 × .1°), which were centered between the sectored circles and had a length equal to 2/3rds of the illusory edge. 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.

2.4. Procedure

The trial presentation sequence (Fig. 1B) was similar to earlier studies (Keane, Lu et al., 2012; Ringach & Shapley, 1996; Zhou et al., 2008) and consisted of a 1000 ms black screen, a 200 ms target presentation, a 50 ms uniform black screen, and 300 ms mask (to cap stimulus processing time). Another black screen would linger until a response, after which an auditory beep sounded for a 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 counter-balanced across subjects. In the illusory condition, the sectored circles were oriented to enable illusory contour formation (i.e., they were "relatable"; Kellman & Shipley, 1991). The elements were individually rotated 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 by the same magnitude to produce a thin shape; see Fig. 1). In the fragmented trials, the elements were oriented downward (to prevent illusory contours) and were individually rotated to the right or left all in the same direction. 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. To reduce the possibility of group differences in key press errors (mismatching a key press with a response), we had subjects verbally say "left"/"right" or "fat"/"thin" after each trial, with the experimenter subsequently entering the response on behalf of the subject. In each half of the experiment, there were 64 practice trials and 84 non-practice trials, the latter half of which presented distractor lines. This number of practice trials—which was slightly smaller than what has been used in other studies (Keane, Lu et al., 2012; Zhou et al., 2008)—allowed subjects to get acclimated to the fast presentation times and slight orientation differences that they would be seeing for the rest of the experiment (see below). The first non-practice trial and the first distractor line trial in a block were excluded for the purposes of threshold estimation since such trials were more often missed by observers. Subjects received a brief break between blocks and immediately preceding the distractor line trials.

Task difficulty depended on rotational magnitude, with larger rotations making the alternatives easier to distinguish. A Bayesian adaptive "Psi" method (Kontsevich & Tyler, 1999) recommended a rotational magnitude on each trial so as to minimize entropy (uncertainty) of the slope and threshold estimates of the psychometric function. Rotational magnitude was expressed in log units given the decelerating function relating this quantity to proportion correct (Zhou et al., 2008). The algorithm assumed a log-Weibull (Gumbel) function (Prins & Kingdom, 2009):

$$\psi(x,\alpha,\beta,\gamma,\lambda) = \gamma + (1-\gamma-\lambda)(1-\exp(-10^{\beta(x-\alpha)}))$$

where ψ is the proportion correct, x is the rotational magnitude, α is threshold, β is slope, γ is the guess rate (.5), and λ corresponds to the proportion of accidental responses (assumed to be .03) (Wichmann & Hill, 2001). Threshold, the most important parameter, establishes the position of the sigmoidal curve along the abscissa and corresponds to the rotational magnitude (in log degrees) needed for 79.7% accuracy. Overall, we selected the Psi method because it makes no assumption about slope—which can change from condition to condition—and because it provides arguably the most efficient means for estimating two parameter psychometric functions (Klein, 2001), yielding a reliable threshold estimate (± 2 dB) with as few as 30 trials.

Instructions were shown immediately before and after the practice trials on each half of the experiment. Special effort was made 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 accommodate to the subtle shape differences and brief stimulus presentation.

2.5. Analyses

Two sets of analyses were performed on the threshold values—one comparing controls and patients, and the other comparing disorganized and non-disorganized patients. For each comparison, we conducted a 2 (relatability: illusory, fragmented) × 2 (distractor: no lines, lines) × 2 (group) mixed-model Type III Sum-of-Squares ANOVA. Filling-in was measured as the relatability × distractor interaction. Accordingly, a three-way interaction (equivalent to a *t*-test on the difference scores) determined whether the groups differed on this variable. Global shape integration was assessed separately and corresponded to the illusory-fragmented threshold difference without distractors. Relationships between symptoms and task performance were evaluated using Spearman rho correlations. *t*-Tests were two-tailed and equal variances were assumed, unless otherwise noted.

3. Results

Fig. 2 shows the threshold results for each condition and group; Fig. 3 directly compares the filling-in and global shape integration metrics for those same groups. There were main effects of relatability, distractor, and group ($F(1,91)=6.85$, $p=.01$, $\eta_p^2=.07$; $F(1,91)=36.42$, $p<.001$, $\eta_p^2=.286$; $F(1,91)=11.88$, $p=.001$, $\eta_p^2=.116$). An expected distractor by relatability interaction ($F(1,91)=18.417$, $p<.001$, $\eta_p^2=.168$) revealed that the distractors raised threshold more in the illusory than the fragmented condition. Importantly, this interaction did not at all depend on whether people had schizophrenia ($F(1,91)=.02$, $p=.638$, $\eta_p^2=.002$; see Fig. 3A). This suggests that the two groups similarly filled-in illusory contours. By contrast, global shape integration was compromised in the clinical group ($t(63.18)=2.20$, $p=.031$, $d=.58$ unequal variances; Fig. 3B) such that controls, but not patients, had lower thresholds in the illusory relative to the fragmented condition.

