A TWO-FACTOR STRUCTURE TO THE SYSTEMIZING QUOTIENT-REVISED DIFFERENTIALLY PREDICTS SUSCEPTIBILITY TO LOCAL AND GLOBAL VISUAL CUES

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DISSERTATION ABSTRACT

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Although Autism Spectrum Disorders (ASD) are often characterized by deficits in social domains, increasing evidence suggests that individuals with ASD have perceptual biases associated with a shift from reliance on global to local visual cues. This dissertation provides evidence for a two-factor structure to the systemizing trait of autism, as measured by the Systemizing Quotient-Revised (SQ-R), which differentially predicts this perceptual shift in the general population. Specifically, an Analytical Tendencies factor within the SQ-R was found to predict attenuated susceptibility to the global contextual cues that drive the rod-and-frame illusion (RFI), while an Insistence on Sameness factor was associated with heightened sensitivity to the local cues that drive the RFI. Furthermore, in a clinical sample of individuals with ASD, both Analytical Tendencies and Insistence on Sameness factors were found to be hyper-expressed, suggesting that perceptual biases in ASD populations can be explained, in part, by heightened systemizing tendencies. In addition, the Analytical Tendencies factor was also found to predict enhanced performance on the Embedded Figures Task, a visual search task commonly used to assess perceptual abilities in ASD. Furthermore, enhanced performance on this task was associated with reduced susceptibility to the global contextual effects of the RFI, suggesting that superior search performance in

individuals with ASD may be due, in part, to attenuated interference from the contextual gestalt of the search array. Importantly, the relationship between heightened systemizing tendencies and attenuated use of global contextual cues was found to reflect a disinclination among high systemizers to use such cues and not a general impairment in processing such cues. Specifically, when contextual cues that benefit performance are available, high systemizers can use these cues to the same extent as low systemizers. Together, these findings implicate a two-factor structure to the SQ-R that is differentially predictive of distinct types of visual processing associated with ASD.

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TABLE OF CONTENTS

Chapter Page

Chapter Page

Chapter Page

Chapter Page

LIST OF FIGURES

Figure Page

LIST OF TABLES

CHAPTER I

INTRODUCTION

Over seventy years ago, a psychiatrist by the name of Leo Kanner working at John Hopkins Hospital examined a small group of young children whom he described as being cut off from the world and lacking the predisposition for social engagement; he described them as 'autistic' (Kanner, 1943). He also noted that these young children, preferring a non-social environment, appeared to be very resistant to change; some children, for example, engaged in repetitive self-stimulation which was interpreted to be the child's attempt at maintaining, or insisting upon, this sameness in the environment. This withdrawal from the social world was in stark contrast to that of typically-developing children, and had a devastating impact on parents and families. Subsequently, as diagnostic models of psychopathology were developed over the proceeding decades, the condition of 'infantile autism' was formally included in the DSM-III in 1980 (Volkmar & McPartland, 2014). In addition to being informed by Kanner's early descriptions of social and repetitive symptoms of children with autism, the diagnostic criteria also included impairments in communicative domains. While additional revisions to the DSM criteria for a diagnosis of autism have taken place over the years (e.g., in the latest edition of the DSM-5, the social and communicative criteria were collapsed into one symptomatic domain), its qualitative impact on children and families has remained constant. Therefore, given the heterogeneity in the severity and types of symptoms that are manifest in autism, it is of the upmost importance to strive to gain a more complete understanding of this often mysterious disorder.

For instance, while autism spectrum disorders (ASD) are often diagnosed based on deficits in social and communicative domains, there is increasing evidence that individuals with ASD exhibit attentional, perceptual, and cognitive biases that are distinct from neurotypical (NT) populations. Examination of atypical functioning in these domains may provide important clues as to how underlying neural mechanisms are affected in ASD, and whether abnormal low-level processes may lead to a broader range of higher-level (i.e., social) impairments. Concurrently, in characterizing atypical functioning in ASD, it is important to evaluate if attentional, perceptual, and cognitive biases may arise from a common underlying neuropathology, or whether these manifest as orthogonal, comorbid symptoms.

This dissertation will specifically focus on understanding how the systemizing trait of autism can account for atypical perceptual processes that are often observed in individuals with ASD. In Chapter II, evidence for distinct types of systemizing that differentially predict a disproportionate reliance on local and global contextual cues will first be presented in experiment 1. In experiment 2, these distinct forms of systemizing will be compared in NT and ASD samples in order to understand whether these systemizing factors may or may not be hyper-expressed in ASD. In Chapter III, the extent to which these systemizing factors can account for performance on a commonly used visuospatial task in autism research – the Embedded Figures Test – will be investigated. Chapter IV will then investigate whether the relationship between systemizing and attenuated use of global contextual cues reflects a bias or a deficit in processing contextual information.

Theoretical Background

While an extensive number of theories have been proposed to account for either a wide range or specific subset of ASD symptoms, only those theories that have attempted to explain or provide predictions as to the attentional, cognitive, and/or perceptual processes that are affected in ASD will be reviewed here. These theoretical models will first be introduced so that as specific findings on these processes are presented in proceeding chapters, the theoretical predictions of each model can be evaluated accordingly.

The Weak Central Coherence Theory

In its original conception, the Weak Central Coherence (WCC) theory of autism proposed that a core deficit in ASD was the failure to use and integrate global contextual form, information, and meaning, resulting in a variety of impairments across perceptual, cognitive, and social domains (Frith, 1989). More recently the theory has emphasized that this failure to use global information may be the result of a detail-focused processing style which places priority on local visual details and information at the cost of global contextual processing, and that this processing bias may be orthogonal to, rather than explain, the social deficits exhibited in ASD (Happe & Frith, 2006). In addition, the WCC theory has been revised to propose that the failure to use global information may be the result of a bias, rather than a deficit *per se*, in ignoring global context (Happe & Frith, 2006). Since specific findings on attentional (e.g., visual search, contextual cueing) and perceptual (e.g., local and global processing, configural face processing) processes in ASD will be reviewed below, the evidence that supports, and constrains, the WCC theory will be discussed in detail where relevant.

The Enhanced Perceptual Functioning Theory

While many symptoms in ASD are associated with *deficits* in different domains of processing, ASD individuals sometimes exhibit preserved and even *enhanced* abilities on certain tasks, such as those that assess low-level perceptual processing. For example, some evidence, reviewed in more detail below, has found that individuals with ASD have superior performance on visual search tasks (O'Riordan, Plaisted, Driver, & Baron-Cohen, 2001), the Embedded Figures Test (Jolliffe & Baron-Cohen, 1997), and on the Wechsler Block Design (Shah & Frith, 1993). The Enhanced Perceptual Functioning (EPF) theory of autism has proposed that superior ASD performance on these tasks is the result of enhanced low-level visual processing (Mottron, Dawson, Soulieres, Hubert, & Burack, 2006). In general, the EPF theory is consistent with findings of increased activation in visuo-perceptual regions during (non-social) perception tasks (e.g., Mottron et al., 2006), and with the notion that hyper-connectivity and -reactivity of neurons in primary sensory cortices may characterize ASD neurophysiology (Markram, Rinaldi, & Markram, 2007). Superior low-level processing in ASD is also thought to manifest as a locally-oriented perceptual bias (i.e., the default setting in autistic perception, Mottron et al., 2006), as evidenced by local biases on drawing tasks (Mottron, Burack, Stauder, & Robaey, 1999) and on performance when processing hierarchical stimuli (e.g., Navon letters), such as faster (O'Riordan et al., 2001) and more accurate (Plaisted, Swettenham, & Rees, 1999) local target detection and greater local-to-global interference (Wang, Mottron, Peng, Bethiaume, & Dawson, 2007). Here, it is important to denote that while the EPF theory similarly proposes that a core characteristic of autistic perception is a locally-orientated bias, the EPF theory differs from the WCC theory in postulating that this local bias is due solely to enhanced low-level processing, as opposed to a bias that that may result from, or occurs alongside, subsequent deficits in processing global context, as proposed by the WCC theory (Mottron et al., 2006). In other words, the EPF theory proposes that higher-order processing (e.g., contextual integration) is optional (or autonomous) in ASD (as opposed to being the default perceptual setting, as it is proposed to be in NT populations), and is likely disregarded when performance on a task can be accomplished using a locally-oriented low-level processing mode (Mottron et al., 2006). Indeed, the prioritized involvement of primary perceptual areas even during higher-order tasks has been proposed to explain both the superior performance on certain visuospatial tasks and the perceptual and/or cognitive expertise (e.g. savant abilities) that individuals with ASD sometimes display (Mottron et al., 2006).

The Intense World Theory

The Intense World (IW) theory of autism proposes that some combination of genetic, pre-natal environmental, and epigenetic factors result in hyper-plastic, hyper-connective, and hyper-functional microcircuits, and that the neurophysiology of these microcircuits is phenotypically expressed as hyper-attention, -perception, -memory, and -emotionality (Markram & Markram, 2010) that predict, and possibly account for, a wide range of symptoms in ASD. One potential pre-natal environmental factor that has been associated with the neurophysiology described above is exposure to valproic acid (VPA), which was once used to treat epilepsy and bipolar disorders and has since been associated with an increased prevalence of autism and autistic tendencies. The evidence for VPA modulating the etiological risk for ASD is based on studies examining the offspring of VPA-exposed rats and the resulting neurobiology and behavioral symptoms that are displayed. Specifically, rat offspring exposed to VPA exhibit a loss of cerebellar neurons and abnormalities in the serotonergic system that result in locomotor hyperactivity and increased repetitive behaviors, two key diagnostic symptoms of ASD in humans. VPA rats also show enhanced connectivity (i.e., VPA rats had a 50% increase in connections between excitatory and inhibitory cells at small intersomatic distances) and hyper-reactivity in sensory cortices. Behaviorally, these rats show impairment in habituation to sensory stimuli and enhanced discrimination abilities, which again parallels human studies of ASD in that individuals with autism often have increased sensitivity to sensory stimulation and lower thresholds for some types of visual discrimination (e.g., orientation; Markram & Markram, 2010). VPA rats also exhibit hyper-activity in the prefrontal cortex and amygdala, which has also been observed in ASD in fMRI studies, though some studies have found ASD hypo-activation in these regions (Markram & Markram, 2010). Behaviorally, VPA offspring exhibit decreased social interaction and enhanced anxiety, which again parallels key symptoms in humans with ASD.

In addition, the IW theory of autism proposes that hyper-reactive and hyper-connective local microcircuits in primary sensory cortices result in enhanced low-level processing, which like the EPF theory, can account for superior performance in low-level perceptual tasks. The IW theory, however, also predicts that long-range connections across cortical areas are underdeveloped and hypo-active due to difficulty in integrating and synchronizing the hyper-active neural signals from local microcircuits. A recent study did find that toddlers with ASD had significantly weaker interhemispheric synchronization (while sleeping) compared to typical and language-impaired controls (Dinstein et al., 2011), which would seem to support this prediction. According to this theory, hypo-active asynchronized long-connections would result in impairments in processing complex, higher-order information (e.g., social and contextual information) due to difficulties in the integration of signals from multiple neural regions that are required to accomplish these processes. Not only would this pattern of disrupted cortical synchronization predict deficits in social domains, as commonly observed in ASD, but when combined with low-level hyper-functional microcircuits would also lead to an intense sensory experience of the world. Specifically, if hyper-active microcircuits in sensory regions result in hyper-sensitivity to stimuli, then, when coupled with deficits in higher-order processes needed to integrate and organize sensory input into expected contextual regularities, this would lead to an intense, disorganized, and piece-meal experience of the world. In addition, if microcircuits in emotion-based regions of the brain (e.g., amygdala) are also hyper-active, intense emotional reactivity (e.g., fear) to everyday stimuli may result in withdrawal (e.g., from social situations) in order to cope with such an intense experience of the world (Markram & Markram, 2010).

The Extreme Male Brain Theory

The Extreme Male Brain (EMB) theory of autism (Baron-Cohen, 2002) proposes that ASD symptomology is the result of an extreme manifestation of the neurotypical male brain. For example, one etiological factor that has been proposed to underlie this extreme manifestation of the male brain is an over-abundance of male sex hormones during prenatal development. Elevated levels of testosterone, for instance, may explain the extreme manifestation of male-biased phenotypes (e.g., cognitive traits) in ASD. For example, the trait of systemizing, or the tendency to perceive, construct, and analyze the structure and operations in complex, rule-based systems, is a trait that is differentially expressed as a function of gender (being more prominent in males), and has subsequently been found to be hyper-expressed in ASD (Baron-Cohen, 2008). Specifically, the magnitude of systemizing tendencies in NT populations vary as a function of gender, with NT males exhibiting stronger systemizing drives than NT females (Baron-Cohen, Richler, Bisarya, Gurunathan, & Wheelwright, 2003). While there is a large amount of overlap in the distributions of systemizing levels across gender, this suggests that this trait, in part, may be driven by the influence of male sex hormones. For example, fetal testosterone levels are strongly predictive of systemizing tendencies (Auyeung, Baron-Cohen, Chapman, Knickmeyer, Taylor, & Hackett, 2006) and autistic traits in general (i.e., as measured by the Autism Quotient; Knickmeyer, Baron-Cohen, Raggatt, & Taylor, 2005; Auyeung, Taylor, Hackett, & Baron-Cohen, 2010), and more recently, sex hormones have been found to differentially modulate the expression of a candidate gene (RORA) in autism (Sarachana, Xu, Wu, & Hu, 2011). However, there are some instances in which the presumed presence of elevated levels of male sex hormones fail to account for behavioral symptoms in ASD. For instance, individuals with ASD often excel at certain visuospatial tasks, such as the Block Design, and in a recent study by Auyeung and colleagues (2009), no association was found between fetal testosterone levels and performance on the Block Design. In addition, the presence of elevated male sex hormones would also predict the hyper-expression of *physical* male traits, which typically are not observed in ASD populations (Barbeau et al., 2009).

Additional evidence for the role of systemizing in the EMB theory of autism comes from analyzing how scores on the Systemizing Quotient (SQ), a 60-item self-report questionnaire developed by Baron-Cohen and colleagues (2003) to measure systemizing tendencies, differ between ASD and NT populations. For example, within NT populations, males on average score higher on the SQ than females, and ASD populations score even higher than NT males (Baron-Cohen et al., 2003; Wakabayashi et al., 2007). While this finding supports the contention of systemizing being a male-typical trait that is hyper-expressed in ASD, another possible explanation for these gender differences is that the SQ consists of more male-typical items on which males would naturally be expected to score higher. To counter this and improve the psychometric properties of this systemizing measure, Wheelwright and colleagues (2006) developed the Systemizing Quotient-Revised (SQ-R), a 75-item self-report questionnaire that retains many of the items from the original SQ but also includes more gender-neutral items that further assess systemizing tendencies. In a large sample of ASD and NT participants, Wheelwright and colleagues (2006) found that NT males still scored higher on average than NT females, and that individuals with ASD scored even higher on the SQ-R than NT males (Wheelwright et al., 2006), supporting the notion that ASD can be characterized by an extreme manifestation of systemizing tendencies. The EMB theory also proposes that different types of hyper-systemizing tendencies can account for a wide-range of ASD symptoms (Baron-Cohen, 2006). For example, the numerical (*e.g., preoccupation with numbers, calendars, and timetables*), spatial (*e.g., fascination with routes*), mechanical (*e.g., drive to understand how mechanical systems operate*), environmental (*e.g., insisting on environmental order and consistent positioning of objects*) and collectible (*e.g., organizing collections, making lists and catalogues*) forms of systemizing strongly correspond with commonly observed ASD symptoms and behaviors, as described parenthetically (Baron-Cohen, Ashwin, Ashwin, Tavassoli, & Charkrabarti, 2009).

Another trait that underlies the tenets of the EMB theory of autism is empathizing – the ability to understand what others are thinking and feeling (Baron-Cohen & Wheelwright, 2004). Empathizing abilities have been found to be stronger in NT females than NT males, and in support of the EMB theory, empathizing drives are even more diminished in ASD populations. Individuals with ASD, for example, typically perform poorly at recognizing complex mental states when only the eyes are presented, such as in the Reading the Mind in the Eyes test (Baron-Cohen, Wheelwright, & Jolliffe, 1997; Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001). They also reliably score lower (than NT males, and especially NT females) on the Empathizing Quotient (EQ), a self-report measure developed by Baron-Cohen and Wheelwright (2004) that assesses empathizing and theory of mind tendencies (Wakabayashi et al., 2007).

In summary, the EMB theory of autism proposes that the cognitive biases exhibited in ASD are the combinatory result of hyper-systemizing and hypo-empathizing tendencies (Baron-Cohen, 2009), relative to NT males, and that this extreme manifestation of male cognitive phenotypes can account for a wide range of social and cognitive symptoms in ASD. However, there is evidence that some aspects of ASD (e.g., autistic traits) may not be related to an extreme manifestation of male neurobiology (Barbeau et al., 2009). Indeed, in Chapter II, we provide evidence for a cognitive phenotype that is more predominant in females, yet nevertheless hyper-expressed in an ASD sample. However, regardless of the extent to which autistic traits can be differentiated or influenced by gender and sex hormones, the traits of empathizing and systemizing still provide useful constructs for characterizing the social and cognitive drives and behaviors in individuals with ASD. Indeed, this trait approach for examining

ASD is most consistent with the conceptualization of autism as reflecting a spectrum, or continuum, of behavioral symptomology, which circumvents some of the difficulties in relying on a discrete categorical assessment as to what constitutes a clinical diagnosis.

Perceptual and Cognitive Processes Affected by ASD

While there are many aspects of perceptual and cognitive processes that may be affected in ASD, a large amount of research has converged on the notion that feature- and context-based perceptual processing is atypical. The evidence for these processes being affected in ASD has frequently come from studies assessing hierarchical processing (i.e., local and global processing), illusion susceptibility, and performance on visual search tasks. Since the perceptual and cognitive processes that underlie performance on these tasks will be examined in Chapters II-IV, the evidence that establishes atypical performance (i.e., deficits, and in some cases enhanced performance) in these visuospatial tasks will first be reviewed.

Local and Global Processing

A fundamental function of the visual system is to process the hierarchical structure in which the world is organized. For example, our visual system can selectively attend to either the leaves that make up a tree, the trees that make up a forest, or the forest and its overall shape and structure. The perceptual processes involved in the selection and identification of a stimulus at the local (e.g., the leaves) or global (e.g., forest) level is a common area of investigation that has demonstrated atypical functioning in ASD. Indeed, perceptual biases in local and/or global processing underlie both the WCC and EPF theories of autism. The initial WCC theory (Frith, 1989) proposed that individuals with

ASD have a deficit in global visual processing, and that such a deficit would lead to difficulties in higher-level cognitive and social processes. Evidence for impaired global processing in ASD, however, has been mixed. Brosnan and colleagues (2004) found that individuals with ASD were less sensitive, and less likely to use, gestalt grouping principles such as proximity (where nearby stimuli are perceived as a group) and similarity (where stimuli with similar featural attributes are perceived as a group). Likewise, individuals with ASD perform better (i.e., faster) in impossible figure-copying tasks, presumably because they are less affected by the impossible gestalt configuration of the stimulus (Mottron et al., 1999). They are also impaired in discriminating global configuration of radial frequency patterns (i.e., they have higher discrimination thresholds) relative to NT controls (Grinter, Maybery, Pellicano, Badcock, & Badcock, 2010). Even NT individuals who exhibit high levels of autistic tendencies (i.e., who score high on the Autism Quotient, Baron-Cohen et al., 2001) have increased thresholds in global motion and global form tasks (Grinter, Maybery, Van Beek, Pellicano, Badcock, & Badcock, 2009) and have attenuated and delayed cortical, magnocellular responses to low contrast stimuli (Sutherland & Crewther, 2010).

