Vagaries of Visual Perception in Autism

Review

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Three classes of perceptual phenomena have repeatedly been associated with autism spectrum disorder (ASD): superior processing of fine detail (local structure), either inferior processing of overall/global structure or an ability to ignore disruptive global/contextual information, and impaired motion perception. This review evaluates the quality of the evidence bearing on these three phenomena. We argue that while superior local processing has been robustly demonstrated, conclusions about global processing cannot be definitively drawn from the experiments to date, which have generally not precluded observers using more local cues. Perception of moving stimuli is impaired in ASD, but explanations in terms of magnocellular/dorsal deficits do not appear to be sufficient. We suggest that abnormalities in the superior temporal sulcus (STS) may provide a neural basis for the range of motion-processing deficits observed in ASD, including biological motion perception. Such an explanation may also provide a link between perceptual abnormalities and specific deficits in social cognition associated with autism.

Introduction

Autism is a developmental disorder of neurological origin that occurs in a large variety of forms from mild to severe, now referred to as autism spectrum disorder (ASD). The estimated prevalence of ASD is between 0.3% and 0.9%. The etiology has not yet been clarified, but genetic factors are likely to play a major role. ASD is currently defined by behavioral criteria, which include impairments in social interaction, impairments in verbal and nonverbal communication, and restricted interests and activities. On the surface, none of these symptom complexes appear to involve perceptual deficits. Increasingly, however, abnormalities of sensory perception have been invoked as possible primary or at least contributory causes of some characteristic features of ASD. For instance, poor processing of eye gaze and facial expressions in ASD have been linked to deficits in low-level perception, which might ultimately result in impairments of social communication. On the other hand, the uneven profile of cognitive abilities, with often

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superior visuospatial skills, has been attributed to particular strengths in perceptual processing.

The idea that individuals with ASD perceive the world differently, reflected in sometimes superior performance on perceptual tasks, is perhaps the most intriguing of all the puzzles thrown up by autism. The list of phenomena that have been systematically investigated is, however, short. Some studies have demonstrated superior performance in tasks requiring recognition for details and ability to find hidden figures (Shah and Frith, 1983). Other studies have shown superior performance in a range of tasks that require attention to small elements, for instance, in visual search (O'Riordan et al., 2001; Plaisted et al., 1998b), and in the learning of highly confusable patterns (Plaisted et al., 1998a). Furthermore, savant capacities, which are frequently associated with ASD, such as exceptional drawing ability, often involve a preference for perceptual detail (Mottron and Belleville, 1993). However, deficits in visual processing have also been found. These suggest that individuals with ASD show raised thresholds for perceiving coherent motion (e.g., Milne et al., 2002; Spencer et al., 2000), and postural hyporeactivity for visual motion (i.e., a reduced change in posture in response to an illusion inducing a sense of self-motion; Gepner and Mestre, 2002a; Gepner et al., 1995).

The phenomena associated with superior performance on visual tasks (see Figure 2 for examples) have been addressed by two theories, the weak central coherence hypothesis (WCC) and the enhanced perceptual function hypothesis (EPF). The WCC hypothesis drew attention to the normally strong drive for meaning (Bartlett, 1932), that is, the tendency to process visual information for overall Gestalt at the expense of details and surface features (Frith, 1989). It highlighted in contrast the performance of individuals with ASD as showing a processing bias for local information and relative failure to extract meaning or "see the big picture." Hence, weak central coherence has been equated with a failure to extract global form. WCC predicts superiority and inferiority of performance on selected perceptual tasks, depending on whether these demand local or global processing, respectively. Happé (1999) modified the WCC account to propose that it describes a processing bias or cognitive style, which can be overcome in tasks with explicit demands for global processing. Furthermore, she presented evidence that this cognitive style is part of the broader autism phenotype and can be observed in clinically healthy relatives of individuals with ASD. An updated review of the WCC account is presented by Happé and Frith (2006).

Another attempt to explain superior local processing is represented by the enhanced perceptual function hypothesis (Mottron and Burack, 2001; Plaisted et al., 1998a). This account, updated by Mottron et al. (2006), proposes that in autism enhanced processing of stimulus elements is facilitated (Bonnel et al., 2003; Plaisted et al., 1998b). This can be seen as an overdevelopment of low-level perceptual operations that cause detection, discrimination, and other low-level abilities to be

enhanced (Mottron et al., 2003). In contrast to WCC, EPF does not assume that there is a failure of global processing. The most recent incarnation of EPF specifically proposes that the automatic progression from local to global visual representation that occurs in normal vision is compromised but that, as a consequence, people with ASD retain access to local structure (which is lost in the course of normal visual processing).

A somewhat different hypothesis has been offered to explain the empirical finding of raised motion thresholds (Milne et al., 2002; Pellicano et al., 2005; Spencer et al., 2000). Here a physiological rather than cognitive account has been proposed, namely, poor functioning of the dorsal/magnocellular system. In contrast to the WCC and EPF hypotheses, this account is not specific to autism, but addresses the same finding in a variety of developmental disorders, such as dyslexia and Williams syndrome.

The remit of this review is work related only to visual processing, both because this is where the bulk of the work has been conducted and because there is a considerable amount of knowledge on the physiology and anatomy of the brain pathways involved in vision. The questions we will address are whether differences in autistic visual function reflect deficits in low-level visual processes in the autistic brain or in behavioral biases toward certain types of information. We will also be considering the question as to whether there are specific deficits in certain pathways of visual function (notably dorsal versus ventral, magnocellular versus parvocellular). After giving some background on human visual processing, we will consider these questions in the light of research conducted with stimuli defined by various visual attributes. We focus on two types of static stimuli that either encourage or discourage global integration, and on moving stimuli. We will argue that the division between local and global requirements in many experiments to date has been poorly defined. For this reason it is not yet possible to adjudicate between the different theoretical accounts sketched out above. While this review is restricted to visual perception, it is important to bear in mind that the main theoretical claims are multimodal and that some of the key evidence is based on tasks in the auditory modality. This will not be reviewed here.