In comparing non-disorganized and disorganized patients, we found main effects of relatability ($F(1,72)=32.21$, $p<.001$, $\eta_p^2=.309$) and distractor ($F(1,72)=20.42$, $p<.001$, $\eta_p^2=.221$), similar to before, but not patient subgroup ($F(1,72)=.967$, $p=.329$, $\eta_p^2=.013$). More importantly, there was an expected interaction between distractor and relatability ($F(1,72)=12.04$, $p<.001$, $\eta_p^2=.143$), which itself did not depend on subgroup ($F(1,72)=2.14$, $p=.158$, $\eta_p^2=.029$; see Fig. 3A). This argues that disorganization exercises no obvious effect on contour filling-in. Global shape integration, by contrast, differed strongly between the subgroups ($t(72)=3.25$, $p=.002$, $d=.95$; see Fig. 3B), with the disorganized group performing worse. Here, it is important to note that, because a number of disorganized patients performed at near-chance levels in the illusory condition, it was difficult for the distractor lines to further elevate thresholds in that case, leading to a probable *under*estimation of filling-in for this subgroup.

We also compared the two most extreme groups, controls and disorganized. There were effects of relatability, distractor, and group ($F(1,31)=19.56$, $p<.01$, $\eta_p^2=.387$; $F(1,31)=21.14$, $p<.001$, $\eta_p^2=.405$; $F(1,31)=10.42$, $p=.003$, $\eta_p^2=252$). There was the expected distractor × relatability interaction ($F(1,31)=5.37$, $p=.027$, $\eta_p^2=.148$), which, again, did not depend on group ($F(1,31)=.36$, $p=.551$, $\eta_p^2=.012$; see Fig. 3C). The shape integration deficit in disorganized patients was large ($t(18.57)=3.814$, $p=.001$, $d=1.12$, unequal variances). In fact, the control subject with the worst global shape integration value still performed better than over half of the disorganized patients (viz., in the upper left half of Fig. 3D, the 8 markers furthest from the diagonal are all disorganized patients). If only patients with negative filling-in were included in the analysis—so that the disorganized group as a whole exhibited *stronger* filling-in than controls—qualitatively the same result emerged ($t(24)=2.29$, $p=.03$, $d=.83$), further demonstrating the specificity of the impairment to global shape integration.

To ascertain whether shape integration impairments can arise without conceptual disorganization, we also compared non-disorganized patients and controls. There were main effects of relatability, distractor, and group ($F(1,75)=4.25$, $p=.043$, $\eta_p^2=.054$; $F(1,75)=3.07$, $p<.001$, $\eta_p^2=.318$; $F(1,75)=10.97$, $p=.001$, $\eta_p^2=.128$). There was an interaction of relatability and distractor ($F(1,75)=21.41$, $p<.001$, $\eta_p^2=.222$), which did not depend on group ($F(1,75)=.70$, $p=.405$, $\eta_p^2=.009$). Global shape integration also did not depend on group ($t(75)=1.01$, $p=.317$, $d=.27$, unequal variances). Thus, it seems that although people with schizophrenia as a whole are worse at shape integration, individuals with moderate to severe levels of conceptual disorganization were primarily driving the effect.

An objection so far is that subjects may be performing worse on Kanizsa shape perception tasks because these individuals have broader orientation tuning curves, making them less sensitive to the slants of the edges that decide contour convexity (Robol et al., 2013; Schallmo, Sponheim, & Olman, 2013). This is unlikely in our case because the highly influential disorganized patients had (non-significantly) *lower* fragmented thresholds than the non-disorganized patients and had similar fragmented thresholds to the healthy controls ($p=.244$).

Clinical and demographic correlates were also considered. Across all patients, neither filling-in nor global shape integration correlated with IQ, age, visual acuity, estimated age of onset of psychotic symptoms, estimated age of first psychiatric hospitalization, estimated total number of psychiatric hospitalizations, schizoaffective vs. schizophrenia diagnosis, handedness, outpatient status, education level (self/mother/father), medication dosage (in CPZ equivalents), premorbid adjustment scale scores (total, and subscores), or past visual hallucinations (all $ps>.07$, uncorrected). Interestingly, global shape integration deficits were more pronounced for patients who smoked ($r=.308$, $p=.008$) and filling-in was less pronounced for male patients ($r=.294$, $p=.01$). Both findings are empirically unprecedented, would not survive multiple corrections, and so must be regarded as preliminary (for a discussion of the relation between sex and perceptual organization in schizophrenia, see Joseph, Bae, and Silverstein (2013)). There were no significant correlations with positive/negative/general/total PANSS scores or with reports of current visual hallucinations ($ps>.11$). It must be acknowledged that our patients were higher functioning, with about 60% receiving treatment on an outpatient basis (requiring at most biweekly doctor visits) and none requiring inpatient psychiatric hospitalization. Inclusion of more severely ill patients would obviously increase sample heterogeneity and make detection of other symptom correlates more likely. Nevertheless, these data replicate past findings of a strong relationship between being able to systematize visual elements into discrete forms and organize thoughts into fluid and coherent speech.

Visual hallucinations were also considered since their severity correlated with occipital oscillation abnormalities in Spencer et al. (2004). We found no correlations with either shape integration or filling-in. This could be because we examined only the presence, not severity, of visual hallucinations or it could be because only subjects with the most pronounced hallucinations produced the overall effect in Spencer et al. (p. 17292). It is worth noting, however, that current visual hallucinations in our study were linked with

