Impairment of perceptual closure in autism for vertex- but not edge-defined object images

Mohammad-Reza A. Dehaqani

School of Cognitive Sciences,
Institute for Research in Fundamental Sciences,
Tehran, Iran ✉

Mehdi Alizadeh Zarei

School of Cognitive Sciences,
Institute for Research in Fundamental Sciences,
Tehran, Iran
Department of Occupational Therapy,
School of Rehabilitation Sciences,
Iran University of Medical Sciences, Tehran, Iran ✉

Abdol-Hossein Vahabie

School of Cognitive Sciences,
Institute for Research in Fundamental Sciences,
Tehran, Iran ✉

Hossein Esteky

School of Cognitive Sciences,
Institute for Research in Fundamental Sciences,
Tehran, Iran
Research Center for Brain and Cognitive Sciences,
Shahid Beheshti University of Medical Sciences,
Tehran, Iran 🏠 ✉

One of the characteristics of autism spectrum disorder (ASD) is atypical sensory processing and perceptual integration. Here, we used an object naming task to test the significance of deletion of vertices versus extended contours (edges) in naming fragmented line drawings of natural objects in typically developing and ASD children. The basic components of a fragmented image in perceptual closure need to be integrated to make a coherent visual perception. When vertices were missing and only edges were visible, typically developing and ASD subjects performed similarly. But typically developing children performed significantly better than ASD children when only vertex information was visible. These results indicate impairment of binding vertices but not edges to form a holistic representation of an object in children with ASD.

Introduction

Recognition of visual objects plays a crucial role in our behavior, but its underlying mechanisms are not well understood. One well-established visual object recognition theory, recognition by component, suggests that objects are represented for purposes of recognition as an arrangement of simple parts, termed geons, and their relationships (Biederman, 1987). The theory suggests that junctions of contours, called vertices, help define the particular part type (or geon) that activates specific neural representations that are invariant with the viewing angle (Hayworth & Biederman, 2006; Kayaert, Biederman, & Vogels, 2003). Matched L-vertices that define deep concavities (or vertices) provide strong evidence for decomposing multipart objects into their component parts at those points (Biederman, 1987; Hoffman & Richards, 1984). It has been shown in adult human subjects that deletion of the vertices results in a larger decline in object recognition performance than that of lines (or edges) connecting these structural components (Biederman & Cooper, 1991; Szwed, Cohen, Qiao, & Dehaene, 2009). An alternative model of object recognition implies that objects are represented by sets of 2-D snapshots

(Poggio & Edelman, 1990; Ullman & Basri, 1991). These image-based 2-D snapshot models do not predict any difference in contribution of different parts of the image and assume a similar role for vertex and edge information in object recognition.

Human fMRI and monkey neurophysiological studies have established that objects are represented in a distributed manner (Haxby et al., 2001; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kriegeskorte et al., 2008; Tsunoda, Yamane, Nishizaki, & Tanifuji, 2001). Neurophysiological studies in nonhuman primates show that neurons in the ventral visual pathway preferentially respond to shapes that form vertices (Brincat & Connor, 2006; Kayaert et al., 2003; Pasupathy & Connor, 1999; Vogels, Biederman, Bar, & Lorincz, 2001). The distributed nature of representation of object features across different cortical areas necessitates a neural mechanism for binding the scattered information related to each object (Reddy & Kanwisher, 2006; Singer & Gray, 1995; Tanaka, 2003). However, the exact nature of the neural mechanism underlying binding of object features remains largely unknown. Synchronized oscillatory activity linking different neural assemblies through horizontal cortical connections has been suggested as a potential binding mechanism (Eckhorn et al., 1988; Engel, Kreiter, König, & Singer, 1991; Gray, Koenig, Engel, & Singer, 1989; Singer & Gray, 1995). An alternative mechanism for binding object features is the spike timing dependent plasticity (STDP). In this scheme, distributed neural representations of salient and consistently present object features bind together using the STDP mechanism, forming a spatially distributed but functionally integrated representation of objects (Masquelier, Guyonneau, & Thorpe, 2008; Masquelier & Thorpe, 2007).

Atypical visual processing has been reported in individuals with autism spectrum disorder (ASD; for a review, see Simmons et al., 2009). Weak central coherence is one of the theories that addresses altered visual processing in ASD (Frith, 1989). Weak central coherence suggests that the process by which diverse information is integrated and higher meaning is constructed into context is impaired in ASD (Frith & Happ, 1994; Happé, 1999; Vanegas & Davidson, 2015). According to this theory, individuals with ASD have problems with global processing and cannot integrate local information to form a coherent percept (Dakin & Frith, 2005; Happé & Frith, 2006; Van der Hallen, Evers, Brewaeys, Van den Noortgate, & Wagemans, 2015; Van Eylen, Boets, Steyaert, Wagemans, & Noens, 2015). They have a bias to local information processing (Happé & Frith, 2006). In recognition of fragmented object images, fragments represent local information that has to be integrated to form a global concept. Previous studies suggest that ASD subjects demon-

strate an atypical visual perception of fragmented objects and visual completion tasks (De Wit, Schlooz, Hulstijn, & Van Lier, 2007; Van Eylen et al., 2015). Vertices and extended contours (edges) convey different types of visual information (Biederman, 1987; Hoffman & Richards, 1984). It has been shown that typically developing subjects have better object recognition performance when the task requires integration of vertices, compared to edge local features (Biederman & Cooper, 1991; Szwed et al., 2009). However, the significance of vertex information for object recognition in ASD subjects is not clear.

Impairment of communication between brain regions has been indicated as the main cause of many cognitive deficits (Ford, Mathalon, Whitfield, Faustman, & Roth, 2002; Konrad & Eickhoff, 2010; Krain & Castellanos, 2006). For example, perceptual processes that require integration of sensory information across different modalities are impaired in ASD (Baum, Stevenson, & Wallace, 2015; Iarocci & McDonald, 2006; Stevenson et al., 2015; Stevenson et al., 2014; Tomchek & Dunn, 2007). It is suggested that neural oscillatory activities that bind related perceptual information from multiple representations across the visual cortex are impaired in individuals with autism (Stroganova et al., 2012; Sun et al., 2012). For example, ASD subjects who show elevated reaction times and reduced detection rates during the perception of upright Mooney faces also show reduction of the amplitude and phase locking of gamma-band activity (Sun et al., 2012). Horizontal corticocortical connections and the inhibitory–excitatory imbalance in cortical circuitry may play a crucial role in mediation of these synchronous activities (Ermentrout & Chow, 2002; Lumer, Edelman, & Tononi, 1997; Van Vreeswijk, Abbott, & Bard Ermentrout, 1994). Atypical horizontal interactions in the visual cortex have been implicated in ASD subjects (Casanova et al., 2006; Hussman, 2001; Vandenbroucke, Scholte, van Engeland, Lamme, & Kemner, 2008). Also modeling (Bakhtiari, Sephavand, Ahmadabadi, Araabi, & Esteky, 2012) and experimental (Levitt, Eagleson, & Powell, 2004; Polleux & Lauder, 2004; Rubenstein & Merzenich, 2003) studies suggest a role for inhibitory–excitatory imbalance in autism.

Here we compared object recognition performances of ASD and typically developing children using line drawings of objects as well as fragmented images of the same objects with either vertex or edge information. Both groups performed equally well in naming complete images. The naming performance of typically developing children was significantly higher for vertex versus edge images. This finding is consistent with recognition by component models of object recognition as it shows greater sensitivity of object naming to deletion of vertices than edges in typically developing

	Children with ASD	Typically developing children	p value (*t* test)
Age (months)	101.25 ± 3.03	98.56 ± 2.48	0.50
Full-scale IQ	103.13 ± 1.99	105.63 ± 1.19	0.28
Verbal IQ	98.75 ± 2.55	100.94 ± 2.07	0.51
Performance IQ	107.25 ± 1.91	109.06 ± 1.86	0.50
ASSQ	35.9 ± 11.3	4.69 ± 0.64	$p < 10^{-5}$

Table 1. Statistics (mean ± *SEM*) for developmental variables for children with autism and typically developing children.

children. But more importantly, and consistent with the expectations of the image-based representation theory, we observed that ASD subjects performed similarly in naming vertex and edge images.