While such findings suggest that individuals with ASD have impairments in processing global information (as predicted by the WCC theory), other studies have failed to find a global deficit in ASD. For example, in a perceptual grouping task in which subjects had to develop and select a perceptual representation of features (i.e., local) or configurations (i.e., global) in hierarchical patterns, no differences were found between an ASD sample and NT controls (Plaisted, Dobler, Bell, & Davis, 2006). In addition, in tasks using visual hierarchical stimuli (e.g., where local shapes form a global shape), individuals with ASD perform similarly to controls in showing faster response times when identifying the global shape relative to the local shape (Mottron, Burack, Iarocci, Belleville, & Enns, 2003; Mottron et al., 1999). Likewise, in other tasks that have been used to assess global processing (e.g., fragmented letters, silhouette identification, and grouping tasks), individuals with ASD perform similarly to NT controls (Mottron et al., 2003). Evidence for intact global processing in ASD has also been found in non-visual tasks. For example, individuals with ASD have similar levels of performance in change detection of global melody manipulations compared to NT controls (Mottron, Peretz, & Menard, 2000).

In light of inconsistent evidence for global processing deficits in ASD, the revised WCC theory (Happe & Frith, 2006) proposed that the perceptual bias in ASD can instead be conceptualized as a locally-oriented processing bias. The notion of a locally-oriented bias in ASD is also consistent with the EPF theory (Mottron et al., 2006), but, unlike the WCC theory, the EPF theory proposes this bias is due solely to superior low-level perceptual functioning. Evidence for a local processing bias in ASD has been more consistent across the literature. For instance, individuals with ASD tend to draw more local features in graphic consistency tasks (Mottron et al., 1999), show enhanced change detection (relative to controls) for local manipulations in melodies (Mottron et al., 2000), and exhibit better discrimination abilities for novel (but not pre-exposed) stimuli (Plaisted, O'Riordan, & Baron-Cohen, 1998). In addition, performance in discrimination of radial frequency patterns defined by local manipulations was found to be intact in ASD relative to controls (Grinter et al., 2010). Increased activations in primary visual areas during performance on the Embedded Figures Test (EFT) has also been taken as evidence of enhanced low-level perceptual functioning indicative of a local processing bias (Lee, Foss-Feig, Henderson, Kenworthy, Gilotty, Gaillard, & Vaidya, 2007; Manjaly, Bruning, Neufang, Stephan, Brieber, Marshall, Kamp-Becker, Remschmidt, Herpertz-Dahlmann, Konrad, & Fink, 2007). In addition, a local processing bias during perception of hierarchical letters, discussed more thoroughly below, is also frequently reported in ASD (Wang et al., 2007). Autistic perception may therefore be better characterized as having a locally-oriented bias as opposed to a global deficit, where failure to use global contextual information may not be reflective of a deficit per se, but rather a preference to attend to local information in a scene (Happe & Frith, 2006).

A greater understanding of perceptual biases in ASD can come from tasks that assess hierarchical visual processes by measuring response times to local and global targets that are competitively embedded in a single stimulus (as opposed to being measured in isolation). The most commonly used paradigm to examine different levels of perceptual processing is through the use of Navon letters, where small letters (i.e., the local shapes) form a configuration of a larger letter (i.e., the global shape). Navon (1977) found that when participants are presented with these compound letters, they are faster to identify the global form (i.e., the large letter) than the local form (i.e., the small letter), a phenomenon known as global precedence. Global precedence is also observed in monkey neurophysiology, in which inferotemporal neurons have been found to respond to the global structure of a hierarchical shape 30ms before they respond to the local structure (Sripati & Olson, 2009). In addition, in conditions in which the local and global levels of a hierarchical stimulus are incongruent (i.e., the letter at the local level differs from the letter at the global letter), NT individuals often experience global interference (i.e., response times are slower when identifying a local target, relative to a global target, in incongruent conditions due to interference from the global shape). Therefore, hierarchical visual processing in NT individuals can be characterized by a global bias, as evident in faster reaction time (RT) to global stimuli and slower RT to local stimuli when global shapes are incongruent.

Although the original WCC theory would predict that global precedence and interference in ASD should be attenuated, evidence for impaired global processing in Navon tasks has been mixed. For example, Mottron et al. (1999) found that although RTs in an ASD group were slower for both congruent and incongruent Navon configurations relative to NT controls, individuals with ASD still exhibited global precedence, suggesting that global processing is intact in ASD. Likewise, Mottron et al. (2003) found that ASD performance in a Navon task and three other tasks used to assess global processing (fragmented letters, silhouette identification, and perceptual grouping) was no different than performance for NT controls. However, Rinehart and colleagues (2000) found that although individuals with ASD exhibited both global precedence and interference in congruent and incongruent conditions, respectively, they made more global errors in both conditions. These results may therefore reflect a speed-accuracy tradeoff in which faster response times to global stimuli in the ASD group may have been achieved at the cost of a decreased level of accuracy. Wang et al. (2007) found similar evidence of a speed-accuracy tradeoff, but with the tradeoff going in the opposite direction – that is, while ASD sample made the same amount of global errors as NT controls, they were slower to respond to global targets than local targets (unlike controls). This suggests that when ASD accuracy for global targets is comparable to NT controls, individuals with ASD are slower to respond to global targets (relative to local targets) and therefore, fail to exhibit global precedence. Finally, the presence of global precedence in ASD has also been found to be modulated by the attentional demands of the task. For example, when individuals with ASD must respond to a target at a pre-specified level (i.e., selective attention is displaced to the pre-specified level), global precedence is observed. However, when they must identify a target that could appear at *either* the local or global level (i.e., when attention must be divided across both levels of the stimulus), then local precedence is observed (Plaisted et al., 1999). Therefore, the degree and consistency of global precedence in ASD may be contingent on whether tasks across studies employ selective or divided attention in assessing hierarchical processing.

Another possibility for lack of consistent findings in ASD hierarchical processing of Navon figures is that different stimulus parameters are often used across studies. For example, global precedence in Navon tasks can be modulated by several factors including the visual angle of the global shape, the exposure time, and the probability that a predefined target (letter) will appear at a specific level (Wang et al., 2007). This latter finding suggests that not only are passive perceptual processes involved in processing the local and global levels of hierarchical visual stimuli, but also controlled attentional processes. For example, evidence from lesion studies has shown that hierarchical processing can be affected in different ways as a function of whether the lesion is known to affect perceptual or attentional processes (Robertson et al., 1988; Robertson & Lamb, 1991). Specifically, these studies have shown that temporal-parietal areas differentially contribute to perceptual and attentional processing of local and global information, and that local/global asymmetries can operate independently from one another (Robertson et al., 1988; Robertson & Lamb, 1991).

In an attempt to account for the modulatory effects of visual angle, exposure time, and attentional processes, Wang and colleagues (2007) examined ASD performance in hierarchical processing by manipulating these stimulus parameters and task demands. Attention to the local or global level was manipulated by a free- vs. forced-choice task in which observers could choose a target at either the local or global level (free-choice) or had to respond to a target at a pre-specified level (forced-choice). In the free-choice condition, the ASD group chose local and global targets randomly (i.e., there was no decreased preference for global targets), but they were faster to respond to the local targets regardless of visual angle or exposure time. In contrast, NT controls exhibited a global advantage in RTs that was modulated by both visual angle (i.e., global RTs were faster at smaller visual angles) and exposure time (i.e., global advantage was only present for shorter exposure times). In the forced-choice condition in which attention was manipulated to respond to a target at a pre-specified level, the ASD group exhibited a local advantage (i.e., they were faster to respond to local targets than global targets) and greater local interference (relative to global interference), whereas NT controls exhibited global advantage and bi-directional interference. The finding of a local bias and local-to-global interference during hierarchical visual processing in ASD is also consistent with other findings on Navon task performance in ASD. For example, in the Rinehart et al. (2000) study discussed above, although global interference was found in the ASD group, increased local interference (relative to controls) was also found. In addition, Billington and colleagues (2008) found that in an NT sample, higher scores on the systemizing quotient (SQ) were associated with increased local precedence and interference, which suggests that heightened systemizing tendencies in ASD may also be modulating their local processing bias.

While individuals with ASD typically exhibit a locally-oriented processing bias, a further question concerns the underlying neurophysiology that would produce such a bias. Aside from differences in low-level primary sensory regions that are often observed in ASD, it may also be the case that the hemispheric lateralization that underlies local and global visual processing may be atypical. As discussed above, evidence for local and global hemispheric lateralization can be found in lesion studies, in which lesions in the right hemisphere have been found to impair performance in identifying global form, while lesions in the left hemisphere have been found to impair performance in identifying local form (Robertson & Delis, 1986). In addition, studies suggest that the hemispheric asymmetries in processing local and global targets may also reflect differences in preferred spatial frequencies across hemispheres that are inherent to the target at each level of processing, and that attentional selection of a corresponding frequency may be the modulating factor in studies that have examined hemispheric asymmetries in local and global processing (Flevaris et at., 2010a, 2010b). Therefore, it is possible that locally-oriented perceptual biases in ASD may be due to a disproportionate reliance on high spatial frequencies (subserved by the left hemisphere, which facilitates local processing) relative to low spatial frequencies (subserved by the right hemisphere, which facilitates global processing), and that the global-to-local shift in perceptual processing may actually reflect biases in processing the spatial frequencies of targets, rather than their hierarchical level, per se.

Another factor that affects the magnitude of local/global hemispheric asymmetries are the attentional demands of the task being performed. For example, local-left hemisphere and global-right hemisphere benefits are often not observed in selective attention tasks (in which participants must report the presence of a target at a pre-specified level) using congruent stimuli, but are present when incongruent stimuli are used. Specifically, in early processing, congruent hierarchical levels activate the same response and therefore, the level at which a target occurs does not need to be processed. When hierarchical levels are incongruent, however, different responses are activated and, at a later stage of processing, need to be binded to their corresponding level in order to accurately identify the target (Hubner, Volberg, & Studer, 2007). Therefore, lack of global precedence (i.e., faster RTs for local levels) in ASD may indicate a local bias that is evident at early stages of processing, while lack of global interference may indicate a local bias at later stages of processing (e.g., across lateralized higher-level cortical regions that are differentially sensitive to local and global attributes). While abnormalities in processing low-level magnocellular input seem most consistent with explaining the local bias (or lack of a global bias) in early stages of processing, the degree to which abnormalities in hemispheric specialization may lead to a local processing bias during later stages of hierarchical processing may be modulated by the attentional demands of the task. For example, hemispheric asymmetries are more reliably observed in divided-attention tasks in which participants do not know the level at which a target will appear (as opposed to selective attention tasks in which participants report if a target appears at a pre-specified level) and must therefore divide attention across both hierarchical levels (Yovel, Yovel, & Levy, 2001). If atypical hemispheric specialization underlies the local processing bias in ASD (during later stages of perceptual processing), this may explain why local precedence was observed in a Navon task under divided, but not selective, attention (Plaisted et al., 1999).

Finally, direct evidence for hemispheric specialization in processing local and global information also comes from neuroimaging studies. For example, in selective-attention tasks, locally-directed attention has been found to activate areas in the left inferior occipital cortex, while globally-directed attention activates areas in the right lingual gyrus (Fink, Halligan, Marshall, Frith, Frackowiak, & Dolan, 1996; Fink, Halligan, Marshall, Frith, Frackowiak, & Dolan, 1997). However, when attention is divided across hierarchical levels, temporal-parietal activations are observed (Fink et al., 1996; Fink et al., 1997), which suggests that these regions may mediate attentional control over local/global processing. Therefore, while local processing biases in ASD during early stages of processing may be *perceptual* in nature, local biases during later stages of processing may reflect *attentional* biases. This interpretation, however, is only partially supported by ASD neuroimaging evidence. For example, during EFT performance, increased activations in left lateralized regions were only found in higher-level areas (e.g., left superior parietal), whereas increased activation in occipital areas were right lateralized (Lee et al., 2007). However, given the role of higher-level parietal regions in hierarchical processing under conditions of divided attention (Fink et al., 1996; Fink et al., 1997), it is plausible that increased left parietal activation in ASD may underlie their local processing bias at later stages of perceptual processing due to attentional selection of preferred local attributes, while local processing biases at earlier stages of processing may be due to superior low-level functioning (as predicted by the

EPF) in regions that are not lateralized for local and global attributes (which is consistent with the lack of hemispheric specialization in congruent Navon tasks).

In summary, evidence in ASD for deficits in processing global context has been inconsistent across studies, while perceptual biases favoring low-level, local elements of a visual stimulus has been more consistently found. Locally-oriented biases in ASD may reflect functional abnormalities during early (e.g., superior low-level processing, and over-reliance on high spatial frequencies) and/or later (i.e., asymmetrical imbalances in lateralized hemispheric activations) stages of perceptual and attentional processing. While stimulus parameters, task demands, and attentional manipulations strongly affect the magnitude of this bias, the current evidence supports the predictions of the EPF theory in postulating that while global processing is optional in ASD, local processing is a mandatory, default setting in autistic perception. Neuroimaging evidence supports the contention that this local bias can be explained by enhanced low-level functioning in ASD (as evidenced by increased activations, relative to NT controls, in primary sensory regions), while behavioral evidence from divided attention tasks suggests that this local bias may also be driven by higher-level attentional processes that modulate lateralized hemispheric specialization in local and global processing.

Illusion Susceptibility

While hierarchical stimuli provide a useful technique for examining the *competition* between local and global processes, a useful technique for assessing the *differential* contributions of local and global processes is to measure susceptibility to visual illusions. While the quantification of susceptibility to illusions provides a general measure of sensitivity to visual context, there are many distinct types of illusions that can be driven by entirely separate perceptual (e.g., local or global) processes. For example, Coren et al. (1976) conducted a factor analysis on susceptibility to a wide range of visual illusions and found that they clustered into five distinct classes: 1) illusions of shape/direction, 2) size contrast illusions, 3) overestimation illusions, 4) underestimation illusions, and 5) frame of reference illusions. Interestingly, susceptibility to this latter class of frame of reference illusions has also been used to provide evidence for the dissociation of perception and action in the ventral and dorsal visual streams, respectively. For example, the induced Roelofs effect – where an offset frame produces perceptual, but not sensorimotor, target mislocalization errors in the direction opposite of the offset frame - is one such illusion that has been taken as evidence for a dissociation between perception and action in the ventral and dorsal streams, respectively. Specifically, Bridgeman et al. (1997) argued that while the ventral pathway enables the perceptual localization of a target and is susceptible to the effect of the offset frame, the dorsal pathway enables the sensorimotor localization of a target and is 'immune' to the distorting effects of the offset frame.

An alternative model that does not require a dissociation in the functional independence of ventral and dorsal cortical streams proposes that the induced Roelofs effect is a frame of reference illusion in which distortion of a *single* reference frame can explain both the perceptual and sensorimotor effects of the illusion (Dassonville & Bala, 2004; Dassonville, Bridgeman, Bala, Thiem, & Sampanes, 2004). Specifically, the offset frame in the induced Roelofs effect has been found to bias an observer's perceived midline in the same direction of the offset frame, which results in perceptual mislocalization of the target (in the opposite direction of the offset frame). When an observer points to the target, the action is guided within the same distorted reference frame that was used to encode the target, which correspondingly results in a veridical pointing movement due to the cancellation of errors. Therefore, the differences in perceptual and sensorimotor localization accuracy in the induced Roelofs effect can be explained by the distortion of a single reference frame that is used to make both perceptual and sensorimotor judgments of a target's remembered location.

The postulation of a single reference frame that drives the induced Roelofs effect is also consistent with a recent neuroimaging study that found that BOLD activations in parietal (i.e., dorsal), but not temporal (i.e., ventral), regions were observed when participants had to judge the location of a target within an offset frame (Walter & Dassonville, 2008). Specifically, bilateral regions in the posterior parietal cortex and precuneus showed significantly greater activation when location judgments were made within the presence of an offset frame compared to when color judgments were made (using identical stimuli), or when location judgments were made without the frame present (Walter & Dassonville, 2008). These results further suggest that the induced Roelofs effect is driven by distortions in a single, egocentric-based reference frame in dorsal regions of the parietal cortex, and are more consistent with a *what* vs. *where* distinction of the functions of the ventral and dorsal streams, respectively, as opposed to a *perception* vs. *action* distinction. Furthermore, although the parietal areas activated in the Walter and Dassonville (2008) study were adjacent to parietal regions found to be involved in attentional processes, attentional demands (i.e., task difficulty) were equated across conditions and therefore, the observed activations are presumed to reflect activity related to contextually modulated location judgments.

While the induced Roelofs effect is one illusion thought to be driven by distortions in an observer's egocentric reference frame as a result of misleading visual context, other illusions have been hypothesized to be driven by similar mechanisms. For example, the Zollner, Poggendorf, and Ponzo illusions are similarly thought to be driven by distortions in an observer's egocentric reference frame, as evidenced by the finding that the magnitude of these illusions increases when reference frames are further distorted through tilting an observer (Prinzmetal & Beck, 2001). The Rod-and-Frame illusion (RFI) – in which the orientation of a rod is mislocalized in the direction opposite of a surrounding tilted frame – is another such illusion thought to be driven by global distortions in an observer's reference frame. Specifically, when the RFI is presented in an open-loop setting (with no visual feedback available), the tilt of the surrounding frame distorts the observer's visuovestibular frame of reference such that their perception of vertical is tilted in the same direction as the tilt of the frame (Ebenholtz & Benzschawel, 1977). This global distortion in the observer's frame of reference causes the rod within the frame to appear tilted in the direction opposite that of the surrounding frame. This component of the illusion – a global visuovestibular distortion in the observer's frame of reference due to the context of the surrounding frame – has also been shown to be modulated by the size of the surrounding frame in that larger frames tend to produce greater distortions in perceived vertical compared to smaller frame sizes (Ebenholtz & Benzschawel, 1977; Spinelli, Antonucci, Daini, & Zoccolotti, 1995).

However, in the case of the RFI, there is an additional mechanism that drives the illusion (independent from the global reference frame distortion) that does affect sensorimotor responses. Specifically, the RFI is also thought to be driven by low-level orientation contrast effects due to mutual inhibition in populations of visual neurons responsible for encoding the orientations of the rod and frame (Chen, 2005). This second mechanism of the RFI results in a qualitatively similar perceptual effect (i.e., an illusory repulsion, relative to the frame tilt, of the orientation of the rod) and, importantly, since sensorimotor responses are prone to these low-level illusory effects, this allows the use of an additional measure of illusion susceptibility (i.e., used in Chapter II). In addition, these orientation contrast effects have also been found to be modulated by the size of the frame in that smaller frame sizes tend to produce greater orientation contrast effects due to the increased proximity of the rod to the frame (Zoccolotti, Antonucci, & Spinelli, 1993). While the RFI is therefore thought to be driven by both local (low-level orientation contrast effects) and global (a visuovestibular distortion in perceived vertical) effects, the local effects primarily drive the RFI with smaller frame sizes, while global distortions primarily drive the RFI with larger frame sizes.

Examination of illusion susceptibility in ASD can provide additional insight into how local and global perceptual processes may be affected. According to the WCC theory (Frith, 1989; Happe & Frith, 2006), individuals with ASD should succumb less to visual illusions driven by contextually-induced distortions (e.g., Roelofs, RFI, Ponzo, Ebbinghaus, surround suppression) due to either a deficit in global processing (Frith, 1989) or an over-reliance on local visual cues that results in a bias to ignore global context (Happe & Frith, 2006). While Happe (1996) initially found support for this prediction in that individuals with ASD were found to succumb less to visual illusions compared NT controls, other studies have failed to replicate this initial finding. Specifically, Ropar and Mitchell (1999; 2001) examined ASD susceptibility to the Ponzo, Muller-Lyer, and Ebbinghaus (Titchner) illusions using both stimulus adjustment and verbal response methods of measurement. They found that individuals with ASD succumbed to the illusory percept (in all illusions) to the same degree as NT controls, which contradicts both Happe's (1996) findings and the WCC theory in general. Furthermore, in the Ropar and Mitchell (2001) study, they included a battery of visuospatial tasks including the Block design, EFT, and the Rey complex figure-copying task, and although individuals with ASD performed significantly better on these visuospatial tasks than NT controls, performance on these visuospatial tasks, while correlated with one another, were not correlated with illusion susceptibility (with the exception of the Muller-Lyer illusion, in which better performance on the visuospatial tasks was associated with decreased susceptibility). However, Bolte and colleagues (2007) examined ASD performance on these same visuospatial tasks (Block design and EFT) and illusions (Ponzo, Muller-Lyer, Titchner, and also the Poggendorff illusion) and found that the ASD group succumbed significantly less to the visual illusions than controls, and that performance on both the Block design and EFT was negatively correlated with illusion susceptibility (i.e., better performance was associated with decreased susceptibility).