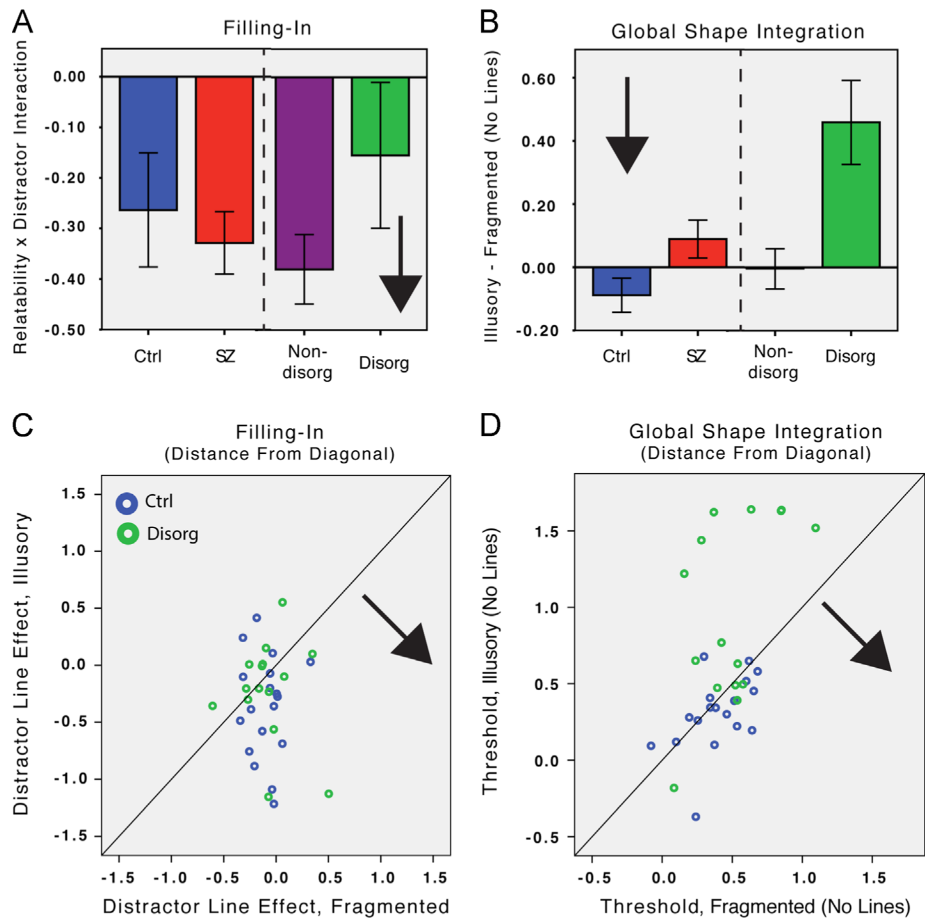

Fig. 3. *Contour filling-in and shape integration for controls and patients*: Values in the direction of the arrow indicate better filling-in (left panels) or better shape integration (right panels). (A, B) Whereas contour filling-in was similar between groups, global shape integration was worse for schizophrenia patients, especially those with conceptual disorganization. (C, D) The distractor line effect—how much performance worsens by adding distractor lines—was similar between controls and disorganized patients for the illusory and fragmented condition. The same two groups differed sharply on their ability to discriminate illusory relative to fragmented configurations.

conceptual disorganization (ρ=.250, p=.033), which is consistent with past reports (Lee, Williams, Loughland, Davidson, & Gordon, 2001). It is also consistent with the hypothesis that hallucinations and other positive symptoms represent responses to an overall state of disorganization, reflecting the compensatory development of hyper-synchronized networks that ultimately lead to symptoms such as hallucinations (Lee, Williams, Breakspear, & Gordon, 2003; Lee, Williams, Haig, & Gordon, 2003; Williams et al. 2009).

4. Discussion

We employed a variant of the well-validated fat/thin discrimination task to improve upon prior schizophrenia studies, which have not yet established the existence, let alone neural locus, of Kanizsa shape perception impairments. We found that, regardless of group, distractors raised thresholds more in the illusory relative to fragmented conditions, suggesting that patients fill-in and rely upon illusory contours during Kanizsa shape discrimination. Yet patients simultaneously demonstrated higher thresholds in the illusory versus fragmented condition, indicating that they could not properly employ illusory contours for distinguishing illusory shape. Shape integration impairments primarily arose among those with moderate to severe levels of conceptual disorganization, underscoring a critical role for this symptom in perception and thought. The group differences could not be attributed to poor motivation or attention since all subjects performed at about the same level of accuracy on all conditions and since integration was always measured as a within-subject difference. These data, we believe, are the first to behaviorally establish Kanizsa shape perception impairment in schizophrenia and to clearly link this deficit to conceptual disorganization.

4.1. Implications for EEG studies

A major goal of our study was to arbitrate between the at times conflicting EEG results from past reports on Kanizsa shape perception in schizophrenia. Our results corroborate Foxe et al.'s (2005) interpretation of the N1 VEP modulation as a signature of intact illusory contour formation in the disorder. Just as their N1 component obtained for Kanizsa shapes regardless of patient status, so too did our distractor line effects arise regardless of clinical status. Foxe et al.'s report of abnormal frontal lobe activation is also consistent with our claim that patients are poor at representing illusory contours at a conceptual stage of analysis.

Our data additionally corroborate certain behavioral and gamma band synchrony results of Spencer et al. (2003, 2004. People with schizophrenia genuinely are worse at detecting Kanizsa shapes, which in turn is intimately linked to levels of conceptual disorganization. However, a birds-eye view of the evidence prevents us from endorsing the claim that these deficits originate in early occipital areas. As noted by others (Foxe et al., 2005), gamma band synchrony commonly arises over frontal areas during illusory shape perception tasks, obtains several hundred milliseconds after stimulus onset, and could mark differences in attention or target selection (Csibra, Davis, Spratling, & Johnson, 2000; Herrmann & Mecklinger, 2000; Herrmann, Mecklinger, & Pfeifer, 1999). Spencer et al. (2004) also acknowledge that gamma irregularities might be ascribed to poor "template matching" in which incoming sensory representations are compared to long-term shape representations. We go even further and argue that it is not any template matching that is impaired (given the relatively normal fragmented discrimination in the disorganized group), but the process of precisely matching illusory contours with the corresponding shape template boundaries maintained in long-term memory. In other words, it is not enough that illusory contours are synthesized reflexively at early stages of perception, since such a process can proceed without any conscious recognition or awareness whatsoever (Keane, Mettler, Tsoi, & Kellman, 2011; Lee & Nguyen, 2001). Successful shape discrimination also requires a non-obligatory process of integrating contours into a high-fidelity shape representation and comparing that shape to the response alternatives. It is this last set of operations that we claim to be most problematic for persons with schizophrenia.