Methods

Sixteen typically developing and 16 high-functioning autistic subjects (both groups 8–12 years old) participated in this study. All ASD participants met the criteria for autism based on the *Diagnostic and Statistical Manual of Mental Disorders* diagnostic (American Psychiatric Association, 2000), according to an independent child psychiatrist. Diagnoses were confirmed with the Autism Diagnostic Observation Schedule–Generic (Lord et al., 2000) by a trained rater. The high-functioning Autism Spectrum Screening Questionnaire (ASSQ) was used to determine the level of functioning in the autism group (Ehlers & Gillberg, 1993; Ehlers, Gillberg, & Wing, 1999). The cutoff score of 19 is suggested as a reasonable score for identifying high-functioning ASD. IQ scores for all participants were measured by the Wechsler Intelligence Scale for Children (Wechsler, 1949; Table 1).

Subjects were asked to name line drawings of familiar object images (Figure 1A). The line drawing images (black lines on a white background) were presented on a computer monitor, which was located about 70 cm from the subjects' eyes. The stimulus presentation was controlled by Matlab software Psychtoolbox (Brainard, 1997). The size of each image was 7° of visual field. Two versions of each stimulus were made by deleting 50% of pixels at either vertices so only edges were visible (herein called EDGE) or deleting the lines (edges) between vertices so only vertices were visible (herein called VERT). Vertices were defined as any junction of two or more lines and any sharp concavity (Biederman, 1987; Szwed et al., 2009). In each fragmented image, 50% of pixels were deleted, making the VERT and EGDE images complementary to each other without any pixel overlap.

Data were collected in two sessions. In the first session, only fragmented object images (VERT and EDGE) were presented to the subjects. In the second session, about 5–10 days later, complete versions of the same images without any part deletion were presented. In each session, a trial started with a red fixation spot (0.5° of visual field radius) at the middle of the monitor. A beep sound that lasted for 500 ms accompanied the onset of each fixation spot to draw subjects' attention to the stimulus. After 1500 ms fixation, a randomly selected stimulus was presented on the center of the computer monitor for 250 ms. Subjects were instructed to name the objects as quickly as possible. After the completion of each trial, subjects could start a new trial by pressing any key on a computer keyboard. No feedback about response accuracy was provided. Each subject only viewed one version of each stimulus (EDGE or VERT) to avoid the potential impact of recognizing the fragmented objects from seeing and recognizing the complementary version of the same object. For each subject, we randomly selected the EDGE or VERT version of each image. Each subject viewed and named 40 EDGE and 40 VERT objects. Subjects' oral responses were monitored online by the experimenter and were also recorded for offline analysis. Subjects' reaction times were acquired by analysis of their vocal response onset, which was recorded and later analyzed by locally made software.

The study was performed in accordance with the principles of the Declaration of Helsinki, and the procedure was approved by the Institute for Research in Fundamental Sciences Ethics Committee. Parents gave consent for their children's participation in the study.

Results

Sixteen typically developing and 16 age (8–12 years old) and IQ matched (Table 1) high-functioning autistic subjects participated in the object naming task experiments (Figure 1A; see Methods). Stimuli were line drawings of 80 familiar objects (Figure 1B). To make sure that differences in familiarity of the presented images among our subjects did not affect the results, we only used data of images for which each subject provided a correct response when naming the complete version of the images. On average, about 12% of images were discarded.

Naming accuracy (percentage correct) were similar for the two groups: the complete (original) and EDGE images (complete images in autism: 0.87 ± 0.02, complete images in typically developing: 0.89 ± 0.01; EDGE images in autism: 0.46 ± 0.05, EDGE images in typically developing: 0.43 ± 0.03; Figure 2). But there
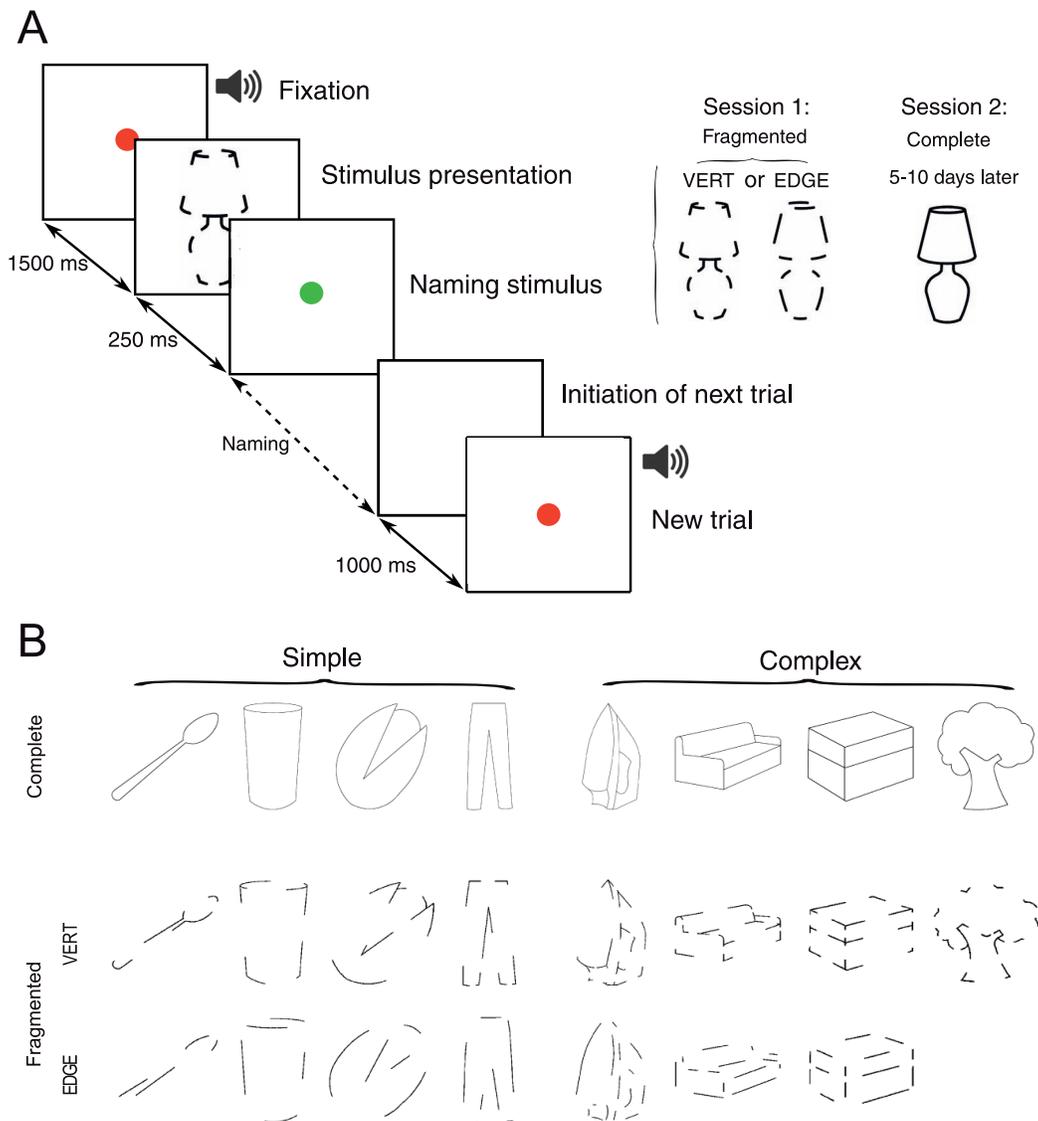
Figure 1. The experimental paradigm and sample of stimuli. (A) The experimental paradigm and image groups. (B) Sample of stimulus images. In the first row, eight representative examples of complete simple and complex stimuli are illustrated. The second and third rows show their fragmented vertex and edge versions.

was a significant difference in the naming performance of the autistic and typically developing groups in naming VERT images (VERT images in autism: 0.52 ± 0.04; VERT images in typically developing: 0.64 ± 0.04, t test $p < 0.001$; Figure 2). Object naming accuracy of typically developing children was significantly lower in EDGE compared with VERT images (EDGE: 0.43 ± 0.03; VERT: 0.64 ± 0.04; $p < 0.001$). Interestingly, in contrast to the typically developing children, autistic subjects' naming performance was similarly affected by deletion of vertices or edges (Figure 2; EDGE: 0.46 ± 0.05; VERT: 0.52 ± 0.04; $p = 0.15$). Note that there was practically no difference between performances of the two groups in naming EDGE images ($p = 0.64$). On the other hand, typically

developing subjects performed significantly better than those with autism in naming VERT images ($p < 0.004$).