One possible source for these inconsistent findings across studies is the variability in ASD severity (i.e., use of different subgroups across the autism spectrum), particularly when small sample sizes are used. For example, in assessing global processing in ASD using a Navon task, Rinehart et al. (2000) found that while a high-functioning ASD group made significantly more global errors than NT controls, there were no differences in global errors made between a subgroup of individuals with Asperger's syndrome and NT controls. This implies that variability in specific traits (i.e., symptoms) across the autism spectrum may modulate the magnitude of observed differences across group comparison studies. Indeed, a consistent finding across a broad range of illusion types is that there are a great deal of individual differences in illusion susceptibility even in NT populations, and the traits that drive these individual differences may be important variables to account for when assessing illusion susceptibility in ASD.

The disparate results on illusion susceptibility in ASD have recently been reconciled by the finding that the autistic trait of systemizing (as measured by the SQ) negatively covaries with susceptibility to visual illusions driven by contextually-induced distortions of an observer's egocentric reference frame, but not with illusions driven by allocentric distortions (Walter et al., 2009). Specifically, these authors examined how autistic tendencies (i.e., as measured by the Autism, Empathizing, and Systemizing Quotients) in the general population are related to illusion susceptibility. Susceptibility to a large subset of visual illusions (RFI, Roelofs, Poggendorff, Ebbinghaus, Muller-Lyer, Zollner, Ponzo, and induced motion) was first subjected to a factor analysis that resulted in two distinct susceptibility factors, which suggests that the illusions that loaded on each factor may be driven by related mechanisms. They found that higher systemizing scores were associated with decreased susceptibility to one factor of illusions (consisting of the RFI, Roelofs, Ponzo, Zollner, and Poggendorff illusions) but were unrelated to susceptibility on the second factor (consisting of the Ebbinghaus, Muller-Lyer, and induced-motion illusions). Given that the Roelofs (Dassonville & Bala, 2004; Dassonville et al., 2004), RFI (Ebenholtz & Benzschawel, 1977; Spinelli et al., 1995), and the Zollner, Poggendorf, and Ponzo illusions (Prinzmetal & Beck, 2001) are all thought to be driven by contextually-induced distortions in *egocentric* reference frames, whereas the Ebbinghaus, Muller-Lyer, and induced-motion illusions may be driven by more contextually-induced distortions in *allocentric* reference frames, this provides some reconciliation as to why there may be inconsistent findings on illusion susceptibility in ASD. Specifically, hyper-systemizing tendencies in individuals with ASD (Baron-Cohen et al., 2003; Wakabayashi et al., 2007) may lead to reduced susceptibility to only visual illusions that are driven by contextually-induced distortions of an observer's egocentric reference frame and therefore, if systemizing tendencies are not matched in NT controls, the magnitude of group differences in susceptibility may be dependent on the levels of systemizing in the NT groups that ASD groups are compared to (e.g., if NT controls have high levels of systemizing, then no differences in illusion susceptibility in ASD may be found, whereas low levels of systemizing in NT controls may result in significant group differences). It is still unclear, however, whether hyper-systemizing tendencies are associated with enhanced local processing, attenuated global processing, or some combination of the two, as either of these perceptual biases would predict decreased illusion susceptibility.

Furthermore, these findings suggest that susceptibility to illusions related to allocentric distortions may be typical in ASD (or at least not modulated by hyper-systemizing tendencies), in which case, inconsistent findings on illusion susceptibility would be expected in studies that make no attempt to distinguish between illusions based in either egocentric vs. allocentric reference frames. Alternatively, if susceptibility to allocentric context is attenuated in ASD, then this would suggest that other traits (other than those measured by the Autism, Empathizing, and Systemizing Quotients) across the autism spectrum may account for variance in illusion susceptibility. For example, Mitchell and colleagues (2010) found that top-down cognitive processes can influence illusion susceptibility. Specifically, they found that susceptibility to a table-version of the Shepard illusion is greater than susceptibility to a parallelogram-version of the illusion due to the top-down influence of the three-dimensional cue (in the table-version) that leads to the higher-level representation of an object (i.e., a table as opposed to shape). They found that while individuals with ASD were more susceptible to the table-version than the parallelogram-version, they were still less susceptible to both versions than NT controls. This suggests that while individuals with ASD are less affected by contextual cues than controls, top-down processes may still contribute to the extent to which observers are affected by illusory stimuli. In addition, other sources of variance (e.g., individual differences in spatial abilities, Coren & Porac, 1987; variability in V1 surface area, Schwarzkopf et al., 2010) may also modulate the magnitude of observed differences in illusion susceptibility.

In summary, different classes of visual illusions are thought to be driven by different underlying perceptual and neurophysiological mechanisms, and examination of susceptibility to different classes of illusions in ASD can offer important clues as to the perceptual processes affected. While the original WCC theory predicts that individuals with ASD should be less susceptible to all classes of visual illusions that are driven by misleading global context, evidence for decreased illusion susceptibility has been mixed. This disparity has recently been informed by the finding that the autistic trait of systemizing is associated with decreased susceptibility to one class of illusions (those driven by distortions in an observer's egocentric reference frame), but not with another class of illusions (those driven by allocentric distortions).

While hyper-systemizing tendencies in ASD can account for decreased susceptibility to a certain class of illusions, it is still unclear as to whether the relationship between systemizing and illusion susceptibility reflects enhanced local processing, attenuated global processing, or some combination of the two. In Chapter II, this question will be examined by comparing scores on the systemizing quotient-revised (SQ-R) to individual differences in susceptibility to the local (low-level orientation contrast effects) and global (visuovestibular distortions in perceived vertical) mechanisms that drive the RFI. Evidence will subsequently be presented suggesting that distinct forms of systemizing (analytical tendencies and insistence on sameness), when hyper-expressed, can differentially account for a heightened processing of local cues and attenuated processing of global cues, with high levels of both types of systemizing resulting in a global-to-local shift in perceptual processing. Given the inconsistent findings regarding the use of global contextual cues in ASD (i.e., whether attenuated use of global information reflects a bias or a deficit), Chapter IV will examine whether individuals with heightened systemizing tendencies can use contextual cues when such cues are beneficial to performance.

Visual Search

Individuals with ASD often demonstrate superior performance in visual search tasks, in which the observer must indicate the presence or absence of a pre-specified target amongst an array of distractors. The most commonly used search paradigm in ASD is the Embedded Figures Test (EFT), in which observers are asked to find a simple target shape within a much more complex image (the EFT is different from other search paradigms in that it requires closure, or the process of integrating line segments in order to identify the target shape). A consistent finding is that individuals with ASD are significantly faster to locate the figure compared to NT controls, despite similar performance in accuracy (de Jonge, Kemner, & van Engeland, 2006; Mottron et al., 2003; Jolliffe & Baron-Cohen, 1997; Shah & Frith, 1983), or in some cases, improved accuracy (i.e., locating the target with a significantly fewer number of incorrect attempts, de Jonge et al., 2006). Faster performance on the EFT is even associated with higher scores on self-report measures of autistic tendencies (i.e., the Autism Quotient, Baron-Cohen et al., 2001) in NT individuals, irrespective of IQ (Grinter et al., 2009). Superior ASD performance on the EFT has been hypothesized to be due to either a decreased bias in attending to global form (i.e., weak central coherence), an increased bias in attending to local form (i.e., enhanced perceptual functioning), or some combination of the two. For example, an observer who experiences decreased interference from the global gestalt of the search array may be more efficient at locating the target shape. Concurrently, a heightened sensitivity to the local form of the target shape would also be expected to facilitate the efficiency of the search process.

Evaluation of these hypotheses can also be informed by past studies that have examined the neural substrates that underlie EFT performance. For example, Lee et al. (2007) used fMRI to examine differences in activity between NT and ASD children during EFT performance. While NT children activated a wide range of neural networks, including left prefrontal, premotor, bilateral temporal, parietal, and occipital cortices, children with ASD failed to activate prefrontal and temporal areas. In addition, BOLD responses in parietal and occipital areas were enhanced in the ASD group, but these activations were unilateral (left superior parietal and right occipital), while activations in these regions were bilateral in the NT group. Importantly, these differences in activation were found despite behavioral performance (accuracy, response time) being equal across groups (though this likely reflects a ceiling effect, as both groups were administered an easier version of the task). The authors interpreted the lack of prefrontal engagement in ASD during EFT performance to suggest deficits in central coherence, or in other words, that NT children were more biased to attend to the global form of the design compared to children with ASD. Manjaly et al. (2007), however, also examined neural activity in NT and ASD groups during EFT performance and came to a different conclusion. In their study, while left lateralized parietal and premotor regions were more active in the NT group (relative to a perceptually similar control task), the ASD group showed greater activation in right primary visual cortex and bilateral extrastriate areas. While behavioral performance (i.e. RT) on the EFT was again similar across groups, the authors interpreted the increased activations in early visual areas as indicative of enhanced (or biased) processing of low-level features, as predicted by the EPF theory of autism.

There is evidence, however, that the magnitude of this local bias may be modulated by explicit or implicit demands in visual search tasks. For example, Iarocci et al. (2006) found that in a visual search task in which the targets (i.e., dot pairs) were based on either local or global configurations, an ASD group exhibited similar sensitivity compared to NT controls for both target levels. This is contrary to the predictions of both the EPF and WCC theories, in which enhanced sensitivity to local targets and decreased sensitivity to global targets, respectively, would be predicted. However, in a second experiment in which target probabilities were manipulated to alter implicit attentional biases (i.e., the global target was present 70% of the time in a global bias condition, while the local target was present 70% of the time in a local bias condition), the ASD group showed an enhanced local task bias compared to NT controls, but a diminished global bias. This suggests that on an explicit level, individuals with ASD may be sensitive to both the local and global attributes of search targets, but when the level of a target is pre-specified, as in the case of the EFT in which the target is always local (in that it is always embedded in the gestalt array), an implicit local bias is manifest that may attenuate sensitivity to global targets and configurations. In tasks in which global sensitivity may hinder or interfere with performance (e.g., as in the EFT), such an implicit local bias, possibly due to superior low-level processes, may then facilitate performance.

Another explanation for preserved and sometimes even superior search abilities in ASD is that perhaps individuals with ASD may be more efficient at storing the relevant target features in working memory so that they are able to disregard distractors with greater efficiency. However, this does not seem to be the case, as there is evidence (from NT populations) that visual search does not recruit working memory processes (Horowitz & Wolfe, 1998; Woodman et al., 2001). Alternatively, there is also evidence that different types of visual search may recruit different processes. For example, in search tasks in which a target is defined by multiple features (i.e., a conjunction), parallel processing of target-distractor features may facilitate the serial deployment of attention to the target (Wolfe et al., 1989). If the efficiency of parallel processes in visual search relies on the accumulation of low-level featural information (that facilitates the serial deployment of attention), then it might be predicted that individuals with ASD should also excel on conjunction search tasks due to greater reliance on low-level perceptual features. O'Riordan et al. (2001) examined NT and ASD accuracy and response times in both featural (in which a target was defined by *either* a color or a form) and conjunctive (in which a target was defined by *both* a color and a form) search tasks across increasing distractor set sizes. They found that while RT (across all set sizes) was similar in both groups for the featural search task, individuals with ASD were significantly faster for conjunction searches, particularly at larger set sizes. Importantly, faster RTs in the ASD group were not due to decreased accuracy, as accuracy in both search tasks was similar across groups. Likewise, ASD and NT children were matched on non-verbal abilities, so faster ASD performance cannot be attributed to higher-level functioning. In addition, the authors suggest that this finding challenges the WCC theory in that perceptual integration does not appear to be compromised in ASD.

Although top-down processes may modulate performance in visual search, the salience of bottom-up signals from the target (which if enhanced, may facilitate the discrimination of a target from a distractor) is presumed to underlie superior ASD performance. For example, O'Riordan et al. (2001) proposed that faster ASD performance on conjunctive search tasks may reflect a greater efficiency in *exogenous* shifts of attention (due to guidance by low-level target feature salience), while *endogenous* shifts of attention (e.g., top-down processes that are operative in NT groups), may be negated or even impaired in ASD. However, enhanced ASD efficiency in shifting exogenous attention could also be due to enhanced low-level target salience that facilitates such rapid shifts, as opposed to the proposition that the shifting of exogenous attention itself is more efficient (which in other tasks may be compromised in ASD).

In summary, performance in visual search tasks in which an observer must locate a target embedded in an array of distractors can be influenced by many factors, including stimulus characteristics and task demands, types of attentional and search processes engaged, and local/global processing biases. Remarkably, studies have found that individuals with ASD often excel in these types of tasks. Since a disproportionate reliance on local and global visual cues is evident in ASD, superior visual search abilities may be accounted for by such a perceptual bias. In Chapter III, this will be investigated by comparing performance on the Embedded Figures Test to distinct forms of systemizing that we have demonstrated (based on findings presented in Chapter II) to be associated with either heightened processing of local cues or attenuated processing of global cues.

Dissertation Overview

The proceeding chapters in this dissertation will examine the extent to which the autistic trait of systemizing, as measured in the general population, is associated with local and global processing (measured through illusion susceptibility) and visual search performance. Chapter II will first provide evidence for a two-factor structure to the Systemizing Quotient-Revised (Wheelwright et al., 2006) that differentially predicts susceptibility to the local and global mechanisms that drive the rod-and-frame illusion, with an Analytical Tendencies factor associated with reduced susceptibility to the global effects of the illusion, and an Insistence on Sameness factor associated with increased susceptibility to the local effects. Both of these systemizing factors will subsequently be shown to be hyper-expressed in a clinical ASD sample. In Chapter III, these systemizing factors, in addition to the susceptibilities to the local and global mechanisms that drive the rod-and-frame illusion, will then be compared to search performance on the Embedded Figures Test, with evidence suggesting that global perceptual (rod-and-frame global effect) and cognitive (Analytical Tendencies) biases can account for individual differences in search performance. In Chapter IV, evidence will be provided suggesting that global processes that covary with systemizing tendencies reflect a *bias*, and not a deficit, in processing global form, with findings having important implications for theories on perceptual processing in autism.

CHAPTER II

A TWO-FACTOR STRUCTURE TO THE SYSTEMIZING QUOTIENT-REVISED PREDICTS ILLUSION SUSCEPTIBILITY

In addition to the social and communicative deficits that provide a basis for an autism spectrum disorder (ASD) diagnosis (American Psychiatric Association, 2004), individuals with ASD often exhibit perceptual biases that are distinct from those found in neurotypical (NT) populations. For example, increased thresholds for processing coherent motion (Bertone, Mottron, Jelenic, & Faubert, 2003), reduced composite effects in face processing (Teunisse & de Gelder, 2003), and reduced perceptual grouping (Brosnan, Scott, Fox, & Pye, 2004) are commonly taken as evidence for weak central coherence, or deficits in processing and integrating global information. In contrast, low-level perceptual processes are often preserved or even enhanced in ASD. For example, individuals with ASD exhibit superior performance on visual search tasks (O'Riordan, Plaisted, Driver, & Baron-Cohen, 2001), the Embedded Figures Test (Jolliffe & Baron-Cohen, 1997), and on the Wechsler Block Design (Shah & Frith, 1993). In addition, individuals with ASD exhibit locally-oriented biases on drawing tasks (Mottron, Belleville, & Menard, 1999) and when processing hierarchical stimuli, as evidenced by faster (O'Riordan et al., 2001) and more accurate (Plaisted, Swettenham, & Rees, 1999) local target detection and greater local-to-global interference on Navon tasks (Wang et al., 2007). Enhanced performance on these tasks has been taken as evidence for superior low-level visual processing (i.e., enhanced local processing).

The Weak-Central Coherence (WCC; Happe & Frith, 2006) and Enhanced Perceptual Functioning (EPF; Mottron et al., 2006) theories have been proposed in order to account for these biases in autistic perception. In its original conception, the WCC theory proposed that individuals with ASD fail to use and integrate global contextual information (Frith, 1989), though more recently the theory has emphasized that this failure to use global information may be the result of a detail-focused processing style which may result in a bias, rather than a deficit *per se*, in ignoring higher-level contextual cues (Happe & Frith, 2006). While the EPF similarly proposes that a core characteristic of autistic perception is a locally-oriented bias, the EPF theory differs from the WCC theory in postulating that this local bias is due specifically to enhanced low-level visual processing that does not arise from, or necessitate, a subsequent deficit in processing global context (Mottron et al., 2006).

One useful technique for assessing biases in local and global processing is to measure susceptibility to visual illusions that are driven by global contextual cues. While both the WCC and EPF theories predict that individuals with ASD should be less susceptible to context-driven visual illusions compared to NT controls (due to either an attenuated global bias or a heightened local bias, respectively), evidence for decreased illusion susceptibility has been mixed. For example, Happe (1996) compared susceptibility to two- and three-dimensional visual illusions in children with and without autism and found that those with autism were less likely to succumb to the illusions. Bolte and colleagues (2007) similarly found reduced susceptibility in individuals with high-functioning autism relative to NT controls. However, two other studies failed to replicate this finding, instead suggesting that those with autism were equally susceptible to illusions as were NT controls (Ropar & Mitchell, 1999, 2001). Here, it is important to consider how heterogeneity in symptom severity, diagnostic criteria, and different experimental methods across studies comparing ASD and NT populations may result in inconsistent findings. For example, age, onset of language delays, and IQ have been shown to strongly interact with the symptoms of ASD resulting in varying degrees of severity and clinical outcomes (Howlin, Goode, Hutton, & Rutter, 2004) that may affect the magnitude of differences observed between clinical and NT samples. Similarly, the use of NT-matched designs can be problematic not only due to different experimental methods, measures, and task parameters across studies (e.g., in Navon tasks, Wang et al., 2007), but also due to confounds in unmatched variables when making group comparisons. Specifically, while it is common for studies to match autistic individuals with NT controls on age, gender, and IQ, variability in additional un-matched traits between NT and ASD samples may confound group differences when such traits may modulate performance on the tasks being measured. For example, if a particular trait was found to modulate sensitivity to global contextual cues, failure to match NT and ASD samples on this trait may result in group differences in some studies and null differences in others, depending on the levels of this trait that are displayed in both NT and ASD samples.

An alternative approach that avoids the confound of variant traits and symptoms in small NT and ASD samples is to measure autistic traits that have been found to form a continuum in the general population, with individuals with ASD occupying the ends of the distributions, and examine the degree to which trait levels can account for the cognitive and perceptual biases thought to be associated with ASD. In first identifying such traits, Baron-Cohen and colleagues found that the traits of empathizing (the ability to understand what others are thinking and feeling) and systemizing (the ability to analyze, integrate, and build complex systems) form a continuum in the general population, with ASD populations disproportionately occupying the extreme ends of these distributions (Wheelwright, Baron-Cohen, Goldenfeld, Delaney, Fine, Smith, Weil, & Wakabayashi, 2006). Specifically, individuals with ASD have been found to exhibit hypo-empathizing (e.g., deficits on 'Reading the Mind in the Eyes' and Theory of Mind tests, Baron-Cohen, 2009) and hyper-systemizing tendencies (e.g., on tests of folk physics, Jolliffe & Baron-Cohen, 1997; Lawson et al., 2004, and picture-sequencing, Baron-Cohen et al., 1986) in comparison to NT populations (Baron-Cohen, Ashwin, Ashwin, Tavassoli, & Chakrabarti, 2009).