The present investigation also sheds light on EEG studies that investigate visual shape completion in healthy adults. Murray et al. (2006) argued on the basis of electrophysiological results that distinguishing Kanizsa shapes comprises an early automatic boundary formation stage followed by a conceptual shape discrimination stage. The current data obviously cohere well with these results: our clinical participants automatically formed illusory contours, but were less able to use those contours to differentiate shape. This two-stage model of Kanizsa shape discrimination is also consonant with a previous behavioral study, as noted (Keane, Lu et al., 2012) and with a visual agnosia investigation in which a brain damaged patient could complete contours but not bind those contours into shapes (Giersch, Humphreys, Boucart, & Kovács, 2000).

4.2. Conceptual and perceptual organization in schizophrenia

Based on multiple published reports, Uhlhaas and Silverstein (2005) posited a subtype of schizophrenia characterized by poor premorbid social functioning, earlier illness onset, poor response to medication and treatment, heightened levels of conceptual disorganization, and impaired perceptual organization (e.g., reduced contour integration or Ebbinghaus-type illusions). Results from the present investigation support most attributes of this hypothesized "disorganized" subtype. In our sample (Table 2), persons who were conceptually disorganized had more severe positive and general symptoms, were more likely to require greater than an outpatient level of care, were less adroit at Kanizsa shape discrimination (relative to fragmented discrimination), and had marginally poorer premorbid social-sexual functioning (p=.095). In contrast to predictions, however, the disorganized and non-disorganized schizophrenia patients were undifferentiated on their age of onset of psychiatric symptoms and age at first hospitalization (both furnished by patient self-report). Other aspects of premorbid functioning (e.g., scholastic performance and peer relationships) were also similar between the two patient groups. Nevertheless, our results reinforce the notion that there may be a genuine etiopathophysiological subtype of schizophrenia, which may be usefully segregated and targeted in genetic and treatment studies (Rietkerk et al., 2008).

So what is the causal relation between shape integration impairments and conceptual disorganization? Does disorganization cause poor perceptual organization or is there a common cause to both? There are no clear answers to these questions at present. Some have argued that there may be a widespread disturbance in "cognitive coordination" (Phillips & Silverstein, 2003) that disrupts perception, thinking, and motor processing, which may all result from hypofunctioning NMDA glutamate receptors. A related possibility is that the underlying neural machinery required for organizing thoughts are also recruited in high-level shape perception, and that disrupting the one is tantamount to disrupting the other. As evidence, healthy people, when biased to conceptualize Kanizsa configurations as fragmented, evince a pattern of results very similar to those produced by the disorganized patients in the present study (Keane, Lu et al., 2012): they normally respond to distractor lines, normally discriminate fragmented arrays, but poorly discriminate illusory shapes. In other words, healthy people can be biased to see Kanizsa shapes like disorganized schizophrenia patients by adopting a fragmented conceptual schema. A specific region that may subserve perception and thought on these tasks may be orbitofrontal cortex. The OFC is active ~300 ms after stimulus onset during certain Kanizsa shape detection tasks (Halgren et al., 2003) and contributes to various forms of object recognition (Bar, 2003). Gray matter volume in the region gradually shrinks over the course of the illness, especially among persons with thought disorder (Nakamura et al., 2008).

4.3. Illusory contour formation and other forms of early integration in schizophrenia

We provided evidence for intact illusory contour formation in schizophrenia by showing that—regardless of clinical status—distractor lines impose a stronger adverse effect when appearing near illusory rather than fragmented contours. We believe it is premature, however, to infer that all forms of the illness leave illusory contour formation unscathed. It is possible that early contour linking could be compromised primarily or even exclusively in so-called Kraepelian patients, who have a unique etiopathological profile, characterized by a greater frequency of long-term inpatient psychiatric care, a deteriorating course, formal thought disorder (i.e., conceptual disorganization), and posteriorization of gray matter loss extending to the occipital lobe (Mitelman & Buchsbaum, 2007). Such patients might be considered as an extreme form of the disorganized subtype described above and might be particularly vulnerable to various forms of early visual processing abnormalities. Consider, for example, a classic surround contrast suppression task, in which the contrast of a central patch is reduced when surrounded by a high-contrast texture (Chubb, Sperling, & Solomon, 1989). The effect is commonly thought to rely upon gain control between spatial frequency-tuned inhibitory neurons in V1. Dakin and colleagues (Dakin et al., 2005) found enormous reductions in surround contrast suppression with chronic inpatient schizophrenia subjects, intermediate effects with a mixture of inpatients and outpatients (Tibber et al., 2013) and very small effects with mostly outpatients (Barch et al., 2012), all of which are consistent with the view that primarily Kraepelian patients generate the effect. Results from illusory contour tasks may take on a similar pattern.