To examine the effect of deletion type (EDGE or VERT), subject type (ASD or typically developing), and their interaction in naming performance, we performed a two-way analysis of variance (ANOVA) with subject type and deletion type variables. This analysis revealed that although the types of deletion (EDGE and VERT) affected performance, accuracy of both subjects (ASD and typically developing) in response to fragmented images was similar (two-way ANOVA: deletion type, $p < 0.002$; subject type, $p = 0.24$). Moreover, the interaction of deletion type and subject type did not describe naming performance (two-way ANOVA: interaction, $p = 0.07$).
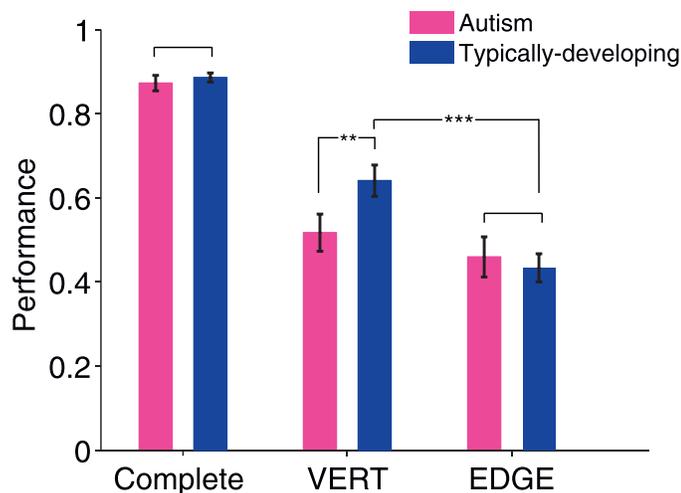
Figure 2. Comparison of naming accuracy of autistic and typically developing subjects. Bar plots show mean performance in naming complete, VERT, and EDGE stimuli for autistic and typically developing subjects. Error bars denote *SEM* and asterisks indicate significant differences between two naming performances (** $p < 0.01$, *** $p < 0.001$).
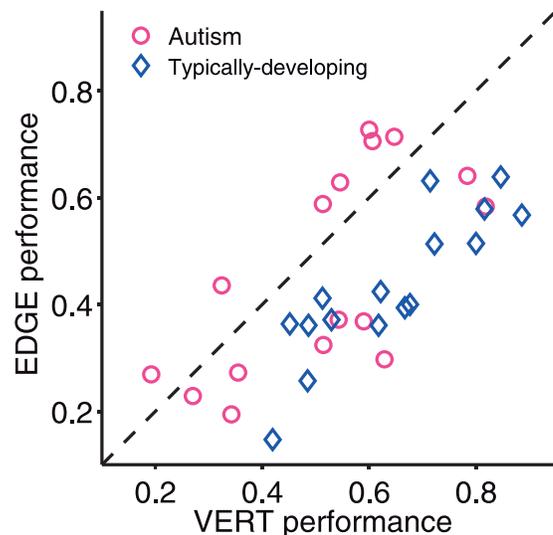

Figure 3. Naming performance of individual subjects. Each symbol on the plot represents one subject. The VERT performance (horizontal axis) was plotted against EDGE performance (vertical axis). Circles show the autistic subjects and diamonds indicate the typically developing subjects. All of typically developing subjects fall below the bisector line ($y = x$ line).

Relative performances of individual subjects in naming EDGE and VERT images are depicted in Figure 3. All of the typically developing subjects performed better in naming VERT images. However, performance of subjects with autism covered a much wider range and included subjects with better performances in VERT or EDGE images. To study the cause of this performance variability, we divided autistic subjects into two groups: seven subjects with higher EDGE/VERT performances and nine subjects with higher VERT/EDGE performances. We compared age (higher EDGE/VERT: 107.3 ± 4.45 months, higher VERT/EDGE: 96.6 ± 4.33 months, $p = 0.1$), IQ (higher EDGE/VERT: 99.4 ± 3.24, higher VERT/EDGE: 104.8 ± 2.56, $p = 0.19$), and verbal IQ (higher EDGE/VERT: 92.1 ± 3.12, higher VERT/EDGE: 101.7 ± 3.62, $p = 0.06$) of these two groups and found no significant difference (*t* test, $p < 0.05$). We also found no significant correlation between VERT and EDGE naming performances of the autistic subjects with IQ (VERT: $r = 0.22$, $p = 0.4$, EDGE: $r = -0.05$, $p = 0.85$), verbal IQ (VERT: $r = 0.09$, $p = 0.75$, EDGE: $r = -0.25$, $p = 0.35$) and age (VERT: $r = 0.38$, $p = 0.15$, EDGE: $r = 0.48$, $p = 0.06$).

Stimulus complexity indexed by the number of components plays a crucial role in visual perception of fragmented object images (Biederman, 1987; Panis & Wagemans, 2009). In our study, the number of fragments in EDGE and VERT images could differentially affect the closure perception. To study and compare the impact of the stimulus complexity in subjects' naming performances of VERT and EDGE images, we divided images into simple (low number of fragments; $n = 33$ for VERT and $n = 34$ for EDGE) and complex (high number of fragments; $n = 32$ for VERT and $n = 31$ for EDGE) groups. We made the fragmented images by deleting (or keeping) the vertices so the number of fragments were an indication of the number of structural features and complexity of images as simple images normally have fewer structural features than complex ones. For this analysis, we excluded object images that yielded VERT and EDGE images with more than three fragment differences ($n = 15$). But using all of the stimuli yielded similar results. Arrows in Figure 4 indicate the median (VERT: six, EDGE: eight) of the distribution of the number of fragments in EDGE and VERT images, which was used to divide the images into simple and complex groups. There was no significant difference between component numbers of EDGE and VERT in the simple and complex image groups (*t* test, $p = 0.13$). As expected, there was a tight positive correlation between the number of fragments of EDGE and VERT images ($r = 0.95$, $p < 0.001$; Figure 4).