Visual Processing: Thinking Locally, Acting Globally
The process of vision begins with the conversion of light into electrical signals at the retina and their transmission, via the dorsal lateral geniculate nucleus (LGN), to the primary visual cortex (V1). While 90% of retinal projections target LGN, those projections account for less than 10% of synapses in that structure, with nearly 60% being due to feedback from V1 (Sherman and Guillery, 2002). Thus, even the very earliest stages of visual processing are reliant on a massive feedback projection. By the stage of V1, the image is effectively represented by a patchwork of neurons, each of which is primarily responsive to visual structure falling within a limited area of space known as its *receptive field* (RF). In V1, cells are particularly responsive to oriented structure within their RFs (Hubel and Wiesel, 1962). The fact that there is a predictable relationship between the neuron's location in cortex and the point in space it responds to
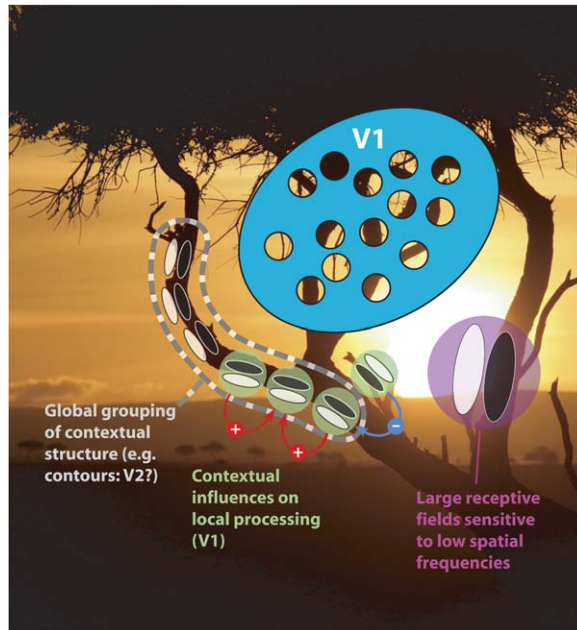

Figure 1. Receptive Fields and Visual Context
Neurons in primary visual cortex (V1) are primarily responsive to locally oriented image structure within a patch of visual space known as their *receptive field* (RF). The view of several V1 neurons is illustrated by the windows cut out from the blue oval. V1 neurons are responsive to different size of features; small RFs (green) and large RFs (purple) confer sensitivity to high and low spatial frequency structure, respectively. In recent years it has become apparent that such neurons do not work in strict isolation, and the wider visual context contributes to processing in two ways. First, it mediates local visual operations (i.e., of the V1 neurons themselves) either through facilitation (e.g., from orientation structure that is consistent with extended contour structure; "+" connections; Polat et al., 1998) or inhibition (e.g., from surround inhibition from neurons with similarly oriented RFs; "−" connections; e.g., Jones et al., 2001). Second, context contributes to the grouping of local structure into more complex, global structures such as spatially extended contours. The mechanism by which such grouping is achieved is not well understood, although it seems likely to involve activation within—and spatially extensive feedback from—later visual areas, such as V2.

(a *retinotopic map*; e.g., Tootell et al., 1982) implies that V1 is forming an essentially "local" representation. However, in recent years the notion that cells could be treated as independent computational entities has collapsed, as it has became increasingly apparent that visual structure falling well outside of a neuron's "classical" RF can massively influence its responses (Figure 1). For example, almost 90% of neurons in V1 are suppressed by the activity of their neighbors (Jones et al., 2001). The source of such contextual influences is controversial but could be due to feedback projections from higher visual areas or from the direct influence of neighboring V1 neurons by way of "long-range" horizontal connections (although the anatomy does not seem to bear the latter hypothesis out; Angelucci and Bullier, 2003). V1 projects into a series of higher visual areas and, in general, neurons in these areas have larger RFs (e.g., in V4; Motter, 2002), indicating more spatially extensive global integration of V1 inputs. For the processing of motion, V1 neurons that are selective for simple translational motion of small local features tend to

project up into areas MT/V5, which have larger receptive fields, and are responsive to more complex, *global motion* (e.g., motion boundaries). With respect to static form, while V1 is interested in simple orientation structure, there is evidence that V2 neurons prefer angles between lines (Ito and Komatsu, 2004), while V4 prefers more complex shape attributes, such as corners that can, through population-coding strategies, be built up into complete codes for complex outline-shape (Pasupathy and Connor, 2002). Beyond V4, the responses of neurons in inferotemporal (IT) cortex show a remarkable degree of scale and position invariance, indicating sensitivity to global form, and, as well as being responsive to objects such as faces, Logothetis et al. (1995) report that they can become selective for any 3D objects that are useful to the animal.

This hierarchical architecture results from the confluence of two different processing streams. At the early stages of visual processing (retina-LGN-V1) there are two distinct subpopulations of neurons responsive to different attributes of the stimulus. Polyak (1941) noted marked differences in the morphology of retinal cells: midget ganglion cells have dense compact dendritic arborization, while parasol cells have much sparser, widely distributed arborization. Midget ganglion cells primarily contact neurons with smaller cell bodies in the four superficial layers of the LGN (to form the *parvocellular stream*), while parasol ganglion cells project to larger cells in the two deeper layers (to form the *magnocellular stream*). A variety of evidence bears on what type of information is carried by these two streams. Lesion studies (e.g., Merigan et al., 1991) indicate that loss of magnocellular neurons compromises sensitivity for low spatial frequency flickering stimuli, indicating an involvement of this stream in motion perception. Loss of the parvocellular stream—which carries almost 70% of the retinal input—affects a variety of color and fine-form discrimination tasks. A further division arises beyond V1 when neurons contribute either to the *dorsal* or *ventral* visual pathways (Goodale and Milner, 1992; Ungerleider and Mishkin, 1982). The dorsal visual stream projects from V1 to the parietal lobe and is thought to play a principal role in the localization of visual stimuli and in the planning of actions toward objects. The ventral stream projects to the temporal lobe and is thought be involved in the recognition of objects and in the encoding of spatial relationships between subparts of scenes.