More generally, data from our study and others do not support the hypothesis of low-level grouping impairments in high-functioning persons with schizophrenia. Two possible counterexamples are worth considering. One derives from a collinear facilitation task in which sensitivity to detect the presence of a central low-contrast oriented element is increased when it is flanked by collinear (versus orthogonal) high contrast elements (Polat & Sagi, 1993). The effect is robust in healthy controls but putatively absent in remitted schizophrenia. The behavioral difference is often attributed to impaired excitatory lateral interactions between orientation tuned spatial frequency filters in V1 (Kéri et al., 2005; Must, Janka, Benedek, & Kéri, 2004). However, patients in one of our on-going studies are managing to achieve normal levels of facilitation, at least in some cases (Keane, Erlikhman, Kastner, Paterno & Silverstein, in preparation), and so we cannot yet embrace the conclusion. Reduced contrast surround suppression, discussed above (Barch et al., 2012), presents another possible counterexample. Here again the data are not entirely compelling since the effect sizes are barely detectable even with large samples (~260 subjects, half patients) and since alternative explanations cast in terms of higher-level "object-knowledge" must still be ruled out, as noted by others (Dakin, Carlin, & Hemsley, 2005; Lotto & Purves, 2001). The foregoing, of course, does not mean that all aspects of early vision are intact in schizophrenia. The P1 component (~54–104 ms) of the VEP, for example, is reliably attenuated along the dorsal pathway (Butler et al., 2013; Foxe et al., 2005) for a variety of stimulus types even for first episode patients (Yeap, Kelly, Thakore, & Foxe, 2008). Our claim here is simply that—of the low-level deficits that exist in the disorder—none have plausibly been shown to be specific to visual grouping when the patients are high-functioning.

4.4. Future directions

Unintelligible thought or speech can be precipitated by injury (stroke victims with Wernicke's aphasia), illness (e.g., influenza patients with delirium), drug intake (Ketamine-induced psychosis: Krystal et al., 2005) or other forms of psychopathology (autism: Solomon, Ozonoff, Carter, & Caplan, 2008). Therefore, we ask: Must disorganization be accompanied by schizophrenia for perceptual organization deficits to arise? Another question alluded to briefly above is: Are acutely ill Kraepelian patients compromised in forming illusory contours? It would additionally be useful to investigate the practical consequences of poor visual shape completion and whether such dysfunction can be remediated by instruction, training, or neurostimulation. Addressing the foregoing issues will shed light on the interrelation of thought and perception for representing a structured distal environment, as well as the plasticity of these relationships in normal and pathological states.

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References

Andreasen, N. C. (1999). A unitary model of schizophrenia: Bleuler's "fragmented phrene" as schizencephaly. *Archives of General Psychiatry*, *56*, 781–787.

Andreasen, N. C., Pressler, M., Nopoulos, P., Miller, D., & Ho, B. C. (2010). Antipsychotic dose equivalents and dose-years: A standardized method for comparing exposure to different drugs. *Biological Psychiatry*, *67*, 255–262.

APA (2000). *Diagnostic and statistical manual of mental disorders*.

Bar, M. (2003). A cortical mechanism for triggering top-down facilitation in visual object recognition. *Journal of Cognitive Neuroscience*, *15*, 600–609.

Barch, D. M., Carter, C. S., Dakin, S. C., Gold, J., Luck, S. J., Macdonald, A., et al. (2012). The clinical translation of a measure of gain control: The contrast-contrast effect task. *Schizophrenia Bulletin*, *38*, 135–143.

Bleuler, E. (1911/1950). *Dementia praecox or the group of schizophrenias*. New York: International Universities Press.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.

Butler, P. D., Abeles, I. Y., Silverstein, S. M., Dias, E. C., Weiskopf, N. G., Calderone, D. J., et al. (2013). An event-related potential examination of contour integration deficits in schizophrenia. *Frontiers in Psychology*, *4*, 132.

Cannon-Spoor, H. E., Potkin, S. G., & Wyatt, R. J. (1982). Measurement of premorbid adjustment in chronic schizophrenia. *Schizophrenia Bulletin*, *8*, 470–484.

Chubb, C., Sperling, G., & Solomon, J. A. (1989). Texture interactions determine perceived contrast. *Proceedings of the National Academy of Sciences of the United States of America*, *86*, 9631–9635.

Csibra, G., Davis, G., Spratling, M. W., & Johnson, M. H. (2000). Gamma oscillations and object processing in the infant brain. *Science*, *290*, 1582–1585.

Dakin, S., Carlin, P., & Hemsley, D. (2005). Weak suppression of visual context in chronic schizophrenia. *Current Biology*, *15*, R822–R824.

Dillenburger, B., & Roe, A. W. (2010). Influence of parallel and orthogonal real lines on illusory contour perception. *Journal of Neurophysiology*, *103*, 55–64.

Doniger, G. M., Foxe, J. J., Murray, M. M., Higgins, B. A., & Javitt, D. C. (2002). Impaired visual object recognition and dorsal/ventral stream interaction in schizophrenia. *Archives of General Psychiatry*, *59*, 1011–1020.

Dresp, B., & Bonnet, C. (1991). Psychophysical evidence for low-level processing of illusory contours and surfaces in the Kanizsa square. *Vision Research*, *31*, 1813–1817.

Dresp, B., & Grossberg, S. (1997). Contour integration across polarities and spatial gaps: From local contrast filtering to global grouping. *Vision Research*, *37*, 913–924.

Dresp, B., & Grossberg, S. (1999). Spatial facilitation by color and luminance edges: Boundary, surface, and attentional factors. *Vision Research*, *39*, 3431–3443.