Analysis of subjects' naming performances revealed similar performance of typically developing and autistic subjects for EDGE images of both simple and complex objects (Figure 5A, B; simple: $p = 0.79$, complex: $p = 0.43$). Among all of the tested conditions, the lowest naming performances were observed for EDGE images of simple objects. Much better performances were observed for naming the EDGE images of complex objects (autism: EDGE simple: 0.33 ± 0.06, EDGE
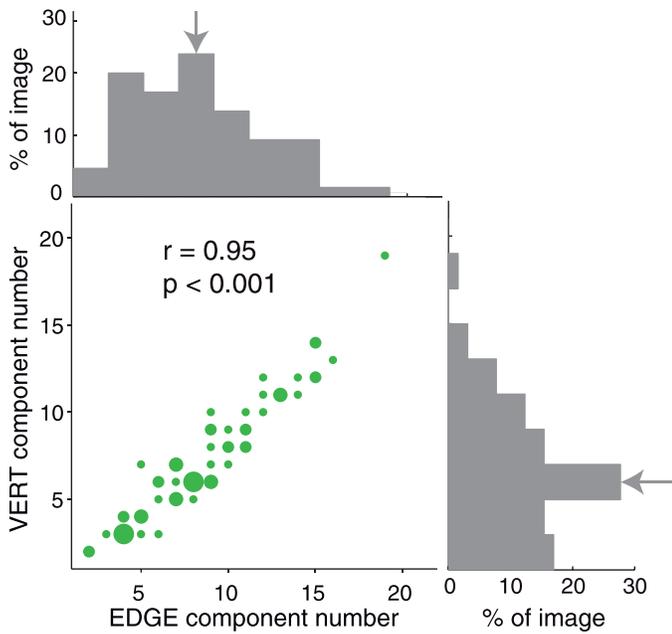
Figure 4. The VERT component number is plotted against the EDGE component number. Each point shows one stimulus. If there was more than one stimulus with similar EDGE and VERT components, the corresponding circle was shown by a bigger circle. Distribution of the component number in EDGE and VERT stimuli are plotted at the top and left of the scatter, respectively. Arrows in distributions show the median of the component number.

complex: 0.56 ± 0.05, $p < 0.001$; typically developing: EDGE simple: 0.31 ± 0.04, EDGE complex: 0.52 ± 0.04, $p < 0.01$). But performances for naming VERT images did not depend on object complexity in both groups (Figure 5A, B; autism: VERT simple: 0.51 ± 0.05, VERT complex: 0.53 ± 0.05, $p = 0.71$; typically developing: VERT simple: 0.6 ± 0.04, VERT complex: 0.66 ± 0.05, $p = 0.14$). Consequently, a significant difference in the performance of autistic subjects was observed in naming VERT and EDGE images of simple ($p < 0.01$) but not complex ($p = 0.50$) objects. Note that typically developing subjects performed better in naming VERT versus EDGE images of both simple and complex objects (simple $p < 0.001$, complex $p < 0.001$). Relative performances of individual subjects for EDGE/VERT of simple (Figure 5C) and complex (Figure 5D) images are shown to reveal individual differences between the subjects.

To test the effect of subjects' response delay time on their performances, we divided the trials based on the response onset time delays. Short and long response onset times were defined as those below or above the median value, respectively. In both conditions, autistic subjects were similarly affected by deletion of vertices or edges (fast trials: VERT: 0.79 ± 0.04, EDGE: 0.75 ± 0.04, $p = 0.48$; slow trials: VERT: 0.6 ± 0.05, EDGE:

0.63 ± 0.06, $p = 0.58$). However, in typically developing children, there was a significant difference in the naming performance of VERT and EDGE (fast trials: VERT: 0.87 ± 0.03, EDGE: 0.76 ± 0.06, $p < 0.01$; slow trials: VERT: 0.63 ± 0.05, EDGE: 0.49 ± 0.04, $p < 0.01$). Both groups performed significantly better in short response latency trials (autism: VERT, $p < 0.01$, EDGE, $p < 0.05$; typically developing: VERT, $p < 0.001$, EDGE, $p < 0.001$). Analysis of response latency of correct trials shows that, compared with typically developing children, autistic subjects' response onsets were significantly longer (EDGE: autism: 2.11 ± 0.18, typically developing: 1.51 ± 0.06, $p < 0.01$; VERT: autism: 1.79 ± 0.1, typically developing: 1.47 ± 0.06, $p < 0.05$). In addition, there was no significant correlation between stimuli complexity and subjects' reaction time (VERT: autism: $r = 0.13$, $p = 0.26$, typically developing: $r = -0.15$, $p = 0.18$; EDGE: autism: $r = -0.23$, $p = 0.06$, typically developing: $r = -0.15$, $p = 0.22$).

Psychophysical, neurophysiological, and imaging studies have proposed specialized neural structures and mechanisms for processing animal objects in humans (Downing, Jiang, Shuman, & Kanwisher, 2001; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Nasr & Esteky, 2009). In our analysis reported thus far, we used inanimate object images. To further test the structural feature (vertices) integration hypothesis, we tested a subset of ASD subjects ($n = 8$) and typically developing ($n = 8$) children in an animal naming task using the same paradigm as in the main study. Naming performance of the complete animal and inanimate images was similar in both groups (autism: animal: 0.84 ± 0.03, inanimate: 0.87 ± 0.02, $p = 0.32$; typically developing: animal: 0.86 ± 0.02, inanimate: 0.89 ± 0.01, $p = 0.23$). Importantly, naming fragmented images of animals yielded higher performances than inanimate objects in both groups (VERT images: autism: animal: 0.61 ± 0.03, inanimate: 0.52 ± 0.02, $p = 0.35$; typically developing: animal: 0.82 ± 0.02, inanimate: 0.64 ± 0.01, $p < 0.05$; EDGE images: autism: animal: 0.64 ± 0.08, inanimate: 0.46 ± 0.04, $p = 0.12$; typically developing: animal: 0.7 ± 0.03, inanimate: 0.43 ± 0.04, $p < 0.01$). The two groups of subjects also performed similarly well in naming the complete and EDGE animal images (complete images in autism: 0.84 ± 0.03, complete images in typically developing: 0.86 ± 0.02, $p = 0.58$; EDGE images in autism: 0.64 ± 0.08, EDGE images in typically developing: 0.7 ± 0.03, $p = 0.60$). Similar to the inanimate images, in the animal naming task, autistic subjects performed similarly in naming animal VERT and EDGE images (VERT: 0.61 ± 0.03, EDGE: 0.64 ± 0.08, $p = 0.17$). In contrast, in the typically developing children there was a significant difference in the naming performance of animal VERT
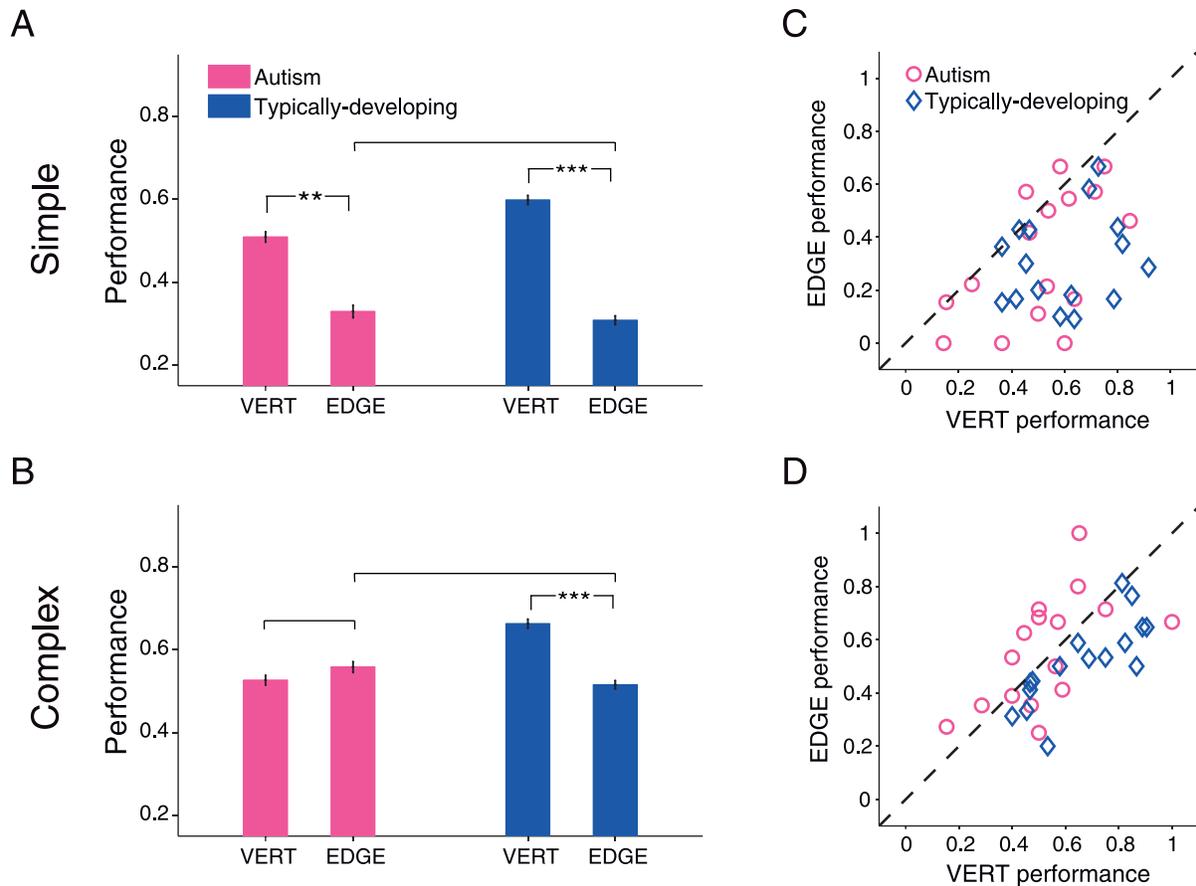
Figure 5. Naming performance of autistic and typically developing subjects in response to simple and complex stimuli. The mean performance (A, B) and scatters of individual subjects' performance (C, D) in simple (low component) and complex (high component) stimuli were computed. The VERT and EDGE stimuli were divided into two groups according to their component numbers (cutoff is median). Asterisks indicate significant difference between two naming performances (** $p < 0.01$, *** $p < 0.001$).