To summarize, the human visual system is hierarchical, with neurons becoming selective for increasingly complex features as one proceeds along the visual pathway. At early stages, two streams deal separately with coarse-scale motion or fine-scale form information. At later stages, two streams deal with the identity or location of features.

It should be clear, even from this thumbnail account, that the context within which a feature arises will greatly influence the way in which it is processed. In this review, we consider two ways in which context can influence functional vision. The first is contextual effects on local visual processing, that is, the way in which processing of information at a particular location within a scene is influenced by surrounding visual structure. For example, the visibility of an oriented feature can improve or deteriorate depending on the proximity to, and arrangement

of, similar visual features within a scene. The second way context influences vision is via global visual grouping; we tend to associate similar features with one another according to principles embodied by the rules described by the Gestalt school of perceptual psychology. Both these categories are linked; identical visual structure may lead to both contextual influences on the elements and grouping phenomena among elements. Strict definition of local and global processing is difficult. Our operational definition is that local structure can be encompassed by the receptive fields of single neurons in the earliest visual cortical area (V1) and so can be signaled by the activity of these neurons. We define global structure as anything that requires the coordinated activity of several neurons.

Ignoring Context: Local Visual Processing
In this section we consider studies that have looked at local visual processing principally by examining the influence of visual context on observers' ability to perform a task based on a local feature within a complex image. Common features of such tasks are (1) that it is to the observer's advantage to ignore distracting global structure and focus on local detail to perform effectively and (2) that they can elicit performance from autistic observers that is substantially better than matched controls. This is of great interest from a theoretical point of view because there are many reasons why a clinical population might be poor at a task, whereas superior performance tends to have a specific cause that can be more easily traced back to specific brain mechanisms (Chapman et al., 1991).

Some of the stimuli used to probe contextual influences on local perception are illustrated in Figures 2A–2F. Participants with ASD are better at constructing arbitrary patterns from simple elements on the Block Design subtest of the Wechsler intelligence test (Figure 2A; Shah and Frith, 1993) and are better at detecting figures embedded in more complex line drawings (Figure 2B; Jolliffe and Baron-Cohen, 1997; Shah and Frith, 1983). Observers with ASD are better at copying impossible figures (Figure 2C; Mottron et al., 1999a), likely resulting from an impaired ability to see, and so be distracted by, the impossible structure (Brosnan et al., 2004). Such findings are consistent with observers with ASD focusing on the detailed structure of the patterns.

Many visual illusions are related to contextual influence upon the appearance of objects. The idea of using illusions to study contextual effects in a clinical population is appealing if one considers illusions as inducing some form of perceptual error. In that case, weaker contextual effects will be manifest as a reduced illusion; i.e., more local visual processing will confer an advantage to clinical subjects over controls. Happé found that people with ASD were immune to many visual illusions (including the Ehrenstein, shown in Figure 2D, and Poggendorf illusions, etc.) and showed reduced benefit from 3D segmentation (Happé, 1996). However, Ropar and Mitchell (1999, 2001) failed to find similar effects. This discrepancy may have been due in part to procedural differences.

Individuals with autism are substantially better than controls at visual search tasks. For a *feature search*, where a target is differentiated from the distracters that surround it by a unique attribute (e.g., only the target is
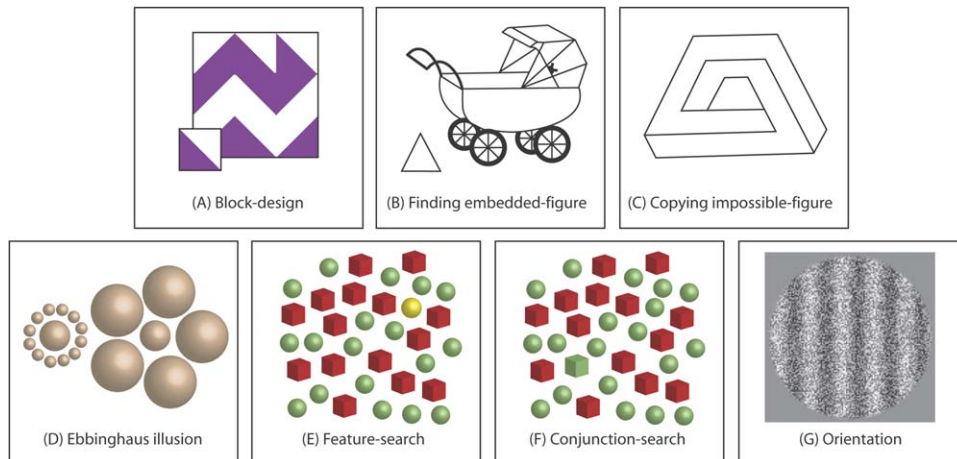
Figure 2. Tasks Used to Probe Perceptual Processing that Elicit Supranormal Performance in Observers with ASD

(A) Block Design subtest of the Wechsler intelligence test, (B) locating embedded figures, (C) copying of impossible figures. (D) Ebbinghaus illusion; the surrounding elements can make the (identical) central targets appear quite different. Some controversy surrounds whether autistic observers are susceptible to this illusion. (E and F) Autistic observers are faster and less error prone at finding the odd-man-out in cluttered displays whether the target is defined by a single feature as in (E) or by a conjunction of features as in (F). (G) Bertone et al. (2005) have reported that observers with ASD can tolerate higher levels of noise in determining the orientation of luminance-defined sine-wave gratings.