Emrich, H. M. (1989). A three-component-system hypothesis of psychosis. Impairment of binocular depth inversion as an indicator of a functional dysequilibrium. *British Journal of Psychiatry Supplement*, 37–39.

Foxe, J. J., Murray, M. M., & Javitt, D. C. (2005). Filling-in in schizophrenia: A high-density electrical mapping and source-analysis investigation of illusory contour processing. *Cerebral Cortex*, *15*, 1914–1927.

Geisler, W. S., Perry, J. S., Super, B. J., & Gallogly, D. P. (2001). Edge co-occurrence in natural images predicts contour grouping performance. *Vision Research*, *41*, 711–724.

Giersch, A., Humphreys, G. W., Boucart, M., & Kovacs, I. (2000). The computation of occluded contours in visual agnosia: Evidence for early computation prior to shape binding and figure-ground coding. *Cognitive Neuropsychology*, *17*, 731–759.

Gold, J. M., Murray, R. F., Bennett, P. J., & Sekuler, A. B. (2000). Deriving behavioural receptive fields for visually completed contours. *Current Biology*, *10*, 663–666.

Gold, J. M., & Shubel, E. (2006). The spatiotemporal properties of visual completion measured by response classification. *Journal of Vision*, *6*, 356–365.

Guttman, S. E., & Kellman, P. J. (2004). Contour interpolation revealed by a dot localization paradigm. *Vision Research*, *44*, 1799–1815.

Hadad, B. S., Maurer, D., & Lewis, T. L. (2010). The development of contour interpolation: Evidence from subjective contours. *Journal of Experimental Child Psychology*, *106*, 163–176.

Halgren, E., Mendola, J., Chong, C. D., & Dale, A. M. (2003). Cortical activation to illusory shapes as measured with magnetoencephalography. *Neuroimage*, *18*, 1001–1009.

Herrmann, C. S., & Mecklinger, A. (2000). Magnetoencephalographic responses to illusory figures: Early evoked gamma is affected by processing of stimulus features. *International Journal of Psychophysiology*, *38*, 265–281.

Herrmann, C. S., Mecklinger, A., & Pfeifer, E. (1999). Gamma responses and ERPs in a visual classification task. *Clinical Neurophysiology*, *110*, 636–642.

Joseph, J., Bae, G., & Silverstein, S. M. (2013). Sex, symptom, and premorbid social functioning associated with perceptual organization dysfunction in schizophrenia. *Frontiers in Psychology*, *4*, 547.

Kanizsa, G. (1955). "Margini quasi-percettivi in campi con stimulazione omogonea". *Rivista di Psicologia*, *49*, 1–30.

Kay, S. R., Fiszbein, A., & Opler, L. A. (1987). The Positive and Negative Syndrome Scale (PANSS) for schizophrenia. *Schizophrenia Bulletin*, *13*, 261–276.

Keane, B. P., Erlikhman, G., Kastner, S., Paterno, D., & Silverstein, S.M. Contour grouping deficits in schizophrenia: What is the role of spatial frequency? Manuscript in preparation.

Keane, B. P., Lu, H., & Kellman, P. J. (2007). Classification images reveal spatiotemporal contour interpolation. *Vision Research*, *47*, 3460–3475.

Keane, B. P., Lu, H., Papathomas, T. V., Silverstein, S. M., & Kellman, P. J. (2012). Is interpolation cognitively encapsulated? Measuring the effects of belief on Kanizsa shape discrimination and illusory contour formation. *Cognition*, *123*, 404–418.

Keane, B. P., Lu, H., Papathomas, T. V., Silverstein, S. M., & Kellman, P. J. (2013). Reinterpreting behavioral receptive fields: Lightness induction alters visually completed shape. *PLoS One*, *8*, e62505.

Keane, B. P., Mettler, E., Tsoi, V., & Kellman, P. J. (2011). Attentional signatures of perception: Multiple object tracking reveals the automaticity of contour interpolation. *Journal of Experimental Psychology. Human Perception and Performance*, *37*, 685–698.

Keane, B. P., Silverstein, S. M., Barch, D. M., Carter, C. S., Gold, J. M., Kovács, I., et al. (2012). The spatial range of contour integration deficits in schizophrenia. *Experimental Brain Research*, *220*, 251–259.

Keane, B. P., Silverstein, S. M., Wang, Y., & Papathomas, T. V. (2013). Reduced depth inversion illusions in schizophrenia are state-specific and occur for multiple object types and viewing conditions. *Journal of Abnormal Psychology*, *122*, 506–512.

Kellman, P. J., Garrigan, P., Shipley, T. F., & Keane, B. P. (2007). Interpolation processes in object perception: Reply to Anderson (2007). *Psychological Review*, *114*, 488–508.

Kellman, P. J., & Shipley, T. F. (1991). A theory of visual interpolation in object perception. *Cognitive Psychology*, *23*, 141–221.

Kéri, S., Kelemen, O., Janka, Z., & Benedek, G. (2005). Visual-perceptual dysfunctions are possible endophenotypes of schizophrenia: Evidence from the psychophysical investigation of magnocellular and parvocellular pathways. *Neuropsychology*, *19*, 649–656.

Klein, S. A. (2001). Measuring, estimating, and understanding the psychometric function: A commentary. *Perception & Psychophysics*, *63*, 1421–1455.

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3? *Perception*, *36*.

Kontsevich, L. L., & Tyler, C. W. (1999). Bayesian adaptive estimation of psychometric slope and threshold. *Vision Research*, *39*, 2729–2737.