Interestingly, the disproportionate expression of empathizing-systemizing tendencies has also been found to characterize differences between males and females in the general population, with NT males, on average, exhibiting an increased drive to systemize and a decreased drive to empathize compared to NT females (see Baron-Cohen, 2009, for a review of the empathizing-systemizing theory of gender differences). In order to quantify how NT and ASD populations differ on these traits, Baron-Cohen and colleagues developed the Autism Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), Empathizing Quotient (EQ; Baron-Cohen & Wheelwright, 2004), and Systemizing Quotient (SQ; Baron-Cohen, Richler, Bisarya, Gurunathan, & Wheelwright, 2003). While the AQ is a measure of general autistic tendencies related to social, communication, and attentional processes, the EQ and SQ measure specific cognitive traits related to theory of mind and systemizing tendencies, respectively. Consistent with the findings above, individuals with ASD tend to score significantly lower on the EQ and higher on the SQ compared to NT males, and especially NT females (Baron-Cohen et al., 2003; Wakabayashi, Baron-Cohen, Uchiyama, Yoshida, Kuroda, & Wheelwright, 2007), though there is substantial overlap in the distributions of these measures across NT and ASD samples. To account for these cognitive differences in ASD, the Extreme Male Brain (EMB) theory of autism (Baron-Cohen, 2002) has proposed that empathizing-systemizing differences in ASD are due to a hyper-manifestation of male-typical traits, with a concurrent hyper-manifestation of male neurophysiology (e.g., fetal testosterone levels, Auyeung et al., 2006). However, the conceptualization of autistic symptoms as reflecting extreme male behaviors has been controversial, and there are many aspects of ASD symptomology that cannot be explained by extreme male neurophysiology (Barbeau, Mendrek, & Mottron, 2009).

Here, use of an individual differences approach in assessing how variability in these traits modulate reliance on local and global visual cues may be beneficial in reconciling some of the inconsistency in the literature as to the extent to which perceptual biases may be manifest in ASD. For example, in considering the inconsistent findings on ASD and illusion susceptibility, Walter, Dassonville, and Boschler (2009) used an individual differences approach to examine how autistic tendencies in the general population (as measured by the AQ, EQ, and SQ) modulate susceptibility to a battery of visual illusions (rod-and-frame, induced Roelofs, induced motion, Zollner, Ponzo, Ebbinghaus, Muller-Lyer, and Poggendorff). They found that higher scores on the SQ were associated with reduced susceptibility to a subset of illusions that loaded on one factor of illusion susceptibility (Zollner, Roelofs, Rod-and-Frame, Ponzo, and

Poggendorff) but not with illusions that loaded on a second factor (Muller-Lyer, induced motion). One possibility for this dissociation is that the illusions in each of these factors may be driven by different mechanisms, which in turn are differentially associated with systemizing. For example, the rod-and-frame (Ebenholtz & Benzschawel, 1977; Goodenough, Oltman, Sigman, Rosso, & Mertz, 1979; Spinelli et al., 1995) and Roelofs (Dassonville, Bridgeman, Bala, Thiem, & Sampanes, 2004) illusions have been found to be driven by contextually-induced distortions in an observer's spatial reference frame, and similar spatial reference frame distortions have been hypothesized to underlie the Zollner, Ponzo, and Poggendorff illusions (Prinzmetal & Beck, 2001). While the mechanisms that drive the Ebbinghaus, Muller-Lyer, and induced motion illusions are less clear, one possibility is that the autistic trait of systemizing is only related to illusions that are driven by global, contextually-induced distortions of an observer's spatial reference frame.

To test this hypothesis in the current study, we measured susceptibility to an illusion known to be driven by both global and local mechanisms. Specifically, the rod-and-frame illusion (RFI), in which a line (rod) appears tilted in the direction opposite the tilt of a surrounding frame (Witkin & Asch, 1948), has been shown to be disproportionately driven by either global or local mechanisms, depending on the size of the inducing frame. In the first of these mechanisms, the tilt of the surrounding frame induces a bias in the observer's sense of vertical, with perceived vertical pulled in the same direction as the frame tilt (Ebenholtz & Benzschawel, 1977; Sigman, Goodenough, & Flanagan, 1979; Cian, Esquivie, Barraud, & Raphel, 1995). This global visuovestibular distortion in the observer's frame of reference causes the rod within the frame to appear tilted in the direction opposite the tilt of the surrounding frame (Ebenholtz & Benzschawel, 1977; Spinelli, Antonucci, Goodenough, Pizzamiglio, & Zoccolotti, 1991; Zoccolotti, Antonucci, Goodenough, Pizzamiglio, Spinelli, 1992). The magnitude of the visuovestibular distortion in perceived vertical has been shown to be modulated by the size of the inducing frame, with larger frames tending to produce greater distortions in perceived vertical compared to smaller frame sizes (Ebenholtz & Benzschawel, 1977).

Another mechanism that is thought to contribute to a subjectively-similar distortion in the perception of the rod's orientation is a low-level orientation contrast effect (Goodenough, Oltman, Sigman, Rosso, & Mertz, 1979; Wenderoth & Johnstone, 1987; Cian et al., 1995; Spinelli, Antonucci, Daini, & Zoccolotti, 1995) brought about by mutual inhibition in populations of neurons in early visual areas responsible for encoding the orientations of the rod and frame (Blakemore, Carpenter, & Georgeson, 1970; Carpenter & Blakemore, 1973; Spinelli et al., 1995; Poom, 2000; Chen, 2005). These orientation contrast effects have also been found to be modulated by the size of the inducing frame, with smaller frames tending to produce greater orientation contrast effects due to the increased proximity of the rod to the frame (Coren & Hoy, 1986; Zoccolotti, Antonucci, & Spinelli, 1993). While the RFI is driven by a weighted summation of both local and global effects at any given frame size, the local orientation contrast effects typically outweigh the global visuovestibular distortions in perceived vertical when the size of the frame has a visual angle of 10° or less (Gogel & Newton, 1975, Zoccolotti et al., 1993), though orientation contrast effects may still be present for larger frames (Goodenough et al., 1979), and visuovestibular distortions in perceived vertical may still occur for smaller frames (Gogel & Newton, 1975, Zoccolotti et al., 1993; Cian et al., 1995). Therefore, while the RFI is driven by both local (low-level orientation contrast effects) and global (visuovestibular distortions in perceived vertical) effects, the local effects primarily drive the RFI with smaller frame sizes, while global visuovestibular distortions primarily drive the RFI with larger frame sizes.

Experiment 1

To test whether the autistic trait of systemizing is related to a heightened processing of local visual cues, attenuated processing of global cues, or some combination of the two, we compared scores on the Autism Quotient (AQ), Empathizing Quotient (EQ), and the Systemizing Quotient-Revised (SQ-R) to measures of susceptibility to small- and large-frame versions of the RFI. In addition to the traditional perceptual version of the RFI, we independently measured susceptibility to the local orientation contrast and global visuovestibular effects of the RFI using recently developed techniques that have been shown to isolate and independently measure these two mechanisms (Dassonville & Williamson, 2010).

Specifically, in the Perception task, we first measured overall susceptibility to the RFI by having participants make a perceptual report as to whether the orientation of a rod was rotated clockwise or counterclockwise in the presence of a tilted frame. Accordingly, susceptibility to the RFI in the Perception task reflects the combined contributions of the local orientation and global visuovestibular effects that drive the illusion (Fig. 1). While, unlike in the traditional version of the RFI, a response circle was also included in the Perception task, the response circle provides no orientation cues that would affect performance, and was included only to maintain consistency in the stimuli across tasks (i.e., the response circle was necessary in the tasks used to independently measure the two mechanisms that drive the RFI).

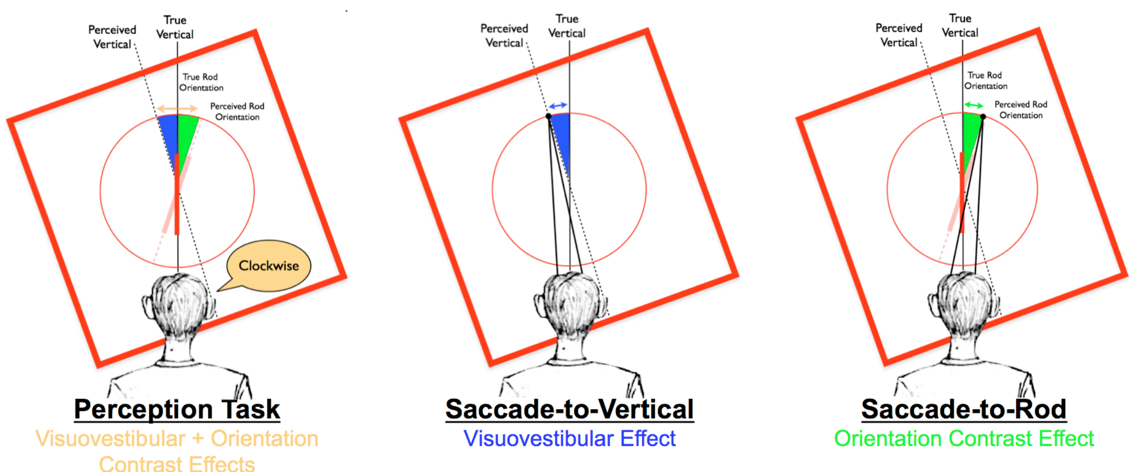

Figure 1. The rod-and-frame Perception, Saccade-to-Vertical, and Saccade-to-Rod tasks. In the Perception task, participants judged whether the central rod was tilted to the left or right, with the overall magnitude of the illusion a combination of global visuovestibular distortions of perceived vertical (blue) and local orientation contrast effects that cause a perceptual repulsion between the rod and the frame (green). In the Saccade-to-Vertical task, participants made a saccade from the fixation point to the point of perceived vertical on the response circle, with the saccade vector prone to a visuovestibular distortion of perceived vertical (blue). In the Saccade-to-Rod task, participants made a saccade from the fixation point to the point on the response circle where they perceived the rod would intersect it if the rod were extended upward. Saccades in this final task are prone only to the perceptual repulsion caused by local orientation contrast effects (green). Solid black lines represent the line-of-sight for the two eyes after the saccadic response in the Saccade-to-Vertical and Saccade-to-Rod tasks.

In order to isolate and measure the global visuovestibular effects of the RFI, each participant performed the Saccade-to-Vertical task. In this task, participants made a saccade from a central fixation point to the point on the response circle perceived to be vertical in the presence of a tilted frame. Since no rod is present in the Saccade-to-Vertical task, and hence no local orientation contrast effects, distortions in perceived vertical induced by the tilt of the surrounding frame (i.e., in the direction of the frame tilt) provide an independent measure of the global visuovestibular distortion that contributes to the RFI (Fig. 1).

In order to independently measure the local orientation contrast effects of the RFI, participants performed the Saccade-to-Rod task (using the same stimuli as in the Perception task) in which they made a saccade from a central fixation point to the point on the response circle where they perceived the rod would intersect if its length were extended upward (Fig. 1). Although the presence of the tilted frame is expected to produce a global visuovestibular distortion, it has been shown that when actions are guided within the same distorted reference frame that is used to perceptually encode a target, the error in motor guidance will cancel with the error in target encoding, resulting in actions that are unaffected by the reference frame distortion (Dassonville & Reed, in preparation). The cancellation of errors in motor guidance and target encoding that occur when both are made within a single distorted reference frame is known as the Two-Wrongs hypothesis, and has been confirmed using another type of illusion that produces a similar distortion in an observer's reference frame (i.e., the induced Roelofs effect, in which an offset frame results in a distortion in perceived straight-ahead; Dassonville & Bala, 2004; Dassonville et al., 2004; Dassonville, 2010). Therefore, in the Saccade-to-Rod task, since the orientation of the rod is encoded in the same distorted reference frame (e.g., distortion in perceived vertical) that is used to guide the saccade, the saccade to the endpoint of the rod is unaffected by the global visuovestibular effects of the frame. Accordingly, since the visuovestibular effects of the frame are cancelled (due to the cancellation of errors in motor guidance and target encoding), only the local orientation contrast effects induced by the rod and frame will remain, with any deviation in the saccade vector from the rod's true orientation therefore reflecting the local orientation contrast effects that contribute the illusion.

Given that the relative contributions of global visuovestibular and orientation contrast effects vary as a function of frame size, with global visuovestibular effects primarily driven by a large-inducing frame, and the local orientation contrast effects strongest with a small-inducing frame, we had participants perform both large- and small-frame versions of the RFI perception, Saccade-to-Vertical, and Saccade-to-Rod tasks. In the study conducted by Walter and colleagues (2009), a relatively large-inducing frame was used to measure RFI susceptibility. Therefore, based on the previous association found between systemizing scores and RFI susceptibility, we hypothesize that systemizing scores will negatively covary with the global visuovestibular effects of the RFI (i.e., as measured by the large-frame Saccade-to-Vertical task), but will be uncorrelated with the local orientation contrast effects (i.e., as measured by the small-frame Saccade-to-Rod task).

Methods

Participants. One hundred and one participants (52 male) were recruited from the University of Oregon Human Subjects Pool and participated in the experiment in exchange for course credit. All participants had normal or corrected-to-normal vision and had no known neurological deficits. The mean age of the sample was 20.5 years (*SD* = 2.7). All participants provided informed consent in accordance with the ethical guidelines and protocol of the University of Oregon Institutional Review Board.

Stimuli and Display. Each participant was seated with the head stabilized in chin and forehead rests, and the eyes 86.4 cm from a screen (Polacoat Ultra projection screen with a DA-100 diffusion coating, Da-Lite, IN, USA) measuring 101.6 cm by 135.9 cm. Stimuli were back-projected (Marquee 8500 projector, with custom-fit HD145 lenses, Electrohome, Niagara Falls, ON, CAN) onto the screen in a darkened room. The RFI stimuli were red in color and consisted of a circular fixation point (0.5° of visual angle) surrounded by a circle measuring 13.7° in diameter with a width of 0.1°. The fixation point was intersected by a rod measuring 6.9° of visual angle in length and 0.2° in width. Surrounding the rod was either a small (8.6° for each side) or large frame (35.9° for each side) that had a stroke width of 1.0° of visual angle and a rotational tilt of either -15° or 15° from vertical (Fig. 2).

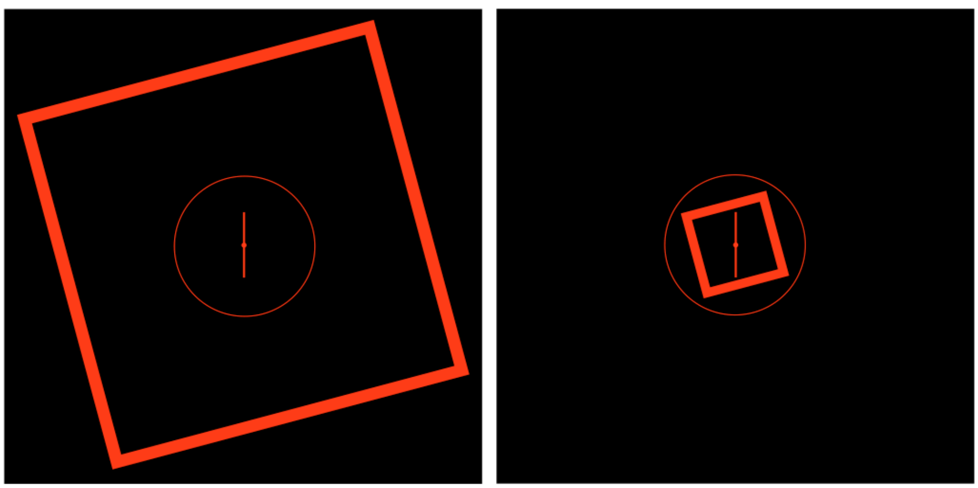

Figure 2. The large- and small-frame versions of the rod-and-frame stimuli used in Experiment 1.

Apparatus. An eye tracker (Eyelink 2000, SR Research, Kanata, ON, CAN) was used to monitor eye movements during all RFI tasks. Before beginning each task, participants were calibrated on the eye tracker using a grid of 13 visual targets. If the average error in fixation was greater than 1° across the 13 targets, the calibration was rejected. The experiment could not proceed until a successful calibration was achieved. If the calibration began to drift mid-task, the experimenter stopped the task, recalibrated, and when calibration was again successfully achieved, the participant continued where he or she had left off.

Measures of Local and Global Processing. All participants completed three RFI tasks: an RFI Perception task, a Saccade-to-Rod task, and a Saccade-to-Vertical task. For each task, following successful calibration of the eye tracker, participants first completed a practice session that only included the fixation point, the response circle, and the rod (with the exception of the Saccade-to-Vertical task in which no rod was presented). No frame was presented on the practice trials so that participants could gain experience in each of the tasks without being exposed to the illusion. During the experimental trials when the frame was present, both frame sizes (8.6° or 35.9°) and tilts (-15° or 15°) were used in all RFI tasks described below. The order of the RFI tasks were counterbalanced across participants.

Perception Task. The Perception task measures the additive sum of the local orientation contrast and global visuovestibular effects that drive the rod-and-frame illusion. On each trial, participants were instructed to make a judgment about the perceived orientation of the rod. At the onset of each trial, the fixation point, reference circle (13.7° in diameter), and the tilted frame (-15° or 15°) would appear on screen. Though the inclusion of the response circle was irrelevant to performance in the Perception task, it was included to maintain consistency in the stimulus parameters used in the other tasks, and does not provide any orientation cues that would affect performance. Participants were instructed to direct their gaze to the fixation point before starting a trial and to maintain this gaze location throughout the task (a trial was aborted if fixation deviated >1° from the fixation point). While fixating on the central fixation point, a button press on a gamepad controller (using the left thumb) initiated the onset of the trial. After 200ms, a rod that was tilted either –6°, –4°, –2°, –1°, 0°, 1°, 2°, 4°, or 6° from vertical would appear on screen (centered on the fixation point) for 300ms (Fig. 3). After 500ms from trial onset, the rod and fixation point were extinguished and participants indicated whether they perceived the rod to be tilted to the counterclockwise or clockwise by pressing the left or right trigger button, respectively, on the gamepad controller. There were 10 trials for each combination of frame tilt (-15° or 15°), frame size (8.6° or 35.9°), and rod orientation (9 tilts), with 360 trials total (10 blocks, 36 trials per block).

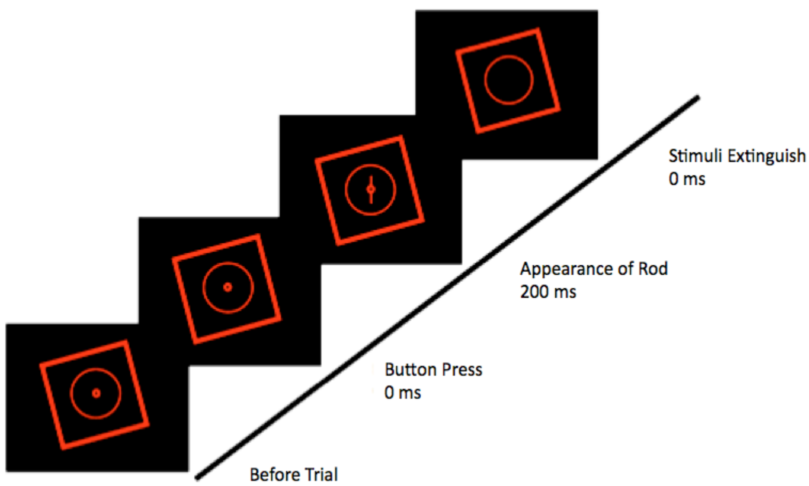

Figure 3. Time course of the rod-and-frame perception task.