yellow; Figure 2E) so that the target "pops-out," the search time for normal participants is independent of the number of distracters. For *conjunction search*—where the target is defined by a pair of attributes, any one of which is shared with the distracters (e.g., a green cube embedded in red cubes and green spheres; Figure 2F)—search time for normal participants depends on the number of distracters. ASD observers are significantly faster on both types of search and in particular do not show any characteristic increase in reaction time as display size increases in the feature-conjunction conditions. As a result, ASD observers are nearly twice as fast as controls in the largest display conditions (O'Riordan et al., 2001). A follow-up study by O'Riordan (2004) reports a statistically significant but somewhat reduced speed advantage, with groups that were matched for nonverbal measures of general ability (confirming that this is not an artifact of the way controls were matched in the earlier study). Critically, these authors also show similar patterns of speed-accuracy trade-off for both groups and that the advantage is reliably observed in feature search, provided ceiling effects are avoided.

Recently, efforts have been made to determine the relationship between fast visual search and other feats of superior visual performance among individuals with ASD. Notably, Jarrold et al. (2005) report that embedded-figure detection is correlated with feature search in autistic subjects, but with conjunction search in controls. These are interesting but preliminary findings, given the rather small, non-age-matched sample and that the feature-search task was unusually difficult, producing a similar dependence of performance on distracter density as the conjunction search. That said, these findings are important for a number of reasons. First, the linkage of performance on embedded figures to feature search in autism suggests superior differentiation of target from distracters, whereas the linkage to conjunction search in controls suggests that they are limited by how well

they can group the background. This goes beyond cognitive bias and suggests that a basic difficulty in grouping may contribute to enhanced pop-out observed in autism.

Finally, Bertone et al. (2005) have reported that observers with ASD produce lower "orientation discrimination thresholds" for stimuli depicted in Figure 2G when defined by modulation in luminance but not contrast. In terms of the experimental task, this meant that autistic observers could tolerate higher levels of luminance noise and still tell the orientation of a luminance-defined target.

To summarize, there is now quite compelling evidence that autistic observers can, under some circumstances at least, make better use of local information than matched control subjects. The stimuli eliciting such performance tend to contain distracting global information, which observers with ASD are better at ignoring. Is this because they simply cannot see global structure or because their cognitive style leads them to ignore it? To evaluate this issue a number of studies have investigated autistic performance on global grouping tasks.

Using Context: Global Visual Processing

Navon (1976) introduced a hierarchical stimulus, consisting of a large/global letter composed of small/local letters, depicted in Figure 3A, to try and separate local and global levels of visual processing. Normal performance with such stimuli is characterized by a simple bias toward the global structure. Because it is widely held that there is a predisposition toward local processing in autism, a number of researchers have used Navon stimuli to manipulate the relevance of either local information (the constituent letters) or global information (the overall shape) to the task at hand. In general, findings have been mixed, indicating impaired global processing under some conditions (Milne et al., 2002; Rinehart et al., 2000) but not others (Mottron et al., 2003, 1999b; Ozonoff et al., 1994).

We note a problem with interpreting studies using Navon stimuli and other variants using "Gestalt
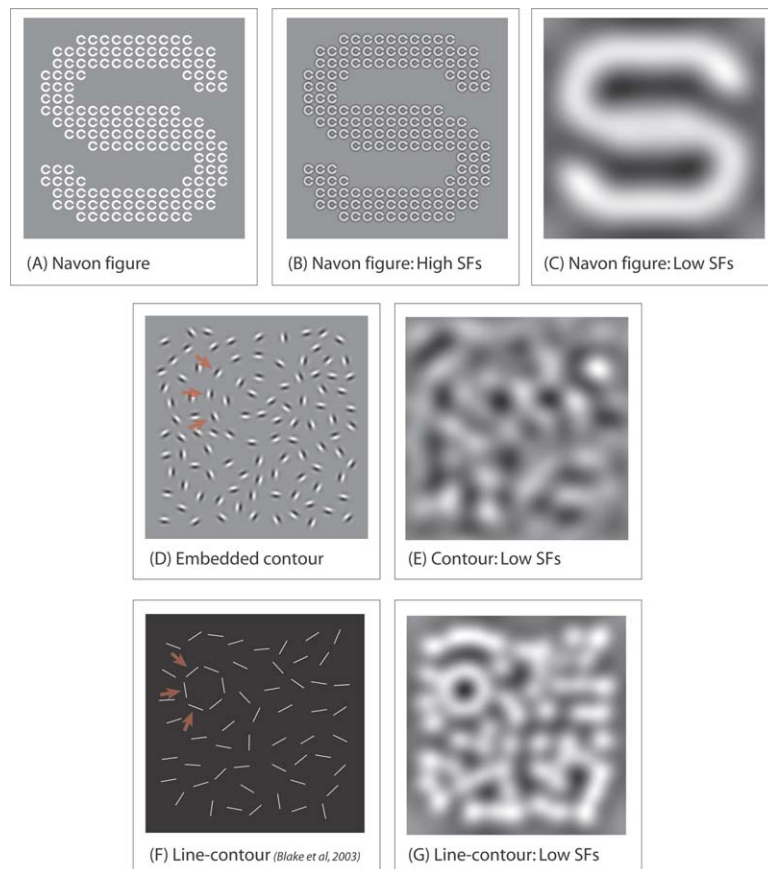
Figure 3. Static Stimuli Used to Probe Global Visual Grouping/Integration