Krystal, J. H., Perry E. B., Jr., Gueorguieva, R., Belger, A., Madonick, S. H., Abi-Dargham, A., et al. (2005). Comparative and interactive human psychopharmacologic effects of ketamine and amphetamine: Implications for glutamatergic and dopaminergic model psychoses and cognitive function. *Archives of General Psychiatry*, *62*, 985–994.

Lee, T. S., & Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 1907–1911.

Lee, K. H., Williams, L. M., Breakspear, M., & Gordon, E. (2003). Synchronous gamma activity: A review and contribution to an integrative neuroscience model of schizophrenia. *Brain Research Reviews*, *41*, 57–78.

Lee, K. H., Williams, L. M., Haig, A., & Gordon, E. (2003). "Gamma (40 Hz) phase synchronicity" and symptom dimensions in schizophrenia. *Cognitive Neuropsychiatry*, *8*, 57–71.

Lee, K. H., Williams, L. M., Loughland, C. M., Davidson, D. J., & Gordon, E. (2001). Syndromes of schizophrenia and smooth-pursuit eye movement dysfunction. *Psychiatry Research*, *101*, 11–21.

Lesher, G. W., & Mingolla, E. (1993). The role of edges and line-ends in illusory contour formation. *Vision Research*, *33*, 2253–2270.

Lotto, R. B., & Purves, D. (2001). An empirical explanation of the Chubb illusion. *Journal of Cognitive Neuroscience*, *13*, 547–555.

Maertens, M., Pollmann, S., Hanke, M., Mildner, T., & Moller, H. (2008). Retinotopic activation in response to subjective contours in primary visual cortex. *Frontiers in Human Neuroscience*, *2*, 2.

Mendola, J. D., Dale, A. M., Fischl, B., Liu, A. K., & Tootell, R. B. (1999). The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *Journal of Neuroscience*, *19*, 8560–8572.

Milne, E., & Scope, A. (2008). Are children with autism spectrum disorders susceptible to contour illusions? *British Journal of Developmental Psychology*, *26*, 91–102.

Mitelman, S. A., & Buchsbaum, M. S. (2007). Very poor outcome schizophrenia: clinical and neuroimaging aspects. *Int Rev Psychiatry*, *19*, 345–357.

Murray, M. M., Foxe, D. M., Javitt, D. C., & Foxe, J. J. (2004). Setting boundaries: Brain dynamics of modal and amodal illusory shape completion in humans. *Journal of Neuroscience*, *24*, 6898–6903.

Murray, M. M., Imber, M. L., Javitt, D. C., & Foxe, J. J. (2006). Boundary completion is automatic and dissociable from shape discrimination. *Journal of Neuroscience*, *26*, 12043–12054.

Murray, R. F., Sekuler, A. B., & Bennett, P. J. (2001). Time course of amodal completion revealed by a shape discrimination task. *Psychonomic Bulletin and Review*, *8*, 713–720.

Murray, M. M., Wylie, G. R., Higgins, B. A., Javitt, D. C., Schroeder, C. E., & Foxe, J. J. (2002). The spatiotemporal dynamics of illusory contour processing: Combined high-density electrical mapping, source analysis, and functional magnetic resonance imaging. *Journal of Neuroscience*, *22*, 5055–5073.

Must, A., Janka, Z., Benedek, G., & Kéri, S. (2004). Reduced facilitation effect of collinear flankers on contrast detection reveals impaired lateral connectivity in the visual cortex of schizophrenia patients. *Neuroscience Letters*, *357*, 131–134.

Nakamura, M., Nestor, P. G., Levitt, J. J., Cohen, A. S., Kawashima, T., Shenton, M. E., et al. (2008). Orbitofrontal volume deficit in schizophrenia and thought disorder. *Brain*, *131*, 180–195.

Nieder, A. (2002). Seeing more than meets the eye: Processing of illusory contours in animals. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural and Behavioral Physiology*, *188*, 249–260.

Nurnberger, J. I., Jr., Blehar, M. C., Kaufmann, C. A., York-Cooler, C., Simpson, S. G., Harkavy-Friedman, J., et al. (1994). Diagnostic interview for genetic studies. Rationale, unique features, and training. NIMH Genetics Initiative. *Archives of General Psychiatry*, *51*, 849–859 (discussion 863–844).

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.

Phillips, W. A., & Silverstein, S. M. (2003). Convergence of biological and psychological perspectives on cognitive coordination in schizophrenia. *Behavioral and Brain Sciences*, *26*, 65–82 (discussion 82–137).

Pillow, J., & Rubin, N. (2002). Perceptual completion across the vertical meridian and the role of early visual cortex. *Neuron*, *33*, 805–813.

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

Prins, N., & Kingdom, F. A. A. (2009). Palamedes: Matlab routines for analyzing psychophysical data. http://www.palamadestoolbox.org.

Ramachandran, V. S., Ruskin, D., Cobb, S., Rogers-Ramachandran, D., & Tyler, C. W. (1994). On the perception of illusory contours. *Vision Research*, *34*, 3145–3152.

Rietkerk, T., Boks, M. P., Sommer, I. E., Liddle, P. F., Ophoff, R. A., & Kahn, R. S. (2008). The genetics of symptom dimensions of schizophrenia: Review and meta-analysis. *Schizophrenia Research*, *102*, 197–205.

Ringach, D. L., & Shapley, R. (1996). Spatial and temporal properties of illusory contours and amodal boundary completion. *Vision Research*, *36*, 3037–3050.