The RFI perception task measures the additive sum of the local orientation contrast and global visuovestibular effects that drive the illusion. Perceptual reports for each frame tilt were quantified by fitting a psychometric function to the proportion of "clockwise" responses in order to derive the point of subjective equality (PSE, the orientation of the rod at which the participant reported it as being rotated clockwise and counterclockwise with equal likelihood) using the equation:

$$\text{proportion "clockwise" responses} = e^{((\text{rodtilt}-\text{PSE})/\text{tau})}/(1+e^{((\text{rodtilt}-\text{PSE})/\text{tau})})$$

where *rodtilt* was the orientation of the rod, *PSE* was the point of subjective equality, and *tau* was the space constant of the psychometric function. Rod-and-frame susceptibility was operationalized as the difference in the PSEs for the clockwise and counterclockwise frame tilts, calculated separately for small and large frames, where higher values indicate greater susceptibility to the illusion and lower values indicate reduced susceptibility to the illusion.

Saccade-to-Vertical Task. The Saccade-to-Vertical task independently measures the global visuovestibular effect that drives the rod-and-frame illusion. The Saccade-to-Vertical consisted of the same stimulus parameters as in the Perception task, but in this task, no rod was presented (and therefore, no local orientation contrast effects could occur). In this task, participants were instructed to make a saccade (cued by the offset of the fixation point after 500ms from trial onset) from central fixation to the top of the response circle (i.e., the location on the response circle directly above the fixation point; Fig. 1). When the saccade was made to the point on the circle that participants perceived to be vertical, a button press (on the gamepad controller) recorded the saccade vector and terminated the trial. Trials were aborted if participants looked away from the fixation point before it was extinguished or if they blinked at any point during the trial (aborted trials were rerun later in the experiment). Since the saccade to perceived vertical is made in the presence of the tilted frame, with no rod present, the global visuovestibular effects of the frame can be measured independent of any local orientation contrast effects that drive the illusion when the rod is otherwise present. There were 10 trials for each combination of frame size (8.6° or 35.9°) and frame tilt (-15° or 15°), with 40 trials total (10 blocks, 4 trials per block).

On each trial, the angle of rotation of a vector plotted from the fixation point to the final eye position on the response circle (the location of the top of the circle, as perceived by the participant) was calculated. Performance in the Saccade-to-Vertical task was operationalized by calculating the difference in the mean rotational errors (the mean difference between the saccade vector plotted from the fixation point to the final eye position and true vertical) between clockwise- and counterclockwise-tilted frames, with positive values indicating a distortion of perceived vertical in the same direction as the frame tilt, and greater values indicating larger errors in perceived vertical, or greater susceptibility to the global visuovestibular effects of the frame. Susceptibility was calculated separately for both small- and large-frame versions of the task. Here, large frames were expected to produce greater visuovestibular distortions in perceived vertical, consistent with the findings of previous studies (Ebenholtz & Benzschawel, 1977).

<u>Saccade-to-Rod Task.</u> The Saccade-to-Rod task independently measures the local orientation contrast effect that drives the rod-and-frame illusion. The Saccade-to-Rod task consisted of the same stimulus parameters as in the Perception task, with the exception of a more narrow array of rod orientations (-5°, -3°, -1°, 0°, 1°, 3°, 5°). In this task, after the rod and fixation point disappeared from the screen (500 ms from trial onset), participants were instructed to make a saccade from the fixation point to the point

on the response circle which would be intersected by the rod if the rod were extended upward (Fig. 1). After this saccade was completed, a button press (on the gamepad controller) cued the recording of the saccade endpoint and terminated the trial. As in the Saccade-to-Vertical task, trials were aborted if participants looked away from the fixation point before initiating the trial or before the offset of the fixation point and were rerun later in the experiment. Participants completed 10 trials for each combination of frame size (8.6° or 35.9°), frame tilt (-15° or 15°), and rod orientation (7 tilts), with 140 trials total (5 blocks, 28 trials per block).

On each trial, the angle of rotation of the vector plotted from the fixation point to the final eye position on the response circle (i.e., where the participant perceived the rod to intersect the circle) was calculated. Performance in the Saccade-to-Rod task was operationalized by calculating the difference between the mean rotational errors (the mean difference between the saccade vector of the final eye position and the rod's true vector) for left- and right-tilted frames, where higher values indicate larger orientation contrast effects (i.e., greater susceptibility to the local effects of the rod-and-frame illusion). Susceptibility was calculated for both small- and large-frame versions of the task, with small frames expected to cause greater local orientation contrast effects due to the greater proximity between the rod and the edges of the frame (Zoccolotti et al., 1993).

Measures of Autistic Tendencies. The Autism Quotient (AQ), Empathizing Quotient (EQ), and Systemizing Quotient-Revised (SQ-R) are self-report questionnaires developed by Baron-Cohen and colleagues for quantifying autistic traits in the general population. Each questionnaire consists of a set of statements in which responses are measured on a 4-point Likert response scale (definitely agree, slightly agree, slightly disagree, definitely disagree). The AQ (Baron-Cohen et al., 2001) consists of 50 questions that measure general autistic tendencies (e.g., "I prefer to do things the same way over and over again, "I am fascinated by dates") and includes 5 subscales (attention switching, attention to detail, social skills, communication, and imagination). The EQ (Baron-Cohen & Wheelwright, 2004) consists of 60 questions that measure empathizing abilities, such as the ability to infer cognitive and emotional states in others (e.g., "I can tune into how someone else feels rapidly and intuitively") and the proclivity to engage in social situations (e.g., "I enjoy being the center of attention at any social gathering"). The SQ-R (Wheelwright et al., 2006) consists of 75 questions that assess systemizing tendencies, such as the ability to analyze, integrate, and systematically perceive the details, variables, and operations in a system (e.g., "In math, I am intrigued by the rules and patterns governing numbers", "When I learn about a new category, I like to go into detail to understand the small differences between different members of that category"). The questionnaires are worded such that in half of the items, agreement with an item constitutes a high score, while in the other half, disagreement with an item constitutes a high score. Total scores on each questionnaire were calculated using the same protocol as described by Baron-Cohen and colleagues. All questionnaires were completed on a Macintosh computer (Apple Computers, Cupertino, CA).

Statistical Analyses. For the RFI measures that showed significant associations with autistic traits, reliability analyses were conducted in order to correct for any attenuations in the correlations (i.e., due to decreased reliability). Specifically, given that illusion susceptibility for each frame size (on each RFI task) was calculated as a difference score (i.e., the difference between left-frame and right-frame susceptibility), reliability analyses were conducted on the measures of local (small-frame Saccade-to-Rod) and global (large-frame Saccade-to-Vertical) RFI effects. Reliability of the difference score on each task was calculated using the standard formula:

$$rDD = \{[(LF_{Rel} + RF_{Rel})/2] - Frame_{Corr}\} / (1 - Frame_{Corr})$$

where LF_{Rel} is the reliability (i.e., internal consistency) of left-frame RFI susceptibility, RF_{Rel} is the reliability of right-frame RFI susceptibility, $Frame_{Corr}$ is the correlation between left- and right-frame susceptibility, and rDD is the reliability of difference scores. Reliability estimates (of the difference scores) were then used to correct for attenuation in correlations using the following formula:

$$rxy_{corr} = rxy / (rxx * ryy)^{1/2}$$

where *rxx* is the reliability of the trait measure, *ryy* is the reliability of RFI susceptibility, *rxy* is the uncorrected correlation between the trait measure and RFI susceptibility, and rXY is the corrected correlation.

Results

Illusion Susceptibility. Initial tests across all participants in the Perception task verified that the small and large frames were capable of inducing a perceptual distortion of the rod in the direction opposite the tilt of the frame (small frame: PSE difference = 4.8°, SD = 2.2°, $t(99) = 21.91$, $p < .001$; large frame: PSE difference = 3.4°, SD = 1.7°, $t(99) = 20.09$, $p < .001$), with susceptibility to the small frame significantly greater than susceptibility to the large frame ($t(99) = 7.05$, $p < .001$). Likewise, significant orientation contrast effects on the Saccade-to-Rod task were found for both frame sizes in that saccades directed to the rod erred in the direction opposite the tilt of the frame (small frame: $M = 2.0°$, $SD = 1.6°$, $t(98) = 12.36$, $p < .001$; large frame: $M = .5°$, $SD = 1.3°$, $t(98) = 3.78$, $p < .001$), with small-frame susceptibility significantly greater than large-frame susceptibility ($t(98) = 9.29$, $p < .001$). Similarly, in the Saccade-to-Vertical task, significant visuovestibular distortions in perceived vertical were found for both frame sizes, with saccades biased in the same direction of the frame tilt (small frame: $M = 1.9°$, $SD = 2.3°$, $t(100) = 8.21$, $p < .001$; large frame: $M = 2.2°$, $SD = 2.2°$, $t(100) = 9.75$, $p < .001$), though no significant difference was found between small- and large-frame susceptibility ($t(100) = -1.16$). The lack of significant frame size effect in the Saccade-to-Vertical task likely reflects the relative proportions of local orientation contrast and global visuovestibular effects that drive the RFI at different frame sizes. Specifically, while the global visuovestibular effects were found to primarily drive the large-frame RFI (i.e., global = 2.2°, local = .5°), the local and global effects are of relatively equal magnitude in the small-frame RFI (i.e., global = 1.9°, local = 2.0°).

In addition, susceptibility to the small-inducing frame in the Perception task was significantly associated with susceptibility to the small frame in both the Saccade-to-Rod ($r(96) = .34$, $p = .001$) and Saccade-to-Vertical ($r(98) = .25$, $p < .02$) tasks, with greater local orientation contrast and global visuovestibular effects predicting greater RFI susceptibility. While greater susceptibility to the large-inducing frame in the Perception task was similarly associated with greater visuovestibular effects in the large-frame Saccade-to-Vertical task ($r(98) = .33$, $p = .001$), large-frame RFI susceptibility was not significantly related to performance on the large-frame Saccade-to-Rod task ($r(96) = .16$). This null association is likely due to the relatively weak local orientation contrast effects that are present with large frame sizes (i.e., greater gaps between the rod and the edges of the frame). Consequently, since the magnitude of local orientation contrast and global visuovestibular effects vary as a function of frame size, we used small-frame Saccade-to-Rod performance and large-frame Saccade-to-Vertical performance as measures of the local orientation contrast and global visuovestibular effects, respectively, of the RFI. Internal consistency analyses indicated that both of these measures were reliable, but attenuated due to both being calculated as a difference score (i.e., susceptibilities on all tasks were calculated based on the difference between left- and right-frame susceptibilities). Specifically, the reliabilities of both the small-frame Saccade-to-Rod (left-frame *alpha* = .968; right-frame *alpha* = .964; reliability of difference scores = .55) and large-frame Saccade-to-Vertical (left-frame *alpha* = .932; right-frame alpha = .932; reliability of difference scores = .55) tasks were attenuated as a difference score. Therefore, in all analyses examining individual differences between RFI susceptibility and autistic tendencies, correlations were corrected for attenuation.

Autistic Tendencies. The mean score on the AQ ($M = 15.7$, $SD = 4.6$) approximated the previously reported mean in NT samples ($M = 16.3$, $SD = 5.9$) by Wheelwright and colleagues (2006). In addition, an internal consistency analysis indicated that the AQ had satisfactory reliability (Cronbach's *alpha* = .75). The mean on the EQ ($M = 47.1$, $SD = 11.1$) also approximated the previously reported mean ($M = 44.3$, $SD = 12.2$; Wheelwright et al., 2006) and demonstrated good reliability (Cronbach's *alpha* = .82). Likewise, the mean score on the SQ-R ($M = 55.5$, $SD = 19.2$) approximated that reported by Wheelwright and colleagues (2006; $M = 55.6$, $SD = 19.7$) and had high internal consistency (Cronbach's *alpha* = .90).

Autistic Tendencies and Illusion Susceptibility. Bivariate correlations were conducted examining whether scores on the AQ, EQ, and SQ-R were associated with small- and large-frame susceptibilities in the three RFI tasks (Perception, Saccade-to-Vertical, and Saccade-to-Rod). Scores on the AQ and EQ were unrelated to performance on any of the RFI tasks (Table 1). In addition, SQ-R scores were unrelated to small- and large-frame susceptibility on the Perception task (small frame: $r(98) = -.12$; large frame: $r(98) = -.13$). While Walter and colleagues (2009) found a significant association between RFI susceptibility and SQ scores, we used the revised measure of systemizing (the SQ-R) that contains additional items that may be differentially related to the mechanisms that drive RFI susceptibility. Indeed, SQ-R scores were found to significantly correlate with *both* the global visuovestibular (large-frame Saccade-to-Vertical performance) and local orientation contrast effects (small-frame Saccade-to-Rod performance) of the illusion (Table 1), but in opposite directions. Specifically, higher systemizing scores were associated with decreased global visuovestibular effects (large-frame Saccade-to-Vertical; $r(99) = -.40$, $p < .01$; Fig. 4) and increased local orientation contrast effects (small-frame Saccade-to-Rod; $r(97) = .31$, $p < .03$; Fig. 5) of the RFI.

Given that SQ-R scores were correlated with both the local (small-frame Saccade-to-Rod) and global (large-frame Saccade-to-Vertical) RFI effects, this could indicate that these RFI effects negatively covary with each other (i.e., enhanced local effects are associated with attenuated global effects). A bivariate correlation was therefore conducted to examine whether the local orientation contrast (small-frame Saccade-to-Rod susceptibility) and global visuovestibular effects (large-frame Saccade-to-Vertical susceptibility) were correlated. No significant correlation, however, was found between these measures of local and global RFI susceptibility, $r(97) = .11$ (Fig. 6). Given that both the local orientation contrast and global visuovestibular effects of the RFI correlated with SQ-R scores but did not correlate with each other, we then examined whether different components within the SQ-R differentially predicted susceptibility to the local and global RFI effects.

Table 1. Correlations (*r* coefficients) between scores on the Autism Quotient (AQ), Empathizing Quotient (EQ), and Systemizing Quotient-Revised (SQ-R) and susceptibilities to the Perception, Saccade-to-Vertical, and Saccade-to-Rod tasks.

	Perception Task		Saccade-to-Vertical		Saccade-to-Rod	
	Small frame	Large frame	Small frame	Large frame	Small frame	Large frame
AQ	.08	.08	-.14	-.02	.02	.15
EQ	-.12	-.01	.05	.14	-.04	.08
SQ	-.13	-.13	-.08	-.40*	.31*	.08

* = $p < .05$

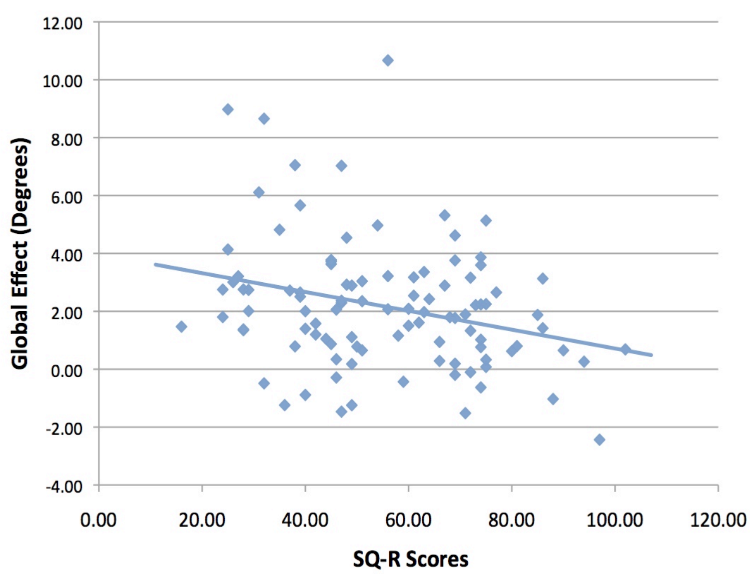

Figure 4. The association between scores on the Systemizing Quotient-Revised (SQ-R) and the global visuovestibular effects of the rod-and-frame illusion, as measured in the large-frame Saccade-to-Vertical task.

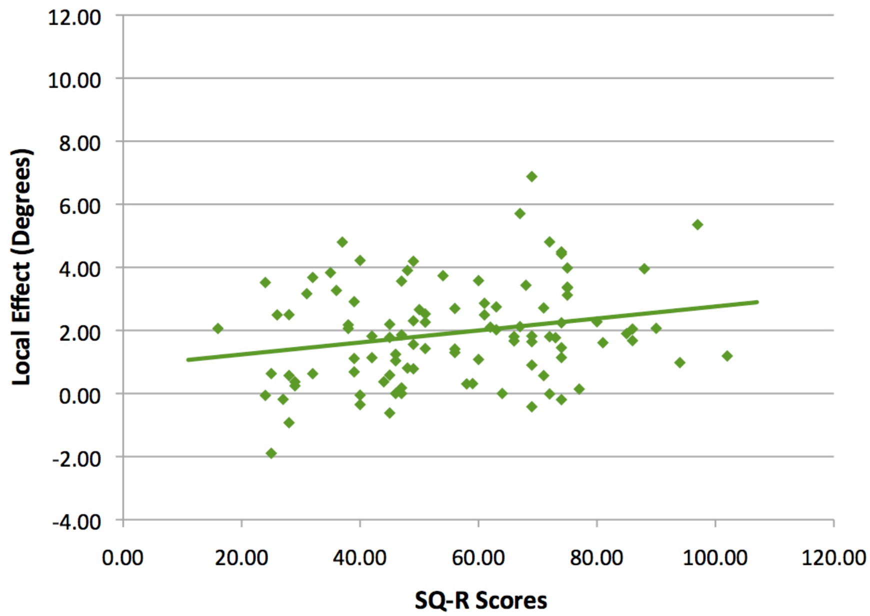

Figure 5. The association between scores on the Systemizing Quotient-Revised (SQ-R) and the local orientation contrast effects of the rod-and-frame illusion, as measured in the small-frame Saccade-to-Rod task.

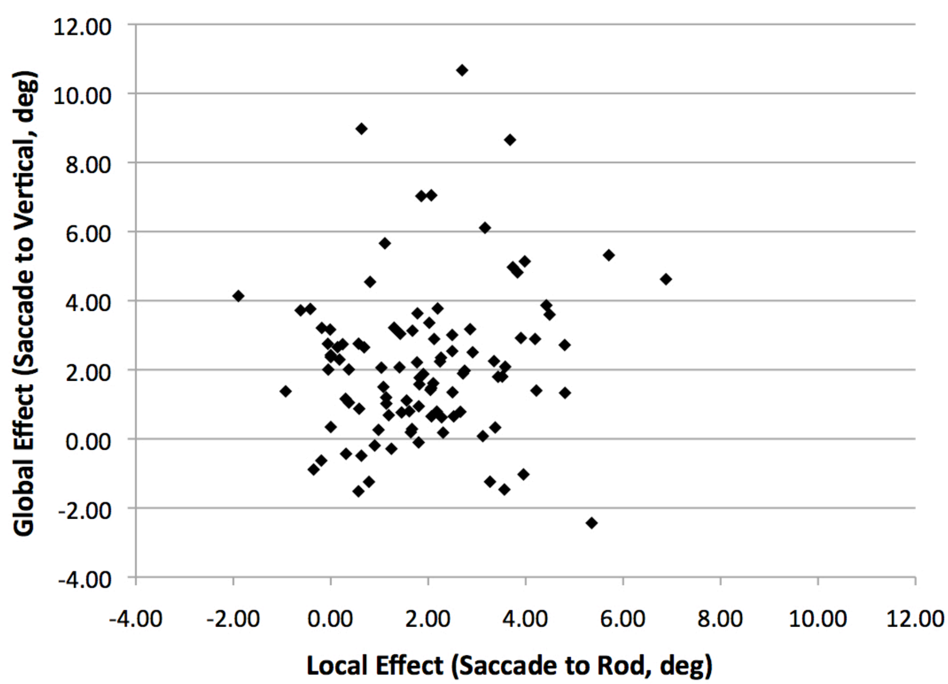

Figure 6. The lack of correlation between the local orientation contrast effects (small-frame Saccade-to-Rod) and the global visuovestibular effects (large-frame Saccade-to-Vertical) of the rod-and-frame illusion, $r(97) = .11$.