(A) Navon stimulus: subjects report either the local component letters ("C") or the global letter ("S"); observers with ASD do not show the normal bias toward the global level. (B) High and (C) low spatial frequency structure of the Navon stimulus highlight local and global structure, respectively. (D) Global grouping stimuli, such as this embedded-contour stimulus (Field et al., 1993; Hess and Dakin, 1997) have been developed that cannot be solved in this manner and require global linking of neural responses across space. The circular contour in (D) is not revealed by (E) low spatial frequency structure. However, the limited testing conducted with people with ASD has used (F) stimuli that contain essentially (G) the same low SF cues to structure as the Navon stimuli.

grouping" of simple dot patterns (e.g., Brosnan et al., 2004) in that these stimuli do not require "global grouping" under our working definition. Figure 3C shows that structure in Navon figures is revealed by the operation of neurons with large receptive fields sensitive to low spatial frequencies (SFs; the purple RFs shown in Figure 1) without recourse to dedicated global grouping mechanisms that link multiple receptive fields across space (Figure 1). Indeed, low spatial frequencies are known to play a major role in processing these stimuli; in particular, no global RT advantage is observed when low SFs are removed (Badcock et al., 1990; LaGasse, 1993). This is consistent with a SF-based explanation of the global bias, based on the notion that low SF information is effectively available faster than high SFs (the "coarse-to-fine" hypothesis; Watt, 1987).

More elaborate grouping stimuli have been developed that require feature linking across space. Notably Field et al. (1993) introduced the embedded contour stimuli depicted in Figure 3D, composed of a field of randomly oriented elements containing an embedded set with positions and orientations consistent with the presence of an elongated contour. These stimuli have a number of attributes that minimize the useful contribution of simple SF filtering as a grouping mechanism, including (1) use of SF band-pass local elements ("Gabors"), (2) substantial interelement separation, and (3) element contrast-polarity alternation along the contour. These steps are crucial in targeting global grouping operations because it is known that observers will use low SF to support grouping when normal global linking operations are un-

available. For example, observers are poor at detecting contours in the periphery except when the stimulus is arranged in such a way as to provide some residual low spatial frequency cues to feature coalignment (Hess and Dakin, 1997).

Remarkably, there has not been, to our knowledge, a single systematic study of global grouping performance of observers with ASD that has used stimuli that entirely prevent observers using local (within receptive field) grouping based on low SFs to perform the task. The only two published applications of embedded contours have used stimuli composed of lines. These patterns are SF broad-band, i.e., contain information at all spatial frequencies. Thus, one instead relies entirely on interelement separation to prevent activation of simple local mechanisms giving away the target location. Figure 3F shows that in one example, from Blake et al. (2003), elements are so close together as to make grouping by a low SF local mechanism trivial (Figure 3G). Thus, reports of normal global grouping performance in ASD have to be treated with caution.

Processing of Visual Motion

Our ability to see movement is a key visual ability that contributes both to the detection and segmentation of objects within natural visual scenes and also to our ability to successfully navigate and maintain posture within complex, constantly changing environments. For example, viewing a large radial flow field produces a compelling impression of self-motion that elicits compensatory postural movements. Gepner et al. (1995) noted that
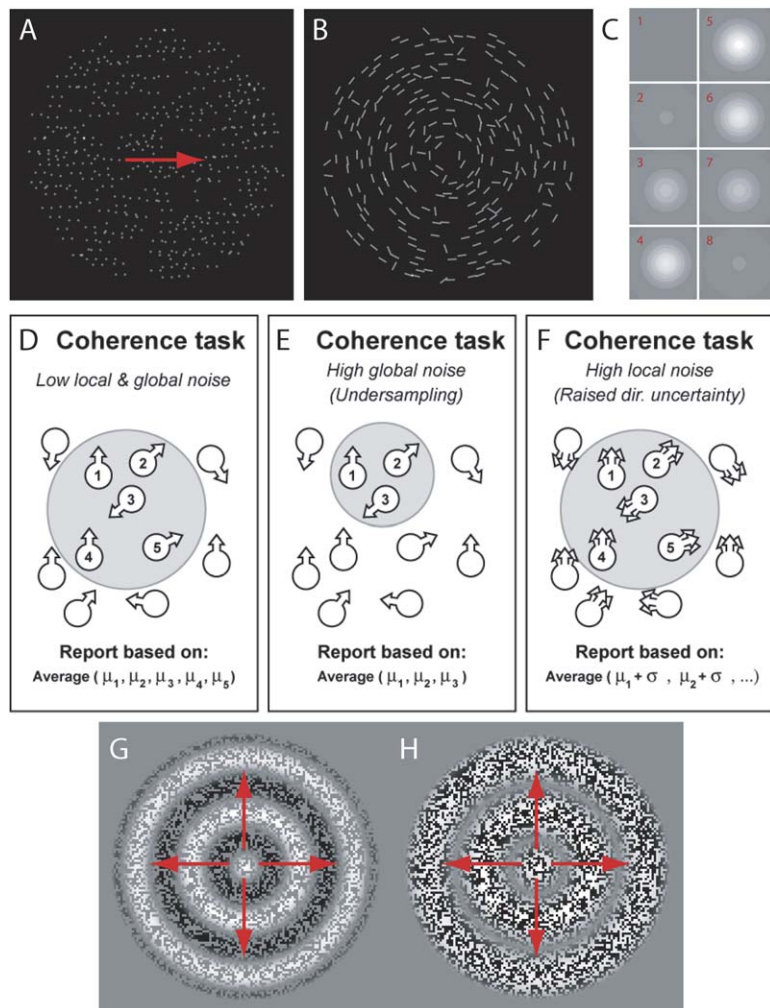
Figure 4. Dynamic Stimuli Used to Probe Visual Function in Autism