and animal EDGE (VERT: 0.82 ± 0.02, EDGE: 0.7 ± 0.03, $p < 0.001$).

Discussion

In this study, we compared object recognition performances of ASD and typically developing children using line drawings of objects as well as fragmented images of the same objects that contained either only vertex (VERT) or edge (EDGE) information. Both groups performed equally well in naming complete object images. Performances of both groups declined when naming fragmented compared to complete images. Typically developing children performed significantly higher for VERT versus EDGE images. This finding is consistent with object recognition theories that expect greater sensitivity of object naming to deletion of vertices than edges (Biederman, 1987; Biederman & Cooper, 1991; Szwed et al., 2009). More importantly, ASD subjects performed similarly in

naming VERT and EDGE images. This finding is consistent with the expectation of the image-based representation theories as these schemes do not assume any difference in contribution of vertices and edges in object recognition performance (Bülthoff, Edelman, & Tarr, 1994; Edelman, 1995; Edelman & Weinshall, 1991; Perrett, Oram, & Ashbridge, 1998). The effect was particularly pronounced for more complex objects with many vertices. Considering the fundamental differences in neural representation of animate and inanimate objects, we also tested animate recognition and found a similar naming performance difference between subject groups for inanimate and animate stimuli.

Human fMRI and monkey neurophysiological studies have established that objects are represented in the ventral visual stream in a distributed manner (Fujita, Tanaka, Ito, & Cheng, 1992; Haxby et al., 2001; Ishai et al., 1999; Tsunoda et al., 2001). The nature of the distributed code is not clear yet, but many neurophysiological studies in nonhuman primates show that neurons in the ventral visual pathway preferen-

tially respond to shapes that normally form vertices (Brincat & Connor, 2006; Kayaert et al., 2003; Pasupathy & Connor, 1999; Vogels et al., 2001). For example, the orientation signals at early stages of visual processing are synthesized into a representation of angle and curvature in V4 (Hegdé & Van Essen, 2007; Yau, Pasupathy, Brincat, & Connor, 2013). The inferior temporal cortex (IT), which is the highest cortical structure involved in pure visual processing of shape information, also contains neurons that are highly sensitive to minor changes in the degree of curvature/angle of partially complex shape features (Tanaka, Saito, Fukada, & Moriya, 1991). To our knowledge, there is no neurophysiological study showing the significance of exclusive edge information in object representation. Indirect evidence suggests that IT neural responses are robust to changes in edge conformation caused by variation in size, aspect ratio, or depth rotation as long as the vertices, which are critical for neuron activation, are visible (Esteky & Tanaka, 1998; Ito, Tamura, Fujita, & Tanaka, 1995; Kayaert et al., 2003).

Neural responses activated by the presentation of incomplete and fragmented images are different (Doniger et al., 2000; Hirsch et al., 1995; Zeki, 1996) and can be noisier than complete images. Because of a more discrete neural representation of vertices, neural activity evoked by VERT images may be more similar to representation of the whole object than that of EDGE images. In such cases, object recognition exclusively based on edge information declines because it relies on matching noisy sensory representation with the related object memory. Similarly, low performances of both subject groups in naming EDGE images suggests that edge-dependent object recognition is a computationally more demanding task potentially due to the noisy nature of the sensory representation of the EDGE stimuli.

When only vertex information was available, ASD subjects performed significantly worse than typically developing children. Integration of the distributed information across the lateral occipital cortex requires linking the activated neurons representing each vertex fragment. Binding and linking the activity of these neurons is critical in recognition of objects. Significantly lower VERT naming performance of autistic subjects suggests that they have a lower capacity to link the distributed neural information of vertices.

This interpretation is consistent with other psychophysical studies on autism and typically developing subjects indicating atypical visuoperceptual integration in autism. For example, although detection of direction of first-order luminance-defined motion and orientation of simple gratings in ASD subjects is not different from typically developing individuals, they are impaired in detection of second-order texture-defined motion (Bertone, Mottron, Jelenic, & Faubert, 2003, 2005) and the more complex motion coherence (Spencer et al., 2000). A distributed neural circuitry is thought to support discrimination of these complex conditions (Badcock & Khuu, 2001; Bertone & Faubert, 2003). Such distributed networks in the dorsal (motion detection) and ventral (object recognition) visual streams require more complex integrative neural processes that seem to be impaired in ASD.

It is widely assumed that synchronized oscillatory activities link different neural assemblies and act as a binding mechanism (Eckhorn et al., 1988; Engel et al., 1991; Gray et al., 1989; Singer & Gray, 1995). Our data suggests that this neural process may be impaired in autism. Several studies have suggested abnormal neural synchronization in the subjects with autism (Brock, Brown, Boucher, & Rippon, 2002; Dinstein et al., 2011). These abnormal oscillatory patterns are observed in many cortical areas, including the visual cortex during the resting state (Cornew, Roberts, Blaskey, & Edgar, 2012) as well as object recognition conditions. For example, a picture naming magnetoencephalography (MEG) study has shown reduced evoked activity of high gamma in the superior temporal gyrus, low gamma power evoked in the left inferior frontal gyrus, and phase-locked beta-band in the occipital lobes of ASD, relative to the control subjects (Buard, Rogers, Hepburn, Kronberg, & Rojas, 2013). Another MEG recording from adults with ASD during the presentation of Mooney faces (a visual closure task) highlights the impaired ASD gamma-band activity in complex visual processing (Sun et al., 2012).

A potential alternative mechanism for impairment of vertex closure in ASD is a deficit in STDP. STDP has been suggested as a mechanism for the emergence of representation of partially complex, informative, and prototypical features that are salient and consistently present in images of an object. Representation of these features enables robust object recognition (Masquelier et al., 2008; Masquelier & Thorpe, 2007). GABA circuitry affects STDP (Lamsa, Kullmann, & Woodin, 2010; Paille et al., 2013). Imbalanced excitation or inhibition across the minicolumn cortex of those with ASD could be due to a reduction in GABAergic neurons (Casanova et al., 2006). Modeling studies consistently suggest that the GABAergic system is impaired in autistic individuals (Bakhtiari et al., 2012; Polleux & Lauder, 2004; Rubenstein & Merzenich, 2003). It is therefore possible that the formation of STDP-dependent prototypical object feature representations is impaired in autistic subjects. Further studies are needed to understand the neural mechanisms of object closure impairment in autism reported in the current study.