SQ-R Factor Analysis. Given that both the local orientation contrast and global visuovestibular effects of the RFI correlated with SQ-R scores but did not correlate with each other, we conducted a principle component analysis (PCA) on the SQ-R. While Wheelwright and colleagues (2006) conducted a similar analysis on the SQ-R and found no underlying factor structure, in our analysis we limited factor extraction to two factors (based on the hypothesis that different SQ-R components are differentially related to the local and global effects of the RFI). Here, in order to increase the statistical power of the analysis, SQ-R data from an additional 161 participants (collected from previous studies) was included in the analysis, resulting in a total sample size of 262 (117 males, 142 females; 3 participants did not specify their gender).

The results of the PCA indicated that, after varimax rotation, the two derived factors accounted for 19.75% of the variance in the SQ-R. Inspection of the items that loaded on each factor (where items with factor loadings < .40 were excluded) indicated qualitatively distinct constructs. Specifically, the first factor contained 26 items that seemed to assess a qualitatively similar dimension (Table 2). For example, items such as "When I look at a building, I am curious about the precise way it was constructed" and "When I listen to a piece of music, I always notice the way it's structured" loaded on this factor, and implicated an underlying systemizing dimension related to 'analytical tendencies' (e.g., tendency to analyze systems, narrowed or focus interests). The second factor contained 12 qualitatively similar items that seemed to measure a different systemizing drive than that measured by the first factor (Table 3). Specifically, items such as "If I had a collection (e.g., CDs, coins, stamps), it would be highly organized" and "I do not find it distressing if people who live with me upset my routines") seemed to implicate a systemizing drive related to an 'insistence on sameness' (e.g., preference for routine, repetition, and organization).

Table 2. SQ-R items that loaded on the Analytical Tendencies Factor (with a factor loading greater than .40).

Items on the Analytical Tendencies Factor
6. I find it difficult to read and understand maps.*
7. When I look at a mountain, I think about how it was formed.
8. I am not interested in the details of exchange rates, interest rates, stocks and shares.*
9. If I were buying a car, I would want to obtain specific information about its engine capacity.
10. I find it difficult to learn how to program video recorders.*
11. When I like something I like to collect a lot of different examples of that type of object, so I can see how they differ from each other.
15. I find it difficult to understand instruction manuals for putting appliances together.*
16. When I look at a building, I am curious about the precise way it was constructed.
17. I am not interested in understanding how wireless communication works (e.g. mobile phones).*
18. When traveling by train, I often wonder exactly how the rail networks are coordinated.
25. I find it easy to grasp exactly how odds work in betting.
26. I do not enjoy games that involve a high degree of strategy (e.g. Risk, chess, Games Workshop).*
27. When I learn about a new category, I like to go into detail to understand the small differences between different members of that category.
30. I can remember large amounts of information about a topic that interests me e.g. flags of the world, airline logos, etc.
32. I am fascinated by how machines work.
34. I know very little about the different stages of the legislation process in my country.*
35. I do not tend to watch science documentaries on television or read articles about science and nature.*
40. I am not interested in how the government is organized into different ministries and departments.*
41. I am interested in knowing the path a river takes from its source to the sea.
45. I rarely read articles or web pages about new technologies.*
46. I can easily visualize how the motorways in my region link up.
50. When I am walking in the country, I am curious about how the various kinds of trees differ.
53. If I were buying a computer, I would want to know exact details about its hard drive capacity and processor speed.
60. If I were buying a stereo, I would want to know about its precise technical features.
70. When I'm in a plane, I do not think about the aerodynamics.*
74. When I listen to a piece of music, I always notice the way it's structured.

* = denotes items that are negatively coded

Since the PCA resulted in additional factors that accounted for the remaining variance in SQ-R scores, we calculated total scores on the two factors derived (i.e., sum of item responses on each of the Analytical Tendencies and Insistence on Sameness factors) and regressed them on to SQ-R scores. Total scores on the Analytical Tendencies factor ranged from 0 to 52, while scores on the Insistence on Sameness factor ranged from 0 to 24. A linear stepwise regression on the SQ-R was then conducted with factor scores from each of the two derived factors as predictors. Both factors produced a significant F change in the model and accounted for 92.8% of the variance in SQ-R scores, $F(2,259) = 1658.5$, $p < .001$.

Table 3. SQ-R items that loaded on the Insistence on Sameness Factor (with a factor loading greater than .40).

Items on the Insistence on Sameness Factor
2. I like music or book shops because they are clearly organized.
14. If I had a collection (e.g. CDs, coins, stamps), it would be highly organized.
20. Whenever I run out of something at home, I always add it to a shopping list.
21. I know, with reasonable accuracy, how much money has come in and gone out of my bank account this month.
28. I do not find it distressing if people who live with me upset my routines.*
31. At home, I do not carefully file all important documents e.g. guarantees, insurance policies.*
44. My clothes are not carefully organized into different types in my wardrobe.*
55. When I get to the checkout at a supermarket, I pack different categories of goods into separate bags.
56. I do not follow any particular system when I'm cleaning my home.*
65. It does not bother me if things in the house are not in their proper place.*
71. I do not keep careful records of household bills.*
72. When I have a lot of shopping to do, I like to plan which shops I am going to visit and in what order.

* = denotes items that are negatively coded

To confirm that the derived factors were consistent across gender, we conducted PCA analyses on SQ-R scores independently for males ($n = 117$) and females ($n = 142$). In addition to qualitative similarities in factor item loadings, the regression coefficients for each factor independently derived from the PCA analyses for males and females were strongly correlated with the regression coefficients of the factors derived from the entire sample ($n = 262$), with significant ($p < .001$) r coefficients all above .93, confirming the consistency in factor extraction across genders. In addition, internal consistency analyses (conducted with the entire sample) indicated that both factors are reliable (Analytical Tendencies *alpha* = .884; Insistence on Sameness *alpha* = .814).

In order to examine whether these two factors differentially accounted for the SQ-R associations with the local orientation contrast and global visuovestibular effects of the RFI, factor scores (sum of item responses) were correlated with susceptibilities in the small-frame Saccade-to-Rod (local effects) and large-frame Saccade-to-Vertical (global effects) tasks. Scores on the Analytical Tendencies Factor were found to negatively correlate with the global visuovestibular effect of the RFI ($r(97) = -.44$, $p < .01$; Fig. 7) but were uncorrelated with the local orientation contrast effect ($r(95) = .12$). In contrast, scores on the Insistence on Sameness factor were positively correlated with the local orientation contrast effects of the RFI ($r(95) = .36$, $p < .02$; Fig. 8), but were uncorrelated with the global visuovestibular effect ($r(97) = -.10$). Remarkably, these associations were stronger than those found with total SQ-R scores and the local/global RFI effects.

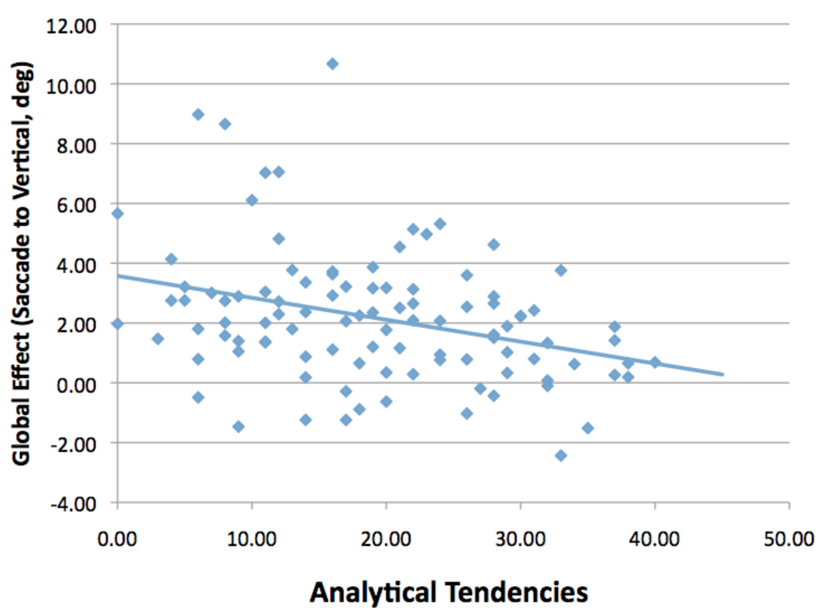

Figure 7. Higher scores on the Analytical Tendencies factor were associated with decreased global visuovestibular effects (large-frame Saccade-to-Vertical) of the rod-and-frame illusion.

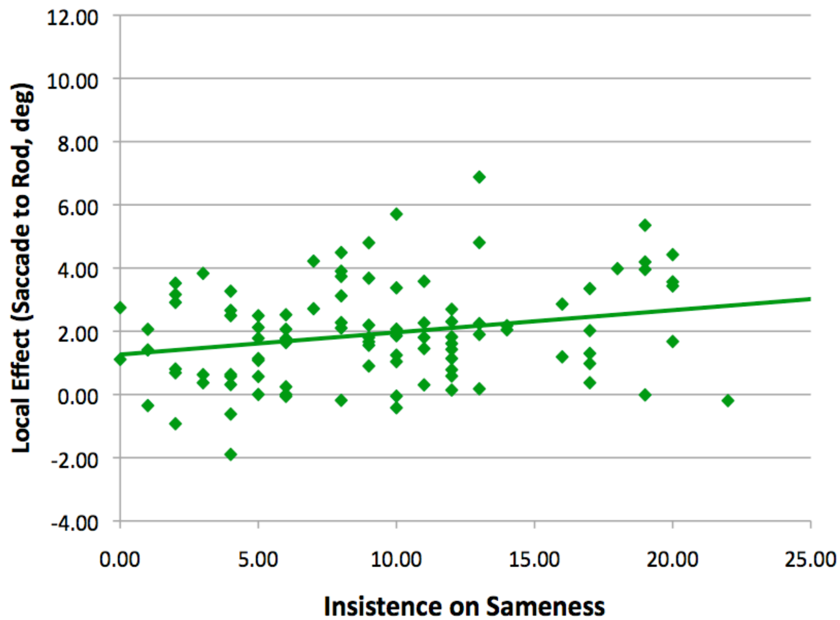

Figure 8. Higher scores on the Insistence on Sameness factor were associated with increased local orientation contrast effects (small-frame Saccade-to-Rod) of the rod-and-frame illusion.

To examine whether the regression slopes for the RFI and SQ-R factor correlations differed as a function of gender, separate ANCOVAs were run on the local and global RFI effects with gender as a fixed factor and Insistence on Sameness and Analytical Tendencies factor scores as covariates, respectively, in each separate analysis. No significant interaction for gender by Insistence on Sameness scores was found for the local RFI effect, indicating that the slope of the correlation did not significantly differ between males and females. However, a significant gender by Analytical Tendencies interaction was found for the global RFI effect in that the slope of the correlation was attenuated for females relative to males, $F(1,93) = 7.53$, $p < .01$. While the expected negative trend in the slope was observed, the correlation between Analytical Tendencies scores and the global RFI effect was not significant for females ($p = .80$).

The lack of correlation between Analytical Tendencies and the global visuovestibular effects for females, however, may reflect an insufficient range of scores on the Analytical Tendencies factor for females (range = 3-29) in that there tends to be relatively few females, relative to males (range = 8-40), that score at the upper end of the SQ-R distribution (indeed, when the range of Analytical Tendencies scores for males was restricted to the range of scores observed for females, the gender by Analytical Tendencies interaction in the ANCOVA was no longer significant). Therefore, to examine gender differences in factor scores, scores on each factor were normalized (items sum / item *n*) and subjected to a 2x2 repeated-measures ANOVA with Gender as a between-subjects variable and Factor (Analytical Tendencies and Insistence on Sameness normalized factor scores) as a within-subjects variable. A significant main effect was found for gender ($F(1,255) = 11.79$, $p = .001$) in that males had higher overall scores ($M = .87$, $SD = .31$) compared to females ($M = .74$, $SD = .30$). A significant main effect was also found for Factor ($F(1,255) = 10.63$, $p = .001$) in that scores on the Analytical Tendencies factor ($M = .76$, $SD = .32$) were lower compared to scores on the Insistence on Sameness factor ($M = .85$, $SD = .45$). A significant Factor by Gender interaction was also found ($F(1,255) = 82.65$, $p < .001$) in that males scored significantly higher on the Analytical Tendencies factor compared to females ($t(255) = 9.82$, $p < .001$; Fig. 10), while females scored significantly higher on the Insistence on Sameness factor compared to males ($t(255) = -2.22$, $p < .03$; Fig. 9).

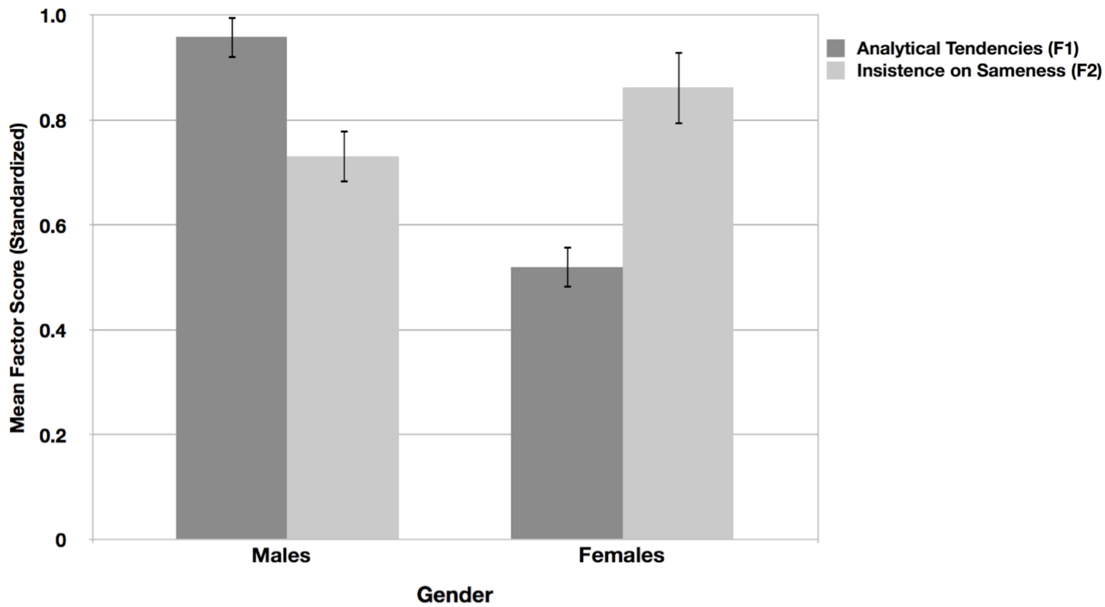

Figure 9. Gender differences in mean systemizing factor scores (standardized). Males scored significantly higher on Analytical Tendencies ($p < .001$), while females scored significantly higher on Insistence on Sameness ($p < .03$). Error bars indicate +/- 1 SEM.

Discussion

In a large sample of neurotypical individuals, we found that systemizing tendencies (as measured by the Systemizing Quotient-Revised) differentially modulated illusion susceptibility as a function of the local (orientation contrast effects) or global (visuovestibular) mechanisms that drive the rod-and-frame illusion (RFI). Specifically, higher systemizing scores were associated with increased local orientation contrast effects and decreased global visuovestibular effects of the illusion. This finding is consistent with both the Weak Central Coherence (WCC) and Enhanced Perceptual Functioning (EPF) theories of perceptual processing in autism spectrum disorders (ASD), where superior, low-level processing (proposed by the EPF) and attenuated global processing (proposed by the WCC) have been postulated to characterize perceptual biases in ASD. Here, we found that qualitatively similar perceptual biases can also be observed in neurotypical (NT) individuals as a function of systemizing tendencies. In addition, consistent with the EPF theory, greater sensitivity to local visual cues (small-frame Saccade-to-Rod susceptibility) did not negatively covary with sensitivity to global visual cues (large-frame Saccade-to-Vertical susceptibility). This suggests that superior low-level perception and deficits in global processing may be two orthogonal, yet comorbid, symptoms of ASD, and that biases in local processing do not necessitate subsequent impairments in processing global context. Instead, these results suggest that a global-to-local shift in perceptual processing, where both increased local processing and an under-reliance on global cues are manifest, may occur as a function of heightened systemizing tendencies, which are known to be hyper-expressed in ASD samples (Wheelwright et al., 2006).

In addition, we found evidence that the Systemizing Quotient-Revised (SQ-R) measures two distinct forms of systemizing: 'analytical tendencies' and 'insistence on sameness'. While the nomenclature of these subscales may necessitate further validation, we found that the derivation of these factors was qualitatively supported, consistent across gender, accounted for a large amount of the variance in overall systemizing tendencies, and had discriminant validity in differentially correlating with behavior (i.e., susceptibility to the mechanisms of the RFI). Although Wheelwright and colleagues (2006) initially examined the factor structure of the SQ-R and, based on the extraction of 18 factors that failed to fall into meaningful clusters, concluded that the SQ-R was a uni-dimensional construct, our data-driven PCA, with extraction restricted to two factors, resulted in qualitatively distinct clusters that may not have been apparent when using exploratory factor analysis. In addition, the original SQ (60 items; Baron-Cohen et al.,

2003) was revised by Wheelwright and colleagues in 2006 (SQ-R) in order to counter the traditionally male-biased items that characterized the original measure by including items that were more gender-neutral, and we found that the factors that were extracted from the SQ-R could be differentiated by the items retained from the original SQ and the newly included items in the SQ-R. Specifically, of the 26 items that loaded onto the Analytical Tendencies factor, 18 came from the original SQ, whereas of the 12 items that loaded onto the Insistence on Sameness factor, only 1 item came from the original SQ. The addition of more gender-neutral items on the SQ-R may also explain the reduced disparity in mean item scores between the SQ and the SQ-R as a function of gender, where Wheelwright and colleagues (2006) reported that females scored higher than males on 13.2% of the items in the SQ and 32% of the items in the SQ-R. The two-factor structure of the SQ-R that was found in the current study may therefore be due in part to the SQ revision process of Wheelwright and colleagues (2006) where more gender-neutral items were included in the SQ-R. Importantly, though, results from the current study suggest that the items that were added to the SQ-R can not only be differentiated as a function of gender biases, but also as a function of the type of systemizing being measured.

As further evidence for a two-factor structure to the SQ-R, we found discriminant validity to these factors in that they differentially covaried with the local orientation contrast and global visuovestibular effects of the rod-and-frame illusion (RFI). Specifically, higher scores on the Analytical Tendencies factor were associated with decreased global visuovestibular effects of the RFI but were uncorrelated with the local orientation contrast effects, while higher scores on the Insistence on Sameness factor were associated with increased local orientation contrast effects but were uncorrelated with the global effects. Together, higher scores on both factors differentially predicted a shift from reliance on global to local visual cues. While the relationship between Analytical Tendencies scores and the global visuovestibular RFI effects was attenuated and non-significant in females, this may reflect an insufficient range in scores in that relatively few females occupy the upper end of the distribution for Analytical Tendencies scores. Indeed, significant gender differences were found on factor scores in that males scored significantly higher on the Analytical Tendencies factor than females, while females scored significantly higher on the Insistence on Sameness factor compared to males.