(A) The stimulus used to measure motion coherence thresholds. A set of randomly moving dots has been displaced to the right; here the two movie frames have been superimposed for illustrative purposes. In this example, 25% of the dot pairs have been replaced with random noise. (B) Form coherence control task used by Spencer et al. (2000) as a static analog of (A). Moving dots are replaced by rotationally organized lines; again 25% have been replaced by randomly oriented elements. (C) Flicker-detection control task used by Pellicano et al. (2005); subjects detected the sinusoidal modulation of luminance of a Gaussian patch over time. Each numbered panel shows one frame of the movie. (D) Notional processing of motion coherence stimuli; subjects are assumed to report direction based on pooled/averaged subset of the local dot directions. Although it is widely held that poor performance on this task is attributable to (E) poor global motion processing (i.e., undersampling), (F) depicts an alternative explanation where global pooling is normal but where each local motion estimate is imprecise. Indeed Barlow and Tripathy (1997) have shown that local noise—specifically an inability to follow individual dot motion across frames—limits MCTs in normal observers under many conditions. Thus, it is unclear if MCTs unambiguously probe global motion processing. Note that neither of the control tasks depicted in (C) or (D) impose any local noise on the subject at all; line orientation is clear in (B), unlike the uncertainty with which one can extract the dot pairings in (A). Bertone et al. (2003) took another approach and used radial motion defined by either (G) first-order/luminance or (H) second-order/contrast. Arrows indicate the direction of motion.

children with autism are less responsive to such stimuli and that the degree of such postural hyporeactivity correlates with the severity of the autistic disorder (Gepner and Mestre, 2002b). In order to rule out higher-order explanations of such phenomena (e.g., that subjects might simply be less *attentive* to the flow field) recent studies have attempted to isolate and study motion perception in more depth.

The most popular psychophysical paradigm for studying motion perception—pioneered in primate electrophysiology (Newsome et al., 1986) but used widely, for example, in the study of dyslexia (e.g., Talcott et al., 2000)—has been based on *motion coherence*. Here, observers must discriminate the overall direction (e.g., "left" versus "right") of a field of coherently moving dots (i.e., moving in the same direction) where some proportion of them has been replaced by randomly moving elements (Figure 4A). The minimum number of coherently moving elements supporting direction discrimination at some criterion level of performance (e.g., 75% correct) is referred to as the *motion coherence threshold* (MCT). Spencer et al. (2000), as well as more recent studies (e.g., Milne et al., 2002), report that autistic observers require about 10% more coherent motion to reliably report direction. However, in order to rule out a simple ex-

planation based on higher-level cognitive factors, one must compare performance on these tasks to control conditions. Thus, Spencer et al. (2000) report that signal-to-noise thresholds measured using an analogous form task (Figure 4B) were normal in autistic observers and suggested that their deficit therefore arose from dysfunction within the dorsal visual stream. However, Pellicano et al. (2005) report that subjects showing elevated MCTs required the same amount of contrast as controls in order to reliably detect the presence of a sinusoidal luminance modulation of a Gaussian patch (Figure 4C; similar findings have since been reported by Bertone et al., 2005). Because such flicker detection is thought to be mediated by the same dorsal-stream neurons that signal motion (indeed, motion detectors are thought to be wired-up using flicker detectors), Pellicano et al. (2005) argued that autistics exhibit not a general dorsal deficit as has been suggested (Braddick et al., 2003; Spencer, 1984) but an impairment in the processing of global motion information (i.e., the ability to combine the individual dot directions together into an estimate of the overall direction).

There has been some work examining integration of direction information not within rigid translational motion but within the more complex motion signals arising

from the kinematics of human motion: so-called *biological motion* stimuli. Moore et al. (1992) initially showed that autistics were not significantly worse than controls at deciding if point-light movies depicted a person or an object. However, using a signal-detection paradigm, Blake et al. (2003) did find autistics to be impaired at recognizing biological motion; the authors proposed that results from the earlier study likely arose from ceiling effects. They go on to propose that such low-level deficits in integrating motion signals could affect ability to recognize dynamic facial expressions.

It is important to note that the conclusions drawn from these studies is typically predicated on the notion that observers' ability to see coherent motion at threshold (i.e., in the presence of high numbers of randomly moving dots) is limited by their ability to pool enough motion signals across space (i.e., a global motion limit). Contrary to this position, Barlow and Tripathy (1997) have presented evidence that it is the observers' inability to track dots across movie frames that limits MCTs; i.e., they are limited by *local motion* processing. Interestingly in order to elicit reliable differences between clinical and control groups many experimenters have converged on motion coherence stimuli containing high levels of intrinsic *local noise*, in particular using large dot displacements within very dense fields of dots (which will lead to high levels of what Barlow and Tripathy (1997) term *correspondence noise*). On a subjective level, performance with such stimuli breaks down not when one sees a field of dots undergoing random local motion but where one sees little or no local motion at all. Since MCTs are likely determined by a mixture of local and global factors, the control tasks used are critical. It is therefore a concern that such tasks are not always well matched to the motion task in that they have tended to minimize local as well as global noise. For example, the static control for the motion coherence stimuli used by Spencer et al. (2000) consists of organized fields of lines (Figure 4B) where local orientation structure is completely noise free. This task is purely limited by global pooling (since there is no uncertainty on the orientation of the elements). Given this, and the balance of evidence from psychophysics, at present it would be quite reasonable to draw the exact opposite conclusion to that advanced in the literature and conclude that poor performance in ASD is wholly due to poor processing of local motion. What is required is that local uncertainty in static control conditions be matched to the motion stimuli. A simple way of doing this would be to use Glass patterns (e.g., the superimposed dot fields depicted in Figure 1A), rather than line stimuli, as control stimuli. Alternatively, it has been shown that an equivalent-noise paradigm—which requires observers to average direction across space in the presence of directional noise—can disentangle local and global limits on motion perception (Dakin et al., 2005).