Impairment of other high-level mechanisms, such as filling-in and illusionary contours, in ASD subjects may

also explain the selective vertex closure impairment observed in our study. The filling-in phenomenon typically occurs when straight edges are missing, such as the Kanizsa figure (Weil & Rees, 2011). Illusionary contour processing is also impaired in the brain of children with ASD (Stroganova et al., 2012). These findings suggest a mechanism for the lower performance of ASD subjects in naming VERT (straight line deleted images) in our study. Further evidence consistent with this notion comes from the fact that spatial integration of shape information, such as contour integration, relies on horizontal connections (Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Li & Gilbert, 2002). The horizontal connections are impaired in ASD (Casanova et al., 2006; Hussman, 2001).

Image-based object recognition theories do not assume any difference in the contribution of different parts of an image in object recognition, and the theories assume a similar role for vertex and edge information (Bülthoff et al., 1994; Edelman, 1995; Kourtzi & Shiffrar, 1999). Unlike typically developing children, the VERT and EDGE object naming performance of ASD subjects in our study were comparable and thus consistent with these models. It should be noted that the establishment of a link between neurophysiological processes or models of object recognition and our observations in ASD children needs further investigation.

The fact that typically developing and autistic subjects' performances were not significantly different in naming complete, simple EDGE, and complex EDGE images suggests that differences in task difficulty and level of required attention to perform the tasks were not responsible for the observed differences between the two groups in naming fragmented VERT images.

Naming performances of complete inanimate and animal images were similar in both typically developing and autistic subjects. However, the performances of both typically developing and autistic subjects were higher in naming fragmented images of animals compared to inanimates for both VERT and EDGE stimuli. The observed effect was not due to higher familiarity of the two subject groups with animal objects because (a) the subjects' performances in naming complete animal and inanimate images were similar, and (b) in both animal and inanimate objects, we only analyzed stimuli for which a correct response was obtained when the complete image was presented. Numerous neurophysiological, psychophysical, and imaging studies have indicated specialized neural structures and mechanisms for processing animal objects in human (Downing et al., 2001; Loffler et al., 2005) and nonhuman (Afraz, Kiani, & Esteky, 2006; Bell et al., 2011; Kiani, Esteky, Mirpour, & Tanaka, 2007) primates. Similar to objects, animate identity

information is shown to be represented in a distributed manner (Kriegeskorte, Formisano, Sorger, & Goebel, 2007). Thus, the similarity of object and animate naming performance reported in our study is expected.

Conclusions

We asked typically developing and ASD subjects to name fragmented visual objects with either missing vertices or elongated edges. We found that when the vertices were missing and only objects' edges were visible, typically developing and autistic subjects' performances were similarly low. But more importantly, ASD children performed significantly worse than typically developing children in naming the fragmented images of objects when only vertices were available. These findings indicate atypical visual processing in ASD individuals. Although the cause of this impairment is not clear and needs further investigation, the potential candidates are impairment in integration of fragmented information due to malfunctioning of neural oscillation, impaired STDP, biased local processing, and image-based object representation in ASD individuals.

Keywords: autism spectrum disorder, visual sensory integration, object naming, edge and vertex information

Acknowledgments

References

Afraz, S.-R., Kiani, R., & Esteky, H. (2006). Microstimulation of inferotemporal cortex influences face categorization. *Nature*, *442*(7103), 692–695, http://doi.org/10.1038/nature05153.

American Psychiatric Association. (2000). *Diagnostic and statistical manual of mental disorders* (4th ed.). Washington, DC: American Psychiatric Publishing, Inc.

Badcock, D. R., & Khuu, S. K. (2001). Independent first- and second-order motion energy analyses of optic flow. *Psychological Research, 65*(1), 50–56.

Bakhtiari, R., Sephavand, N. M., Ahmadabadi, M. N., Araabi, B. N., & Esteky, H. (2012). Computational model of excitatory/inhibitory ratio imbalance role in attention deficit disorders. *Journal of Computational Neuroscience, 33*(2), 389–404, doi:10.1007/s10827-012-0391-y.

Baum, S. H., Stevenson, R. A., & Wallace, M. T. (2015). Behavioral, perceptual, and neural alterations in sensory and multisensory function in autism spectrum disorder. *Progress in Neurobiology, 134*, 140–160.

Bell, A. H., Malecek, N. J., Morin, E. L., Hadj-Bouziane, F., Tootell, R. B. H., & Ungerleider, L. G. (2011). Relationship between functional magnetic resonance imaging-identified regions and neuronal category selectivity. *Journal of Neuroscience, 31*(34), 12229–12240, doi:10.1523/JNEUROSCI.5865-10.2011.

Bertone, A., & Faubert, J. (2003). How is complex second-order motion processed? *Vision Research, 43*(25), 2591–2601, doi:10.1016/S0042-6989(03)00465-6.

Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2003). Motion perception in autism: A "complex" issue. *Journal of Cognitive Neuroscience, 15*(2), 218–225.

Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2005). Enhanced and diminished visuo-spatial information processing in autism depends on stimulus complexity. *Brain, 128*(10), 2430–2441, doi:10.1093/brain/awh561.

Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review, 94*(2), 115–147, doi:10.1037/0033-295X.94.2.115.

Biederman, I., & Cooper, E. E. (1991). Priming contour-deleted images: Evidence for intermediate representations in visual object recognition. *Cognitive Psychology, 23*(3), 393–419, doi:10.1016/0010-0285(91)90014-F.

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

Brincat, S. L., & Connor, C. E. (2006). Dynamic shape synthesis in posterior inferotemporal cortex. *Neuron, 49*(1), 17–24.

Brock, J., Brown, C. C., Boucher, J., & Rippon, G. (2002). The temporal binding deficit hypothesis of autism. *Development and Psychopathology, 14*(2), 209–224, doi:10.1017/S0954579402002018.

Buard, I., Rogers, S. J., Hepburn, S., Kronberg, E., & Rojas, D. C. (2013). Altered oscillation patterns and connectivity during picture naming in autism. *Frontiers in Human Neuroscience, 7*, 742, doi:10.3389/fnhum.2013.00742.

Bülthoff, H. H., Edelman, S. Y., & Tarr, M. J. (1994). How are three-dimensional objects represented in the brain? *Cerebral Cortex, 5*(3), 247–260, doi:10.1093/cercor/5.3.247.

Casanova, M. F., van Kooten, I. A., Switala, A. E., van Engeland, H., Heinsen, H., Steinbusch, W. M., . . . Schmitz, C. (2006). Minicolumnar abnormalities in autism. *Acta Neuropathologica, 112*(3), 287–303, doi:10.1007/s00401-006-0085-5.

Cornew, L., Roberts, T. P. L., Blaskey, L., & Edgar, J. C. (2012). Resting-state oscillatory activity in autism spectrum disorders. *Journal of Autism and Developmental Disorders, 42*(9), 1884–1894, doi:10.1007/s10803-011-1431-6.

Dakin, S., & Frith, U. (2005). Vagaries of visual perception in autism. *Neuron, 48*(3), 497–507, doi:10.1016/j.neuron.2005.10.018.

De Wit, T. C., Schlooz, W. A., Hulstijn, W., & Van Lier, R. (2007). Visual completion and complexity of visual shape in children with pervasive developmental disorder. *European Child and Adolescent Psychiatry, 16*(3), 168–177, doi:10.1007/s00787-006-0585-9.

Dinstein, I., Pierce, K., Eyler, L., Solso, S., Malach, R., Behrmann, M., & Courchesne, E. (2011). Disrupted neural synchronization in toddlers with autism. *Neuron, 70*(6), 1218–1225, doi:10.1016/j.neuron.2011.04.018.

Doniger, G. M., Foxe, J. J., Murray, M. M., Higgins, B. A., Snodgrass, J. G., Schroeder, C. E., & Javitt, D. C. (2000). Activation time course of ventral visual stream object-recognition areas: high density electrical mapping of perceptual closure processes. *Journal of Cognitive Neuroscience, 12*(4), 615–621.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001, Sept 28). A cortical area selective for visual processing of the human body. *Science, 293*(5539), 2470–2473.

Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., & Reitboeck, H. J. (1988). Coherent oscillations: A mechanism of feature linking in the visual cortex? Multiple electrode and

correlation analyses in the cat. *Biological Cybernetics, 60*(2), 121–130, doi:10.1007/BF00202899.

Edelman, S. (1995). Class similarity and viewpoint invariance in the recognition of 3D objects. *Biological Cybernetics, 72*(3), 207–220.

Edelman, S., & Weinshall, D. (1991). A self-organizing multiple-view representation of 3D objects. *Biological Cybernetics, 64*(3), 209–219.

Ehlers, S., & Gillberg, C. (1993). The epidemiology of Asperger syndrome. *Journal of Child Psychology and Psychiatry, 34*(8), 1327–1350.

Ehlers, S., Gillberg, C., & Wing, L. (1999). A screening questionnaire for Asperger syndrome and other high-functioning autism spectrum disorders in school age children. *Journal of Autism and Developmental Disorders, 29*(2), 129–141.

Engel, A. K., Kreiter, A. K., König, P., & Singer, W. (1991). Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat. *Proceedings of the National Academy of Sciences, USA, 88*(14), 6048–6052, doi:10.1073/pnas.88.14.6048.

Ermentrout, G. B., & Chow, C. C. (2002). Modeling neural oscillations. *Physiology and Behavior, 77*, 629–633, doi:10.1016/S0031-9384(02)00898-3.

Esteky, H., & Tanaka, K. (1998). Effects of changes in aspect ratio of stimulus shape on responses of cells in the monkey inferotemporal cortex. *Society of Neuroscience Abstracts, 24*, 899.

Ford, J. M., Mathalon, D. H., Whitfield, S., Faustman, W. O., & Roth, W. T. (2002). Reduced communication between frontal and temporal lobes during talking in schizophrenia. *Biological Psychiatry, 51*(6), 485–492, doi:10.1016/S0006-3223(01)01335-X.

Frith, U. (1989). *Autism, explaining the enigma.* Oxford, UK: Basil Blackwell.

Frith, U., & Happ, F. (1994). Autism: Beyond "theory of mind." *Cognition, 50*(1), 115–132, doi:10.1016/0010-0277(94)90024-8.

Fujita, I., Tanaka, K., Ito, M., & Cheng, K. (1992, Nov 26). Columns for visual features of objects in monkey inferotemporal cortex. *Nature, 360*(6402), 343–346, doi:10.1038/360343a0.

Gilbert, C. D., Das, A., Ito, M., Kapadia, M., & Westheimer, G. (1996). Spatial integration and cortical dynamics. *Proceedings of the National Academy of Sciences, USA, 93*(2), 615–622, doi:10.1073/pnas.93.2.615.

Gray, C., Koenig, P., Engel, A., & Singer, W. (1989, Mar 23). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronisation which reflects global stimulus properties. *Nature, 338*(6213), 334.

Happé, F. (1999). Autism: Cognitive deficit or cognitive style? *Trends in Cognitive Sciences, 3*(6), 216–222, doi:10.1016/S1364-6613(99)01318-2.

Happé, F., & Frith, U. (2006). The weak coherence account: Detail-focused cognitive style in autism spectrum disorders. *Journal of Autism and Developmental Disorders, 36*(1), 5–25.

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001, Sept 28). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science, 293*(5539), 2425–2430, doi:10.1126/science.1063736.

Hayworth, K. J., & Biederman, I. (2006). Neural evidence for intermediate representations in object recognition. *Vision Research, 46*(23), 4024–4031.

Hegdé, J., & Van Essen, D. C. (2007). A comparative study of shape representation in macaque visual areas V2 and V4. *Cerebral Cortex, 17*(5), 1100–1116.

Hirsch, J., DeLaPaz, R. L., Relkin, N. R., Victor, J., Kim, K., Li, T., ... Shapley, R. (1995). Illusory contours activate specific regions in human visual cortex: Evidence from functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences, USA, 92*(14), 6469–6473.

Hoffman, D. D., & Richards, W. A. (1984). Parts of recognition. *Cognition, 18*(1), 65–96.

Hussman, J. P. (2001). Suppressed gabaergic inhibition as a common factor in suspected etiologies of autism. *Journal of Autism and Developmental Disorders, 31*(2), 247–248, doi:10.1023/A:1010715619091.

Iarocci, G., & McDonald, J. (2006). Sensory integration and the perceptual experience of persons with autism. *Journal of Autism and Developmental Disorders, 36*(1), 77–90.

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, USA, 96*(16), 9379–9384, doi:10.1073/pnas.96.16.9379.

Ito, M., Tamura, H., Fujita, I., & Tanaka, K. (1995). Size and position invariance of neuronal responses

in monkey inferotemporal cortex. *Journal of Neurophysiology, 73*(1), 218–226.

Kayaert, G., Biederman, I., & Vogels, R. (2003). Shape tuning in macaque inferior temporal cortex. *The Journal of Neuroscience, 23*(7), 3016–3027.

Kiani, R., Esteky, H., Mirpour, K., & Tanaka, K. (2007). Object category structure in response patterns of neuronal population in monkey inferior temporal cortex. *Journal of Neurophysiology, 97*(6), 4296–4309, doi:10.1152/jn.00024.2007.

Konrad, K., & Eickhoff, S. B. (2010). Is the ADHD brain wired differently? A review on structural and functional connectivity in attention deficit hyperactivity disorder. *Human Brain Mapping, 31*(6), 904–916, doi:10.1002/hbm.21058.

Kourtzi, Z., & Shiffrar, M. (1999). The visual representation of three-dimensional, rotating objects. *Acta Psychologica, 102*(2), 265–292.

Krain, A. L., & Castellanos, F. X. (2006). Brain development and ADHD. *Clinical Psychology Review, 26*(4), 433–444, doi:10.1016/j.cpr.2006.01.005.

Kriegeskorte, N., Formisano, E., Sorger, B., & Goebel, R. (2007). Individual faces elicit distinct response patterns in human anterior temporal cortex. *Proceedings of the National Academy of Sciences, USA, 104*(51), 20600–20605, doi:0705654104. [pii] \r10.1073/pnas.0705654104

Kriegeskorte, N., Mur, M., Ruff, D. A., Kiani, R., Bodurka, J., Esteky, H., . . . Bandettini, P. A. (2008). Matching categorical object representations in inferior temporal cortex of man and monkey. *Neuron, 60*(6), 1126–1141, doi:10.1016/j.neuron.2008.10.043.

Lamsa, K. P., Kullmann, D. M., & Woodin, M. A. (2010). Spike-timing dependent plasticity in inhibitory circuits. *Frontiers in Synaptic Neuroscience, 2*, 8, doi:10.3389/fnsyn.2010.00008.

Levitt, P., Eagleson, K. L., & Powell, E. M. (2004). Regulation of neocortical interneuron development and the implications for neurodevelopmental disorders. *Trends in Neurosciences, 27*(7), 400–406, doi:10.1016/j.tins.2004.05.008.

Li, W., & Gilbert, C. D. (2002). Global contour saliency and local colinear interactions. *Journal of Neurophysiology, 88*(5), 2846–2856, doi:10.1152/jn.00289.2002.

Loffler, G., Yourganov, G., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience, 8*(10), 1386–1390, doi:10.1038/nn1538.

Lord, C., Risi, S., Lambrecht, L., Cook, E. H., Jr., Leventhal, B. L., DiLavore, P. C., . . . Rutter, M. (2000). The Autism Diagnostic Observation Schedule–Generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders, 30*(3), 205–223.

Lumer, E. D., Edelman, G. M., & Tononi, G. (1997). Neural dynamics in a model of the thalamocortical system. II. The role of neural synchrony tested through perturbations of spike timing. *Cerebral Cortex, 7*(3), 228–236, doi:10.1093/cercor/7.3.228.