While both an analytical drive (e.g., tendency to analyze systems, narrowed or focus interests) and an insistence on sameness (e.g., preference for routine, repetition, and organization) characterize some of the symptoms associated with ASD, the finding that NT females exhibited a greater insistence on sameness drive than NT males has important implications for the Extreme Male Brain (EMB) theory of autism (Baron-Cohen, 2002). The EMB theory proposes that the cognitive biases in ASD represent an extreme manifestation of NT male traits, such as a heightened drive to systemize and an attenuated drive to empathize, relative to NT females. The results from experiment 1, however, suggest that some forms of systemizing (i.e., insistence on sameness) may be more dominant, or expressed in higher levels, in NT female populations. Consequently, if the autistic brain is an extreme manifestation of the NT male brain, then hyper-systemizing tendencies in ASD should only manifest as extreme scores on the Analytical Tendencies factor of the SQ-R, while ASD scores on the Insistence on Sameness factor (which we found in Experiment 1 to be associated more strongly with female cognitive phenotypes) should be hypo-expressed. However, ASD symptomology would suggest that individuals with ASD are strongly "resistant to change" and exhibit a greater "insistence on sameness" (Kanner, 1943) than NT individuals. In this view, individuals with ASD would be expected to score higher on the Insistence on Sameness factor of the SQ-R compared to NT individuals, despite the finding that this trait is stronger in females. Experiment 2 therefore examined how scores on the two SQ-R factors, and in particular on the Insistence on Sameness factor, differ between and within NT and ASD groups as a function of gender.

Experiment 2

In Experiment 1, we found evidence for a two-factor structure to the systemizing trait of autism, as measured by the Systemizing Quotient-Revised. Systemizing, or the process of observing, analyzing, and deriving the structure and operations in complex, rule-based systems, has been a useful construct in understanding some of the cognitive biases associated with autism spectrum disorders (Baron-Cohen, 2008). The hyper-systemizing theory of autism (Baron-Cohen, 2006) proposes that many of the symptoms associated with ASD, such as repetitive behaviors, narrow interests, and an insistence on sameness, are the result of a systemizing mechanism that is set too high in ASD. For example, individuals with ASD exhibit superior performance on tasks that require systemizing abilities, such as on tests of folk physics (Jolliffe & Baron-Cohen, 1997; Lawson et al., 2004) and picture-sequencing (Baron-Cohen et al., 1986), and in neurotypical (NT) populations, autistic traits are predictive of higher systemizing tendencies (Baron-Cohen, 2008; Wheelwright et al., 2006). Hyper-systemizing drives consequently may explain why individuals with ASD often develop narrow interests or an insistence on sameness, as such a cognitive bias would naturally lead to an analytical focus on specific types of systems (i.e., narrow interests) that have minimal variance (i.e., insistence on sameness; Baron-Cohen, 2006). Hyper-systemizing tendencies also predict a proclivity to attend to the details in a visual scene, and this perceptual bias is frequently observed in ASD populations (Mottron et al., 2003; O'Riordan, et al., 2001; Plaisted, O'Riordan, & Baron-Cohen, 1998; Shah & Frith 1993) and in NT populations as a function of autistic tendencies (Grinter et al., 2009; Grinter et al., 2009).

Hyper-systemizing tendencies in ASD have been hypothesized to be the result of an extreme manifestation of the neurotypical male brain (EMB theory of autism, Baron-Cohen, 2002). For example, fetal testosterone levels are strongly predictive of systemizing tendencies (Auyeung et al., 2006) and autistic traits in general (Knickmeyer et al., 2005; Auyeung, Baron-Cohen, Ashwin, Knickmeyer, Taylor, & Hackett, 2009; Auyeung et al., 2010), and recently, sex hormones have been found to differentially modulate the expression of a candidate gene (RORA) in autism (Sarachana et al., 2011). Given that the hyper-systemizing theory of autism predicts that a hyper-systemizing mechanism that is set too high can produce a wide-range of autistic symptoms (Baron-Cohen, 2006), including narrow interests (e.g., analytical focus on specific systems) and an insistence on sameness (e.g., preference for routines and systems with minimal variance), the finding from Experiment 1 that different types of systemizing are embedded within the SQ-R as two distinct factors may not be surprising. For instance, Baron-Cohen and colleagues (2009) described several types of systemizing that are associated with core autistic behaviors, and the two factors found in the SQ-R can be qualitatively differentiated by these different types of systemizing. For example, the numerical (*e.g., preoccupation with numbers, calendars, and timetables*), spatial (*e.g., fascination with routes*), and mechanical (*e.g., drive to understand how mechanical systems operate*) types of systemizing strongly correspond with items on the Analytical Tendencies factor of the SQ-R, while the environmental (*e.g., insisting on environmental order and consistent positioning of objects*) and collectible (*e.g., organizing collections, making lists and catalogues*) forms of systemizing strongly correspond with items on the Insistence on Sameness factor of the SQ-R. The two-factor structure of the SQ-R can therefore be differentiated by these different types of systemizing, which further supports the qualitative factor structure of the instrument.

Unexpected results from Experiment 1, however, were the gender differences that emerged on these factors. While the EMB theory of autism would predict that NT males should exhibit greater manifestations of both types of systemizing, it was found that NT males only scored higher on the Analytical Tendencies factor, while NT females scored higher on the Insistence on Sameness factor. Although this result may not be too surprising given that the majority of items that loaded on the Insistence on Sameness factor were the more recent, gender-neutral items that were added to the SQ-R in the revision process, this finding does have important implications for the EMB theory of autism in that some forms of systemizing (i.e., an insistence on sameness) may be stronger in females than in males. Consequently, if ASD is an extreme manifestation of NT male traits, then hyper-systemizing tendencies in ASD should only be reflected in higher scores on the Analytical Tendencies factor of the SQ-R, while ASD scores on the

Insistence on Sameness factor should be at similar levels as NT males. On the other hand, if a systemizing mechanism that is set too high in ASD leads to heightened forms of all aspects of systemizing (e.g., numerical, mechanical, environmental), then ASD groups should score higher than NT groups on *both* the Analytical Tendencies and Insistence on Sameness factors, regardless of gender. This result would suggest that while many aspects of ASD are influenced by extreme male neurophysiology, some forms of hyper-systemizing in ASD may not be due to the influence of male sex hormones but rather may arise from other etiological sources. Experiment 2 therefore sought to replicate the two-factor structure of the SQ-R found in Experiment 1 and to examine how these factors differ between NT and ASD samples as a function of gender. Furthermore, analysis of the covariation between SQ-R factors may indicate whether different types of systemizing (e.g., spatial, mechanical, environmental) may arise from a common epigenetic source (e.g., an extreme male brain, or high levels of fetal testosterone) or may be similar cognitive phenotypes that arise from different, yet comorbid, etiologies in ASD.

Methods

Overview. A large data set comprising NT and ASD groups previously collected from Wheelwright et al. (2006) was used in Experiment 2 in order to verify the two-factor structure of the SQ-R. After independent verification of the factor structure in this data set, the Wheelwright et al. (2006) data from the NT group (n = 1761) was combined with the NT data from Experiment 1 (n = 262) in order to compare factor scores across the ASD group (from the Wheelwright et al., 2006 data set; n = 125) and NT group (from the combined data sets; n = 2023).

Participants. The data set from Wheelwright et al. (2006) consisted of an NT group (*n* = 1761; 41% male) with a mean age of 21.0 years (*SD* = 2.58 years) who were previously recruited by various means (e.g., email, newspaper advertisements, university postings) and had no known psychiatric conditions. A second group comprised of an additional 125 participants (55.2% male) with an ASD diagnosis (based on DSM-IV or ICD-10 criteria) was also recruited and had a mean age of 37.6 years (*SD* = 13.1 years). Within the ASD group, 110 had a diagnosis of Asperger Syndrome and 15 had a diagnosis of high-functioning autism (see Wheelwright et al., 2006 for further details). Participant characteristics from the data set used in Experiment 1 (*n* = 262) are reported above.

Materials. Although all participants in both data sets completed three questionnaires on autistic tendencies (the Autism Quotient, Empathizing Quotient, and Systemizing Quotient-Revised), only the data from the SQ-R were analyzed and reported here. In the Wheelwright data set, participants completed the questionnaire online via a website. In the data set from Experiment 1, participants completed the questionnaire in person on a Macintosh computer (Apple Computers, Cupertino, CA).

Design and Procedure. All analyses in the current study are based on archival data that was collected from a previous study (Wheelwright et al, 2006). Principal components analysis on the NT SQ-R data from Wheelwright et al. (2006) was first conducted to verify the factor structure of the SQ-R. The NT data from both data sets were then combined and compared to the ASD group in order to examine how SQ-R factor scores differ across NT and ASD groups as a function of gender.

Results

Verification of the Two-Factor Structure of the SQ-R. A principal components analysis (PCA) using varimax rotation and restriction of factor extraction to two was first conducted on SQ-R data from the NT group in Wheelwright et al. (2006). Initial extraction of the two factors resulted in eigenvalues of 10.40 and 4.36 and cumulatively accounted for 13.88% of the variance in total SQ-R scores. However, given that additional components with eigenvalues > 1 accounted for the remainder of the variance in SQ-R scores, a linear regression on SQ-R scores was conducted. Specifically, scores on the two derived factors were computed (i.e., sum of item responses on each factor) and used as predictors in a linear regression on SQ-R scores. Scores on both factors produced a significant F change in the model and accounted for 83.2% of the variance in total SQ-R scores, $F(2,1760) = 4354.45$, $p < .001$.

Comparison of the items that loaded on each factor in the PCA (from the Wheelwright data set) were highly similar to the factor items derived separately in Experiment 1. Specifically, using a factor-loading cutoff of .40, 16 of the 26 items from the Analytical Tendencies factor were retained (Table 4). The items that did not load on the factor were due to the relatively high factor-loading cutoff (.40), as when the PCA was rerun with a factor-loading cutoff of .30, 21 of the 26 items were retained in the Analytical Tendencies factor. In addition, the new items that loaded on this factor were qualitatively similar to the items retained in both experiments in that all these items appear to measure analytical forms of systemizing. On the Insistence on Sameness factor, 10 of the 12 items derived from Experiment 1 were retained using a .40 factor-loading cutoff (Table 5). When the PCA was rerun with a .30 factor-loading cutoff, all 12 of the items on the Insistence on Sameness factor from Experiment 1 were retained, with only one new item (corresponding to insistence on sameness) loading on this factor.

Table 4. SQ-R items that loaded on the Analytical Tendencies factor (with a factor loading greater than .40) in both Experiments, and those that only loaded on this factor in Experiment 1 or Experiment 2 (i.e., from the Wheelwright data set).

Items on the Analytical Tendencies Factor in Both Experiments
6. I find it difficult to read and understand maps.*
9. If I were buying a car, I would want to obtain specific information about its engine capacity.
10. I find it difficult to learn how to program video recorders.*
15. I find it difficult to understand instruction manuals for putting appliances together.*
16. When I look at a building, I am curious about the precise way it was constructed.
17. I am not interested in understanding how wireless communication works (e.g. mobile phones).*
18. When traveling by train, I often wonder exactly how the rail networks are coordinated.
25. I find it easy to grasp exactly how odds work in betting.
26. I do not enjoy games that involve a high degree of strategy (e.g. Risk, chess, Games Workshop).*
32. I am fascinated by how machines work.
35. I do not tend to watch science documentaries on television or read articles about science and nature.*
45. I rarely read articles or web pages about new technologies.*
46. I can easily visualize how the motorways in my region link up.
53. If I were buying a computer, I would want to know exact details about its hard drive capacity and processor speed.
60. If I were buying a stereo, I would want to know about its precise technical features.
70. When I'm in a plane, I do not think about the aerodynamics.*

Items Only on the Analytical Tendencies Factor in Experiment 1
7. When I look at a mountain, I think about how it was formed.
*8. I am not interested in the details of exchange rates, interest rates, stocks and shares.**
11. When I like something I like to collect a lot of different examples of that type of object, so I can see how they differ from each other.
27. When I learn about a new category, I like to go into detail to understand the small differences between different members of that category.
30. I can remember large amounts of information about a topic that interests me e.g. flags of the world, airline logos, etc.
34. I know very little about the different stages of the legislation process in my country.*
40. I am not interested in how the government is organized into different ministries and departments.*
41. I am interested in knowing the path a river takes from its source to the sea.
50. When I am walking in the country, I am curious about how the various kinds of trees differ.
74. When I listen to a piece of music, I always notice the way it's structured.

Items Only on the Analytical Tendencies Factor in Experiment 2
1. I find it very easy to use train timetables, even if this involves several connections.
43. If there was a problem with the electrical wiring in my home, I'd be able to fix it.
*51. I find it difficult to understand information the bank sends me on different investment/saving systems.**
*52. If I were buying a camera, I would not look carefully into the quality of the lens.**
*64. When I hear the weather forecast, I am not very interested in the meteorological patterns.**
66. In maths, I am intrigued by the rules and patterns governing numbers.
*67. I find it difficult to learn my way around a new city**

* = denotes items that are negatively coded; *italics* denote items that would be retained in both experiments using a .30 factor-loading cutoff.

Table 5. SQ-R items that loaded on the Insistence on Sameness factor (with a factor loading greater than .40) in both Experiments, and those that only loaded on this factor in Experiment 1 or Experiment 2 (i.e., from the Wheelwright data set).

Items on the Insistence on Sameness Factor in Both Experiments
14. If I had a collection (e.g. CDs, coins, stamps), it would be highly organized.
20. Whenever I run out of something at home, I always add it to a shopping list.
21. I know, with reasonable accuracy, how much money has come in and gone out of my bank account this month.
31. At home, I do not carefully file all important documents e.g. guarantees, insurance policies.*
44. My clothes are not carefully organized into different types in my wardrobe.*
55. When I get to the checkout at a supermarket, I pack different categories of goods into separate bags.
56. I do not follow any particular system when I'm cleaning my home.*
65. It does not bother me if things in the house are not in their proper place.*
71. I do not keep careful records of household bills.*
72. When I have a lot of shopping to do, I like to plan which shops I am going to visit and in what order.

Items Only on the Insistence on Sameness Factor in Experiment 1
2. I like music or book shops because they are clearly organized.
*28. I do not find it distressing if people who live with me upset my routines.**

Items Only on the Insistence on Sameness Factor in Experiment 2
*39. I do not always check off receipts etc. against my bank statements.**

* = denotes items that are negatively coded; *italics* denote items that would be retained in both experiments using a .30 factor-loading cutoff.

In addition, when factor scores were calculated (sum of item responses from the PCA with a .40 factor loading cutoff) for the two factors derived from Experiment 1 and correlated with factor scores derived independently from the Wheelwright data set, they were strongly correlated. Specifically, the correlation between the Analytical Tendencies factors derived from the two data sets was $r(2020) = .941$, $p < .001$ (Fig. 10A), while the correlation between the Insistence on Sameness factors from both data sets was $r(2020) = .974$, $p < .001$ (Fig. 10B). In addition, when internal consistency analyses were conducted on each of the factors (using the factor items derived from the PCA in Experiment 1) for the NT data combined ($n = 2021$), both factors were found to be reliable (Cronbach's alpha for the Analytical Tendencies factor = .872; Cronbach's alpha for the Insistence on

Sameness factor = .795), with the higher reliability on the Analytical Tendencies factor likely due to a greater number of questions that loaded onto this factor.

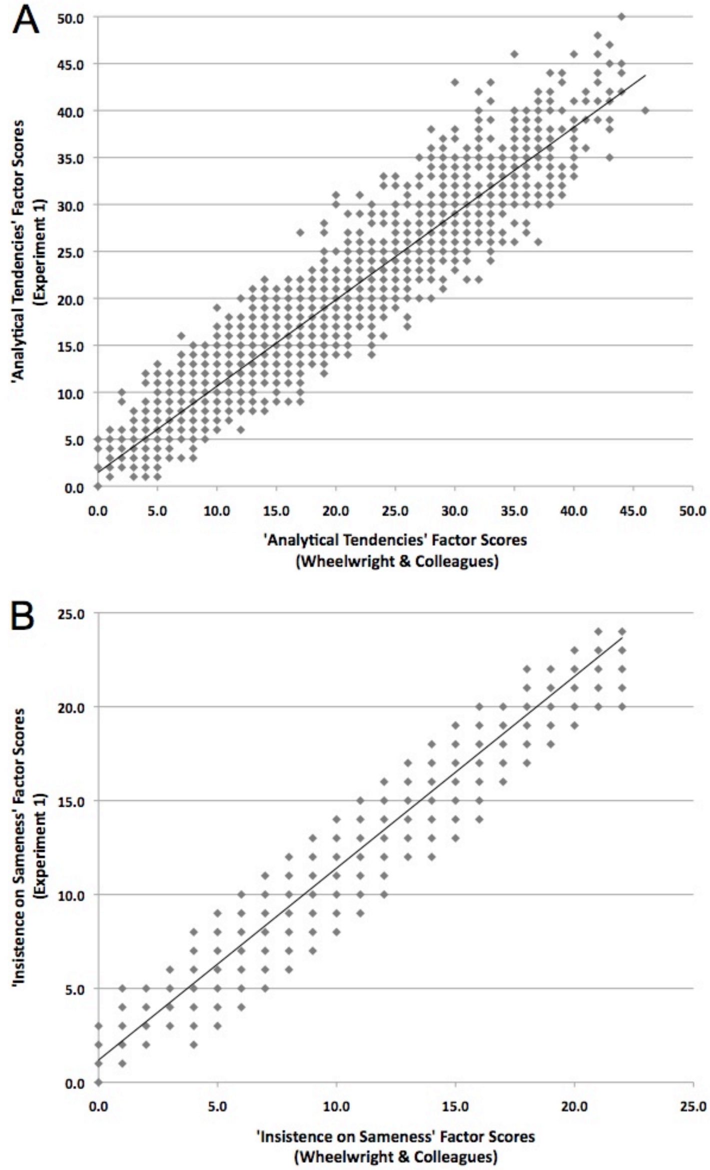

Figure 10. Verification of the two-factor structure of the SQ-R through comparison of factor scores independently extracted from two SQ-R data sets (Experiment 1 and Wheelwright et al., 2006). A, Correlation between raw scores on the Analytical Tendencies factor from the two data sets [$r(2020) = .941$, $p < .001$)]. B, Correlation between raw scores on the Insistence on Sameness factor from the two data sets [$r(2020) = .974$, $p < .001$)]. Note that each data point includes multiple participants due to limited range of scores.

In order to examine whether these two types of systemizing covary, a bivariate correlation was conducted between scores on the Analytical Tendencies and Insistence on Sameness factors. Although a significant correlation was found between the two factors [$r(2020) = .253$, $p < .001$], only 6.4% of the variance in each factor was accounted for. In addition, inspection of the scatterplot of this association (Fig. 11) further suggests that these two SQ-R factors (i.e., types of systemizing) may be largely independent from one another and that each is accounting for unique variance in the SQ-R.

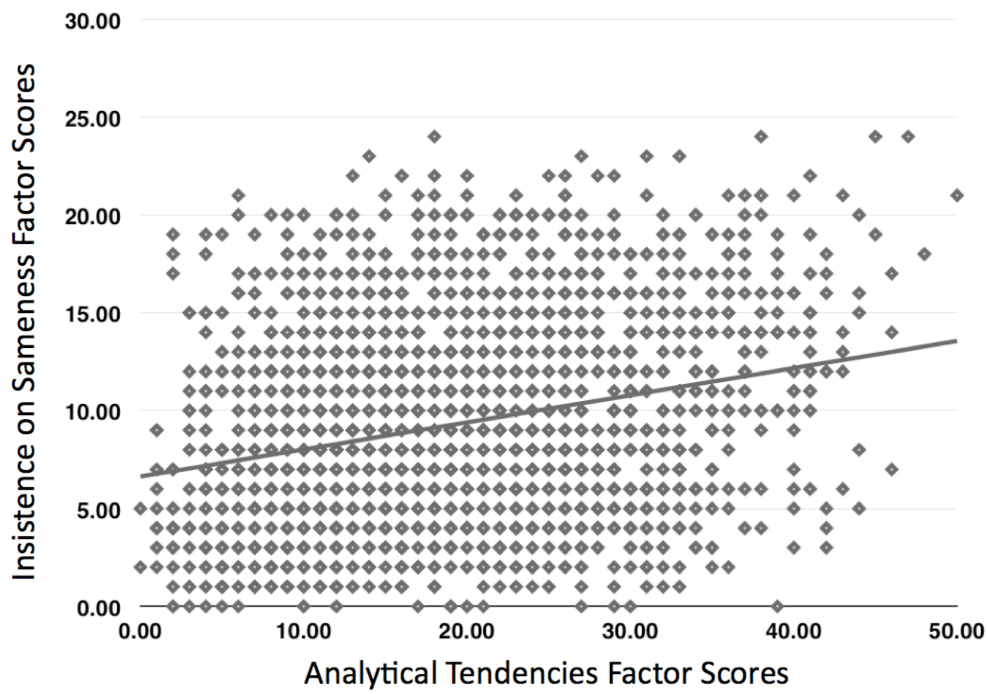

Figure 11. Scatterplot of the correlation [r(2020) = .253, p < .001)] between scores on the Analytical Tendencies and Insistence on Sameness factors in Experiment 2.