An alternative approach, taken by Bertone et al. (2003), has been to use stimuli which contain minimal local uncertainty but which probe different types of motion information, and which the authors characterize as requiring more or less "complex" processing. Specifically, the motion signal in dot patterns is carried by a change in luminance over time (essentially, the shift in dot position from one frame to the next, known as "first-order" mo-

tion), but the human visual system is also capable of detecting the motion of other stimulus attributes such as contrast ("second-order" motion; Chubb and Sperling, 1988). Examples of first- and second-order motion stimuli are shown in Figures 4G and 4H, respectively. While the neural substrate and computational principles underlying first-order motion processing are fairly well understood (e.g., motion energy filtering; Adelson and Bergen, 1985) the mechanism responsible for signaling second-order motion is more contentious. The most widely accepted view is the two-stream "filter-rectify-filter" (FRF) model (Wilson et al., 1992). Wilson proposes that there are two motion streams. In the first, motion energy filtering signals first-order motion. In the second, a sequence of prefiltering and the application of a rectifying nonlinearity essentially turn second- into first-order motion, which is then signaled by another population of motion-energy mechanisms, operating at a coarse spatial scale. The two directional estimates obtained from these streams are then combined to signal complex two-dimensional motion. Bertone et al. (2003) report lower sensitivity of autistic observers to second- compared to first-order motion, using stimuli (Figures 4G and 4H) composed of a static noise pattern ("carrier") whose contrast or luminance was modulated by a moving pattern. This the authors attribute not to a dorsal stream deficit—which would equally affect first- and second-order processing—but to the *complexity* of their stimuli.

There are two problems with this conclusion. First, the notion of complexity in these stimuli is poorly defined. If there is an idea that second-order motion processing and global motion processing (i.e., requiring more extensive pooling) might be linked, this is unlikely to be true because a feature of second-order motion processing seems to be that it employs only limited pooling over space (Allen and Derrington, 2000). Second, it has been proposed that attentional demands from second-order motion processing are higher (Derrington et al., 2004), so that attentional deficits associated with autism (Burack, 1994) may have confounded the results. The latter is an important point and suggests a need for work examining whether attentional deficits associated with ASD are linked to particular classes of stimuli (e.g., dynamic patterns). It has to be said that almost all psychophysical studies that report inferior performance in a clinical group suffer from this limitation. In other words, it can always be surmised that the reason for elevated perceptual thresholds is not due to the nature of the perceptual discrimination, but due to poorer ability to stay "on task." In the absence of additional tasks to control for attentional demand, we make the following procedural suggestion. Many studies of visual function in ASD employ adaptive psychophysical procedures that quickly measure performance/thresholds. Such procedures assume that observers will make few "key-press" errors, unassociated with the stimulus, but likely due to atentional lapse. If the observer violates these assumptions, then this can lead to underestimation of their true performance (Stuart et al., 2001). Measuring full psychometric functions, across the range of stimulus values, is more time consuming but allows one to quantify the rate of these random errors and by inference, the rate of attentional lapses across conditions.

Returning to the issue of stimulus complexity, dot patterns are complex in the sense that they contain information at many spatial scales and that they contain both first- and second-order motion cues. What is not yet understood is the relative contribution of these sources of information to a judgment of global motion. Given that many of the motion coherence stimuli employed in the studies described above used large dot displacements (high speeds) and that it has been proposed that second-order motion processing may be particularly useful for dealing with fast-moving stimuli, a parsimonious interpretation can be derived. Thus, the results described suggest there is a generalized deficit in processing of second-order information and that this influences the processing of dot patterns under conditions that effectively target that system. We return to this point in the discussion.

In summary, people with ASD are poor at motion coherence tasks, biological motion, and second-order motion processing. It has been assumed that the limiting factor on the first task is global integration, but we have argued that the experimental stimuli used have failed to fully disentangle local and global motion and that control stimuli frequently involve much lower levels of local noise. For this reason one cannot definitely conclude that it is a global and not a local deficit that underlies these results.

Conclusions and Future Directions

Individuals with ASD really do see the world differently, or else, attend in a radically different manner to features of the visual environment. Thus, elements that might be hard to extract and may therefore remain hidden from the experience of normal observers might be perceived very easily by observers with ASD. The literature on low-level visual perception in individuals with ASD has convincingly demonstrated normal or superior local visual processing. This allows them to excel on tasks where global information interferes with normal visual performance.

The suggestions of the WCC and EPF theories are that this superiority reflects a cognitive style that entails poor global processing or the ability to ignore context or else that it simply reflects enhanced perception of local features. An evaluation of the theories would require robust testing of global grouping performance of static stimuli. We are unaware of any perceptual study of global grouping performance in autism that has used stimuli that are not compromised by the presence of low SF structure (allowing the subject to perform the task using simple low SF information, that can be signaled by local mechanisms). This gap in the literature needs to be filled before we can differentiate between competing accounts of autistic perceptual processing (e.g., WCC and EPP). To this end, it would be interesting to know how observers with ASD perform with spatial-frequency band-pass contour stimuli of the sort described by Field et al. (1993). We also suggest the use of more "stripped down" versions of pop-out tasks to look at how well individuals with ASD are able to discount disruptive backgrounds. In particular, it is known that the recognition of visual stimuli, such as letters, presented in the peripheral visual field, is compromised by the presence of nearby irrelevant structures, a phenomenon known as "crowding." It is unknown if autistic observers' ability to localize "odd-man-out" stimuli in complex centrally presented displays generalizes to enhanced recognition of such simple configurations of letters. These tests would be revealing because there is a burgeoning literature on crowding and the cortical mechanisms involved in it (for a recent review see Pelli et al., 2004).