Robol, V., Tibber, M. S., Anderson, E. J., Bobin, T., Carlin, P., Shergill, S. S., et al. (2013). Reduced crowding and poor contour detection in schizophrenia are consistent with weak surround inhibition. *PLoS One*, *8*, e60951.

Schallmo, M. P., Sponheim, S. R., & Olman, C. A. (2013). Abnormal contextual modulation of visual contour detection in patients with schizophrenia. *PLoS One*, *8*, e68090.

Seghier, M. L., & Vuilleumier, P. (2006). Functional neuroimaging findings on the human perception of illusory contours. *Neuroscience & Biobehavioral Reviews*, *30*, 595–612.

Sheehan, D. V., Lecrubier, Y., Sheehan, K. H., Amorim, P., Janavs, J., Weiller, E., et al. (1998). The Mini-International Neuropsychiatric Interview (M.I.N.I.): The development and validation of a structured diagnostic psychiatric interview for DSM-IV and ICD-10. *Journal of Clinical Psychiatry*, *59*(*20*), 22–33 (quiz 34–57).

Shipley, T. F., & Kellman, P. J. (1992). Strength of visual interpolation depends on the ratio of physically specified to total edge length. *Perception &Psychophysics*, *52*, 97–106.

Silverstein, S. M., Berten, S., Essex, B., Kovács, I., Susmaras, T., & Little, D. M. (2009). An fMRI examination of visual integration in schizophrenia. *Journal of Integrative Neuroscience*, *8*, 175–202.

Silverstein, S. M., & Keane, B. P. (2011). Perceptual organization impairment in schizophrenia and associated brain mechanisms: Review of research from 2005 to 2010. *Schizophrenia Bulletin*, *37*, 690–699.

Silverstein, S. M., Keane, B. P., Barch, D. M., Carter, C. S., Gold, J. M., Kovács, I., et al. (2012). Optimization and validation of a visual integration test for schizophrenia research. *Schizophrenia Bulletin*, *38*, 125–134.

Silverstein, S. M., Keane, B. P., Wang, Y., Mikkilineni, D., Paterno, D., Papathomas, T. V., et al. (2013). Effects of short-term inpatient treatment on sensitivity to a size contrast illusion in first-episode psychosis and multiple-episode schizophrenia. *Frontiers in Psychology*, *4*, 466.

Silverstein, S. M., Kovács, I., Corry, R., & Valone, C. (2000). Perceptual organization, the disorganization syndrome, and context processing in chronic schizophrenia. *Schizophrenia Research*, *43*, 11–20.

Slaghuis, W. L. (1998). Contrast sensitivity for stationary and drifting spatial frequency gratings in positive- and negative-symptom schizophrenia. *Journal of Abnormal Psychology*, *107*, 49–62.

Solomon, M., Ozonoff, S., Carter, C., & Caplan, R. (2008). Formal thought disorder and the autism spectrum: Relationship with symptoms, executive control, and anxiety. *Journal of Autism and Developmental Disorders*, *38*, 1474–1484.

Spencer, K. M., Nestor, P. G., Niznikiewicz, M. A., Salisbury, D. F., Shenton, M. E., McCarley, R. W., et al. (2003). Abnormal neural synchrony in schizophrenia. *Journal of Neuroscience*, *23*, 7407–7411.

Spencer, K. M., Nestor, P. G., Perlmutter, R., Niznikiewicz, M. A., Klump, M. C., Frumin, M., et al. (2004). Neural synchrony indexes disordered perception and cognition in schizophrenia. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 17288–17293.

Spitzer, R. L., Williams, J. B., Gibbon, M., & First, M. B. (1992). The Structured Clinical Interview for DSM-III-R (SCID). I: History, rationale, and description. *Archives of General Psychiatry*, *49*, 624–629.

Tibber, M. S., Anderson, E. J., Bobin, T., Antonova, E., Seabright, A., Wright, B., et al. (2013). Visual surround suppression in schizophrenia. *Frontiers in Psychology*, *4*, 88.

Uhlhaas, P. J., Phillips, W. A., Mitchell, G., & Silverstein, S. M. (2006). Perceptual grouping in disorganized schizophrenia. *Psychiatry Research*, *145*, 105–117.

Uhlhaas, P. J., & Silverstein, S. M. (2005). Perceptual organization in schizophrenia spectrum disorders: Empirical research and theoretical implications. *Psychological Bulletin*, *131*, 618–632.

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, *63*, 1293–1313.

Williams, L. M., Whitford, T. J., Gordon, E., Gomes, L., Brown, K. J., & Harris, A. W. (2009). Neural synchrony in patients with a first episode of schizophrenia: Tracking relations with grey matter and symptom profile. *Journal of Psychiatry & Neuroscience*, *34*, 21–29.

Wokke, M. E., Vandenbroucke, A. R., Scholte, H. S., & Lamme, V. A. (2013). Confuse your illusion: Feedback to early visual cortex contributes to perceptual completion. *Psychological Science*, *24*, 63–71.

Yeap, S., Kelly, S. P., Thakore, J. H., & Foxe, J. J. (2008). Visual sensory processing deficits in first-episode patients with Schizophrenia. *Schizophrenia Research*, *102*, 340–343.

Zachary, R. A. (1991). *The manual of the Shipley Institute of Living Scale*. Los Angeles, CA: Western Psychological Services.

Zhou, J., Tjan, B. S., Zhou, Y., & Liu, Z. (2008). Better discrimination for illusory than for occluded perceptual completions. *Journal of Vision*, *8*(26), 1–17.