Masquelier, T., Guyonneau, R., & Thorpe, S. J. (2008). Spike timing dependent plasticity finds the start of repeating patterns in continuous spike trains. *PLoS ONE, 3*(1), e1377, doi:10.1371/journal.pone.0001377.

Masquelier, T., & Thorpe, S. J. (2007). Unsupervised learning of visual features through spike timing dependent plasticity. *PLoS Computational Biology, 3*(2), e31, doi:06-PLCB-RA-0472R2.

Nasr, S., & Esteky, H. (2009). A study of N250 event-related brain potential during face and non-face detection tasks. *Journal of Vision, 9*(5):5, 1–14, doi:10.1167/9.5.5. [PubMed] [Article]

Paille, V., Fino, E., Du, K., Morera-Herreras, T., Perez, S., Kotaleski, J. H., & Venance, L. (2013). GABAergic circuits control spike-timing-dependent plasticity. *The Journal of Neuroscience, 33*(22), 9353–9363, doi:10.1523/JNEUROSCI.5796-12.2013.

Panis, S., & Wagemans, J. (2009). Time-course contingencies in perceptual organization and identification of fragmented object outlines. *Journal of Experimental Psychology: Human Perception and Performance, 35*(3), 661–687.

Pasupathy, A., & Connor, C. E. (1999). Responses to contour features in macaque area V4. *Journal of Neurophysiology, 82*(5), 2490–2502.

Perrett, D. I., Oram, M. W., & Ashbridge, E. (1998). Evidence accumulation in cell populations responsive to faces: An account of generalisation of recognition without mental transformations. *Cognition, 67*(1), 111–145.

Poggio, T., & Edelman, S. (1990, Jan 18). A network that learns to recognize 3D objects. *Nature, 343*(6255), 263–266.

Polleux, F., & Lauder, J. M. (2004). Toward a

developmental neurobiology of autism. *Mental Retardation and Developmental Disabilities Research Reviews, 10*(4), 303–317, doi:10.1002/mrdd.20044.

Reddy, L., & Kanwisher, N. (2006). Coding of visual objects in the ventral stream. *Current Opinion in Neurobiology, 16*(4), 408–414, doi:10.1016/j.conb.2006.06.004.

Rubenstein, J. L. R., & Merzenich, M. M. (2003). Model of autism: Increased ratio of excitation/inhibition in key neural systems. *Genes, Brain, and Behavior, 2*(5), 255–267, doi:10.1046/j.1601-183X.2003.00037.x.

Simmons, D. R., Robertson, A. E., McKay, L. S., Toal, E., McAleer, P., & Pollick, F. E. (2009). Vision in autism spectrum disorders. *Vision Research, 49*(22), 2705–2739, doi:10.1016/j.visres.2009.08.005.

Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience, 18*(1), 555–586, doi:10.1146/annurev.ne.18.030195.003011.

Spencer, J., O'Brien, J., Riggs, K., Braddick, O., Atkinson, J., & Wattam-Bell, J. (2000). Motion processing in autism: Evidence for a dorsal stream deficiency. *Neuroreport, 11*(12), 2765–2767, doi:10.1097/00001756-200008210-00031.

Stevenson, R. A., Segers, M., Ferber, S., Barense, M. D., Camarata, S., & Wallace, M. T. (2015). Keeping time in the brain: Autism spectrum disorder and audiovisual temporal processing. *Autism Research*, 9(7), 720–738.

Stevenson, R. A., Siemann, J. K., Schneider, B. C., Eberly, H. E., Woynaroski, T. G., Camarata, S. M., & Wallace, M. T. (2014). Multisensory temporal integration in autism spectrum disorders. *The Journal of Neuroscience, 34*(3), 691–697.

Stroganova, T. A., Orekhova, E. V., Prokofyev, A. O., Tsetlin, M. M., Gratchev, V. V., Morozov, A. A., . . . Obukhov, Y. V. (2012). High-frequency oscillatory response to illusory contour in typically developing boys and boys with autism spectrum disorders. *Cortex, 48*(6), 701–717, doi:10.1016/j.cortex.2011.02.016.

Sun, L., Grützner, C., Bölte, S., Wibral, M., Tozman, T., Schlitt, S., . . . Uhlhaas, P. J. (2012). Impaired gamma-band activity during perceptual organization in adults with autism spectrum disorders: Evidence for dysfunctional network activity in frontal-posterior cortices. *The Journal of Neuroscience, 32*(28), 9563–9573.

Szwed, M., Cohen, L., Qiao, E., & Dehaene, S. (2009). The role of invariant line junctions in object and visual word recognition. *Vision Research, 49*(7), 718–725, doi:10.1016/j.visres.2009.01.003.

Tanaka, K. (2003). Columns for complex visual object features in the inferotemporal cortex: Clustering of cells with similar but slightly different stimulus selectivities. *Cerebral Cortex, 13*(1), 90–99, doi:10.1093/cercor/13.1.90.

Tanaka, K., Saito, H. A., Fukada, Y., & Moriya, M. (1991). Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology, 66*(1), 170–189.

Tomchek, S. D., & Dunn, W. (2007). Sensory processing in children with and without autism: A comparative study using the short sensory profile. *American Journal of Occupational Therapy, 61*(2), 190–200.

Tsunoda, K., Yamane, Y., Nishizaki, M., & Tanifuji, M. (2001). Complex objects are represented in macaque inferotemporal cortex by the combination of feature columns. *Nature Neuroscience, 4*(8), 832–838, doi:10.1038/90547.

Ullman, S., & Basri, R. (1991). Recognition by linear combination of models. *IEEE Transactions on Pattern Analysis and Machine Intelligence, 13*(10), 992–1006.

Vandenbroucke, M. W. G., Scholte, H. S., van Engeland, H., Lamme, V. A. F., & Kemner, C. (2008). A neural substrate for atypical low-level visual processing in autism spectrum disorder. *Brain, 131*(4), 1013–1024, doi:10.1093/brain/awm321.

Van der Hallen, R., Evers, K., Brewaeys, K., Van den Noortgate, W., & Wagemans, J. (2015). Global processing takes time: A meta-analysis on local–global visual processing in ASD. *Psychological Bulletin, 141*(3), 549.

Vanegas, S. B., & Davidson, D. (2015). Investigating distinct and related contributions of weak central coherence, executive dysfunction, and systemizing theories to the cognitive profiles of children with autism spectrum disorders and typically developing children. *Research in Autism Spectrum Disorders, 11*, 77–92.

Van Eylen, L., Boets, B., Steyaert, J., Wagemans, J., & Noens, I. (2015). Local and global visual processing in autism spectrum disorders: Influence of task and sample characteristics and relation to symptom severity. *Journal of Autism and Developmental Disorders, 1*–23.

Van Vreeswijk, C., Abbott, L. F., & Bard Ermentrout, G. (1994). When inhibition not excitation synchronizes neural firing. *Journal of Computational Neuroscience, 1*(4), 313–321, doi:10.1007/BF00961879.

Vogels, R., Biederman, I., Bar, M., & Lorincz, A. (2001). Inferior temporal neurons show greater sensitivity to nonaccidental than to metric shape differences. *Journal of Cognitive Neuroscience, 13*(4), 444–453, doi:10.1162/08989290152001871.

Wechsler, D. (1949). *Wechsler intelligence scale for children*. New York: The Psychological Corporation.

Weil, R. S., & Rees, G. (2011). A new taxonomy for perceptual filling-in. *Brain Research Reviews, 67*(1), 40–55.

Yau, J. M., Pasupathy, A., Brincat, S. L., & Connor, C. E. (2013). Curvature processing dynamics in macaque area V4. *Cerebral Cortex, 23*(1), 198–209, doi:10.1093/cercor/bhs004.

Zeki, S. (1996). Brain activity related to the perception of illusory contours. *Neuroimage, 3*(2), 104–108.