The story regarding motion processing is a little clearer. People with ASD exhibit clear problems when dealing with complex moving stimuli, but their contrast-detection thresholds for flickering stimuli are normal (Bertone et al., 2005; Pellicano et al., 2005). Thus, their deficit is unlikely to be linked to a general dorsal/magnocellular deficit. The issue of whether poor perception of motion is due to local or global processing is yet to be convincingly resolved. The fact that observers with ASD produce normal contrast-detection thresholds for first-order motion would seem to push this issue more toward a problem with global motion integration. What is required is either (1) that one accepts that integration of complex motion is always in part limited by local and global constraints and develop suitable static control tasks that fully match local uncertainty in static and dynamic stimuli or (2) use more time-consuming paradigms, such as equivalent noise, that can separate the influence of local and global motion processes (Dakin et al., 2005).

What kind of neural processing abnormality underlies the range of motion-processing deficits associated with ASD? We suggest that a common underlying factor could be atypical operation of an area within the dorsal visual stream known as the superior temporal sulcus (STS). A variety of evidence already suggests abnormal operation of STS in autism. For example, a symptom of ASD is poor monitoring of gaze (e.g., Leekam et al., 1998), and STS is concerned with coding facial properties—e.g., direction of gaze and mouth movements—linked to social interaction (Hoffman and Haxby, 2000). Recently, direct evidence from fMRI indicated that reduced activity in the STS was linked to poor gaze processing in individuals with ASD (Pelphrey et al., 2005). There is also evidence from fMRI that children and adolescents with ASD exhibit structural abnormalities in STS (Boddaert et al., 2004b; Waiter et al., 2004). Furthermore, we consider that there is now (direct or indirect) evidence implicating STS in nearly every motion task that is problematic for people with ASD. Thus, experiments using fMRI (Grossman et al., 2005; Michels et al., 2005; Puce et al., 1995; Sekuler, 1994; Servos et al., 2002; Vaina et al., 2001) and, more recently, TMS (Grossman et al., 2005) have shown that STS is central to the integration of biological motion. Puce and Perrett (2003) suggested that if this is the case, then dysfunction in STS could contribute to disorders of social communication.

In line with this notion, Noguchi et al. (2005) have recently presented evidence that STS plays a role in the processing of second- but not first-order motion. They report no significant activation in the anterior region of STS in response to first-order motion, even when visibility was equated to the second-order stimuli. Thus, dysfunction in STS could potentially contribute to poor perception of second-order motion in autism (Bertone et al., 2003), but what about poorer performance with the dot patterns used to measure motion coherence thresholds?

fMRI data indicate that STS responds weakly to dot stimuli moving at around 4 deg/s (Grossman et al., 2000). However, while moving dot patterns contain both first- and second-order motion components, psychophysical evidence on the motion after-effect indicates that the perceived direction of motion in fast-moving dot patterns is determined largely by the second-order motion component (Nishida and Sato, 1992, 1995). We make the following suggestion: the conditions under which motion coherence paradigms have been conducted in the past (i.e., fast two-dimensional motion) may have inadvertently favored subjects relying on second-order motion cues to perform the task. If that were the case then poor processing by STS of these cues could contribute to poor performance on these tasks.

It remains to be seen if such findings might also bear on sensory abnormalities within other modalities associated with ASD. A tantalizing finding in this respect is abnormal auditory processing in speech related areas of STS (Boddaert et al., 2004a) in individuals with autism. Likewise, Gervais et al. (2004) have shown that individuals with autism failed to activate STS voice-selective regions in response to vocal sounds, but showed normal activation to nonvocal sounds. While a detailed review of nonvisual sensory processing falls outside the remit of this paper, it is notable that enhanced processing of musical stimuli has been shown (Heaton, 2003; Mottron et al., 2000), as well as lack of interference from the context of melodic structure (Foxton et al., 2003). Such notions may explain the raised incidence of perfect pitch, stable memory for exact pitches (Heaton et al., 1998), and higher pitch sensitivity (Bonnel et al., 2003) in ASD.

Another class of sensory-processing abnormalities associated with autism that we have not reviewed is the phenomenon of hypersensitivity, i.e., intolerance to certain tactile stimuli, tastes, smells, and sounds (Rogers et al., 2003). Overreaction to sensory stimuli and apparent lack of habituation with repeated exposure has been vividly described in biographical accounts (Gerland, 1997; Grandin, 1986), and it is possible that the notions of enhanced perceptual function, and an ability to ignore context, that we have discussed within the domain of visual processing could also provide an explanation of these phenomena.

Such sensory phenomena are still much in need of investigation, and it remains unclear whether they result from abnormal basic stimulus processing, "stimulus overload," or inappropriate allocation of top-down attentional processes, which are failing both to inhibit repeated and expected stimuli, but also fail to enhance novel and unexpected stimuli. As we hinted already, the role of high-level attentional processing may turn out to be crucial in the explanation of the perceptual phenomena that we discussed. Many aspects of autism seem well characterized as manifestations of reduced top-down modulation (Frith, 1993) and locally oriented processing as postulated by the WCC theory. Thus, local processing could be a default when high-level control is weakened or absent (Happé and Frith, 2006). Possibly, the combined study of problems in high-level mechanisms of attentional modulation and low-level mechanisms of basic perception has the potential to provide a unifying account for both social and nonsocial features of autism.

In conclusion, we believe that this review has shown that investigations of visual perception in ASD can be highly rewarding and that future investigations are likely to allow us to penetrate deeply into some of the most puzzling phenomena of this disorder. The combined study of problems in high-level mechanisms of attentional modulation and low-level mechanisms of basic perception has the potential to provide a unifying account for both social and nonsocial features of autism.

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