Analysis of Analytical Tendencies Factor in NT and ASD Groups. For the Analytical Tendencies factor, a 2x2 ANOVA was conducted with Gender (male, female) and Group (NT, ASD) as between-subjects variables (Fig. 12A, Table 6). A significant main effect was found for Gender, $F(1, 2139) = 56.34$, $p < .001$. Planned comparisons revealed that NT males scored significantly higher on the Analytical Tendencies factor than NT females [$t(2016) = 23.68$, $p < .001$], with males scoring higher on 96.1% of the items on this factor than females. No significant differences in mean factor scores were found between males and females with ASD. A significant main effect was also found for Group in that the ASD group scored significantly higher on the Analytical Tendencies factor than the NT group, $F(1,2139) = 87.77$, $p < .001$. Planned comparisons indicated that males with ASD scored significantly higher than NT males [$t(907) = -3.98$, $p < .001$], while females with ASD scored significantly higher than NT females [$t(1232) = -9.13$, $p < .001$]. A significant Gender-by-Group interaction was also found in that the increase (slope) in factor scores from NT to ASD groups was greater for females than for males, $F(1,2139) = 15.11$, $p < .001$.

Analysis of Insistence on Sameness Factor in NT and ASD Groups. A 2x2 ANOVA was conducted on Insistence on Sameness factor scores with Gender (male, female) and Group (NT, ASD) as between-subjects variables (Fig. 12B, Table 6). A significant main effect was found for Gender, $F(1, 2139) = 12.45$, $p < .001$. Planned comparisons revealed that NT females scored significantly higher on the 'insistence on sameness' factor than NT males [$t(2016) = -6.00$, $p < .001$], with females scoring higher on 83.3% of the items on this factor than males. Similarly, females with ASD scored significantly higher than males with ASD [$t(123) = -1.98$, $p = .05$], with ASD females scoring higher on 83.3% of the items on this factor compared to ASD males. A significant main effect was also found for Group in that the ASD group scored significantly higher on the Insistence on Sameness factor than the NT group, $F(1,2139) = 92.24$, $p < .001$. Planned comparisons indicated that males with ASD scored significantly higher than NT males [$t(907) = -6.95$, $p < .001$], while females with ASD scored significantly higher than NT females [$t(1232) = -6.73$, $p < .001$]. No interaction was found between gender and group indicating that Insistence on Sameness factor scores increased by the same magnitude from NT to ASD groups in both males and females.

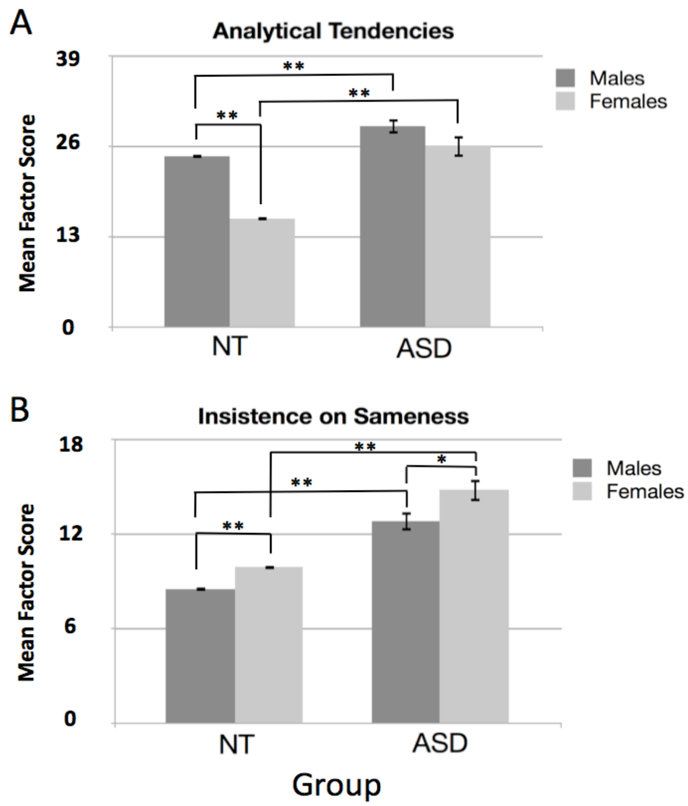

Figure 12. Mean scores on the Analytical Tendencies (A) and Insistence on Sameness (B) SQ-R factors as a function of gender (male, female) and group (NT, ASD) in Experiment 2 (* $p < .05$; ** $p < .01$). Error bars indicate +/- 1 SEM.

Differences in SQ-R Factors. In order to examine differences in the magnitude of factor scores within each group, planned comparisons (using independent-samples *t*-tests) between standardized factor scores (i.e., comparing Analytical Tendencies and Insistence on Sameness) were conducted as a function of gender and group. For NT males, scores on the Analytical Tendencies factor were significantly higher than on the Insistence on Sameness factor [$t(839) = 15.89$, $p < .001$], though this difference was not found in males with ASD ($p > .40$), who had similar scores on both systemizing factors (Table 6). For both NT and ASD females, scores on the Insistence on Sameness factor were significantly higher than on the Analytical Tendencies factor [NT females: $t(1177) = -17.62$, $p < .001$; ASD females: $t(55) = -3.16$, $p < .01$; Table 6]. Results from these analyses are summarized in Figure 13.

Table 6. Mean raw and standardized scores on the Analytical Tendencies and Insistence on Sameness SQ-R factors as a function of gender and group (NT, ASD) in Experiment 2. Standard deviations are in parentheses.

SQ-R Factor	NT		ASD	
	Males	Females	Males	Females
Analytical Tendencies				
Raw Score	24.77 (8.63)	15.61 (8.20)	28.88 (9.04)	26.04 (11.12)
Standardized Score	.94 (.33)	.60 (.32)	1.11 (.35)	1.00 (.43)
Insistence on Sameness				
Raw Score	8.50 (4.92)	9.89 (5.31)	12.81 (5.42)	14.80 (5.78)
Standardized Score	.71 (.41)	.82 (.44)	1.07 (.45)	1.14 (.47)

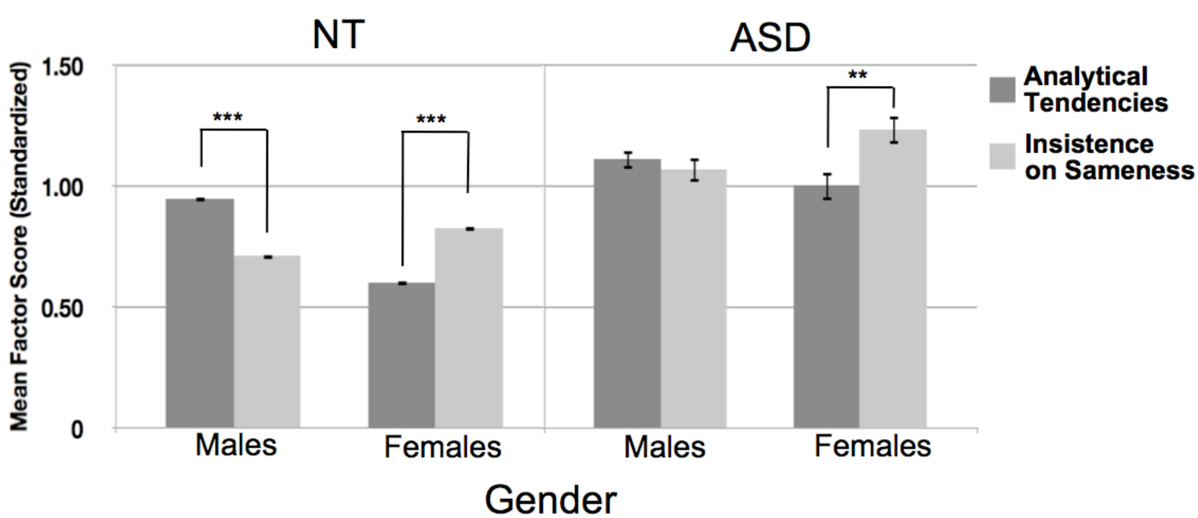

Figure 13. Differences in dominant types of systemizing factors (Analytical Tendencies and Insistence on Sameness) as a function of gender and group (NT, ASD) in Experiment 2. Mean scores on the Analytical Tendencies factor were higher in NT males, while mean scores on the Insistence on Sameness factor were higher in both NT and ASD females (** $p < .01$; *** $p < .001$). Error bars indicate +/- 1 SEM.

Discussion

In a large sample of neurotypical (NT) participants (from Wheelwright et al., 2006), the two-factor structure to the SQ-R reported in Experiment 1 was verified. These two factors (Analytical Tendencies and Insistence on Sameness) were found to account for most of the variance in overall SQ-R scores and appear to measure distinct types of systemizing. Specifically, items on the Analytical Tendencies factor are fairly consistent with numerical, spatial, and mechanical types of systemizing as described by Baron-Cohen and colleagues (2009), while items on the Insistence on Sameness factor are consistent with environmental and collectible types of systemizing. In addition, the two systemizing factors in the SQ-R were only weakly associated with one another, suggesting that they may be relatively distinct cognitive processes that while comorbid in ASD populations, are differentially expressed (in magnitude) in the general population as a function of gender. Specifically, systemizing mechanisms related to analytical tendencies are more predominant in NT males, while systemizing mechanisms related to an insistence on sameness are more predominant in NT females.

This finding has important implications for the Extreme Male Brain (EMB, Barron-Cohen, 2002) theory of autism. This theory postulates that in NT populations, the systemizing mechanism is set higher in males than in females, and that an even stronger systemizing mechanism is present in ASD due to extreme male neurophysiology. The present results constrain this theory in that some forms of systemizing (e.g., systemizing related to an insistence on sameness) appear to be stronger in females than in males, regardless of clinical diagnosis. This suggests that not all forms of systemizing may be influenced by male neurophysiology, and consequently, that some forms of hyper-systemizing in ASD populations may be characterized by extreme manifestations of more predominant female traits or cognitive phenotypes. This interpretation is consistent with the current results in that, in comparison to males, scores on the Insistence on Sameness SQ-R factor were higher in females, compared to males, in both NT and ASD groups. This also suggests that while ASD is four to five times more prevalent in males than in females (Center for Disease Control, 2007), there may be important etiological differences in the types of systemizing that are displayed in ASD populations, which may be related to some of the subtle gender differences which have been reported in ASD behaviors (Hartley & Sikora, 2009).

It is important to emphasize that the current results do not discount the EMB theory of autism but only constrain it. There is much evidence that key behaviors in ASD, and systemizing in NT populations, are influenced by extreme male neurophysiology (e.g., fetal testosterone levels, Auyeung et al., 2006). In addition, the significant gender-by-group interaction for scores on the Analytical Tendencies factor does implicate the influence of extreme male neurophysiology in ASD. Specifically, while Insistence on Sameness scores showed the same linear increase from NT to ASD groups in both males and females, scores on the Analytical Tendencies factor increased at a greater rate in females with ASD compared to males with ASD. Consistent with the EMB theory of autism, this suggests that in females with ASD, male-predominant forms of systemizing are manifest at more extreme levels in comparison to NT females, possibly proportionate to gender differences in fetal testosterone levels across NT and ASD populations. The current results do, however, constrain the EMB theory by proposing that not all forms of systemizing are predominant in males, and consequently, that not all forms of systemizing are influenced by male sex hormones. This is further supported by the finding that the types of systemizing that are more predominant in females (i.e., insistence on sameness) appear to be relatively distinct (i.e., only weakly related) to the more traditional types of systemizing that are predominant in males (i.e., analytical tendencies).

General Discussion

Results from two experiments suggest that the systemizing trait of autism, as measured by the Systemizing Quotient-Revised (Wheelwright et al., 2006), contains a two-factor structure that differentially predicts a shift from reliance on global to local visual cues in individuals who score high on both factors. Importantly, susceptibilities to the local orientation contrast and global visuovestibular RFI effects were uncorrelated, suggesting that these may be two orthogonal perceptual processes. This finding has important implications for the Weak Central Coherence (WCC, Happe & Frith, 2006) and Enhanced Perceptual Functioning (EPF, Mottron et al., 2006) theories of autism in that it suggests that the local processing biases commonly reported in ASD may not arise due to global impairments (or reduced global biases). Rather, attenuated use of global information and over-reliance on local information can, in part, be explained by hyper-systemizing tendencies in ASD populations that are associated with both types of perceptual processing. Here, we found that different types of systemizing (analytical tendencies and insistence on sameness) differentially predict this global-to-local shift, with higher systemizing scores related to analytical tendencies predictive of attenuated susceptibility to the global visuovestibular effects of the rod-and-frame illusion, and higher systemizing scores related to insistence on sameness predictive of heightened susceptibility to the local orientation contrast effects. While these results were more strongly apparent for males, they nevertheless suggest that cognitive traits associated with ASD may, in part, account for distinct perceptual biases and processing styles observed in clinical populations. In addition, future studies examining local and global perceptual biases in ASD populations using NT-matched designs would benefit by using the SQ-R as a matched group variable in order to avoid the confound of variant systemizing tendencies and its modulatory relationship with local and global processing.

The finding of heightened systemizing tendencies in NT and ASD females related to an insistence on sameness also constrain the Extreme Male Brain (EMB, Baron-Cohen, 2002) theory of autism in suggesting that some forms of ASD symptomology may not always reflect extreme manifestations of male-typical traits, and consequently, that ASD may be better conceptualized as an extreme manifestation of a *systemizing* brain as opposed to an extreme manifestation of a *male* brain. Of course, since these results are based on examination of the distributions of the two SQ-R factors, confirmation of the factor structure of the SQ-R through replication and analysis of convergent associations with theoretically overlapping constructs is needed. The original SQ – from which the majority of items from the Analytical Tendencies factor are drawn – has been shown to correlate with performance on tests of intuitive physics (Dassonville et al., 2007), for which analytical abilities are a prerequisite. Similar analyses of convergent validity with constructs theoretically similar to the Insistence on Sameness factor (e.g., comparison with the Insistence on Sameness subscale of the ADI-R) would be beneficial in verifying the convergent validity of this factor. Here, it is interesting to note that autistic tendencies are often comorbid with obsessive-compulsive tendencies (Ivarsson & Melin, 2008; Russell, Mataix-Cols, Anson, & Murphy, 2005), and there are conceptual similarities between items on the Insistence on Sameness factor and items on self-report measures of obsessive-compulsive tendencies (e.g., the OCI-R, Foa, Huppert, Langner, Kichic, Hajcak, & Salkovskis, 2002). Indeed, both appear to measure specific aspects of restricted and repetitive behavior (e.g., the necessity to have items arranged in a particular way), and, consistent with the gender differences we observed on the Insistence on Sameness factor, some types of obsessive-compulsive tendencies have been found to be more prevalent in females (Labad, Menchon, Alonso, Segalas, Jimenez, Jaurrieta, Leckman, & Vallejo, 2008; Angst, Gamma, Endrass, Goodwin, Ajdacic, Eich, & Rossler, 2004). Interestingly, obsessive-compulsive tendencies have also been associated with a locally-oriented perceptual bias (Rankins, Bradshaw, & Georgiou-Karistianis, 2005), which closely resembles the relationship we found between Insistence on Sameness scores and heightened susceptibility to the local contextual cues of the rod-and-frame illusion.

These results also build upon the hyper-systemizing theory of autism (Baron-Cohen, 2006), which postulates that all types of systemizing (e.g., spatial, numerical, environmental) are amplified in ASD populations and lead to key behaviors in ASD. Specifically, consistent with this prediction, we found that the ASD group scored higher on both systemizing factors in comparison to the NT group, regardless of gender. In addition, the hyper-systemizing theory of autism suggests that the etiology of hyper-systemizing mechanisms in ASD may be explained by assortative mating (Baron-Cohen, 2006), in which ASD may be the result of having two high systemizers as parents. For example, both mothers and fathers of children with ASD tend to have occupations associated with high systemizing (Baron-Cohen et al., 1997) and show strong systemizing on the Embedded Figures Test (Baron-Cohen & Hammer, 1997), where performance on this test is predictive of autistic tendencies (as measured by the Autism-Quotient, Grinter et al., 2009; Grinter et al., 2009). Therefore, a possible implication of the current results is that hyper-systemizing tendencies related to both analytical tendencies and an insistence on sameness in ASD may result from the differential contributions of each type of systemizing from parents as a function of their gender, with systemizing in mothers of children with ASD predominantly characterized as an 'insistence on sameness' and systemizing in fathers of children with ASD predominantly characterized as an 'analytical' drive. While speculative, an individual with ASD may consequently inherit a distinct type of hyper-systemizing mechanism from each parent, the combinatory result of which may lead to several key behaviors in ASD (Baron-Cohen, 2006). One way in which this prediction could be tested would be to compare SQ-R factor scores in children with ASD with factor scores in their parents; it would be predicted that while both factor scores in children with ASD should correlate with parent scores, ASD scores on the Insistence on Sameness factor should correlate more strongly with their mothers' scores on this factor, while ASD scores on the Analytical Tendencies factor should correlate more strongly with their fathers' scores. This would explain why some types of systemizing that are more predominant in female cognitive phenotypes are present alongside extreme male neurophysiology in ASD, and further contribute to our understanding of the genetic influences associated with ASD.

CHAPTER III

INDIVIDUAL DIFFERENCES IN SYSTEMIZING TENDENCIES RELATED TO ‘ANALYTICAL TENDENCIES’ PREDICTS PERFORMANCE ON THE EMBEDDED FIGURES TEST

While Autism Spectrum Disorders (ASD) are often characterized by impairments or deficits in functioning, there are, remarkably, some tasks in which individuals with ASD exhibit preserved and sometimes even enhanced performance. For example, visual search abilities are often spared or even superior in individuals with ASD (O’Riordan, Plaisted, Driver, & Baron-Cohen, 2001), with such enhanced abilities being observed even at a very young age (Kaldy, Kraper, Carter, & Blaser, 2011). The most commonly used visual search task to assess such abilities in ASD is known as the Embedded Figures Test (EFT), in which an individual must locate a simple geometric shape embedded within a complex figure. In the original version of the task used by Witkin (1950), observers were shown a set of complex figures and had to identify which figure contained the simple target shape (Fig. 14A). In a modified version of the task, known as the Hidden Figures Test (Ekstrom et al., 1976), observers are shown five target shapes and must identify which target shape is located within the complex array (Fig. 14B). Due to the similarities in both versions of the task, we shall not distinguish them further (unless otherwise noted), but rather use the term Embedded Figures Test to refer to both variations of the task. Remarkably, individuals with ASD often exhibit superior performance on this task in that they locate the target faster (de Jonge, Kemner, & van Engeland, 2006; Mottron, Burack, Iarocci, Belleville, & Enns, 2003; Jolliffe & Baron-

Cohen, 1997; Shah & Frith, 1983) or more accurately (de Jonge et al., 2006) compared to neurotypical (NT) individuals.

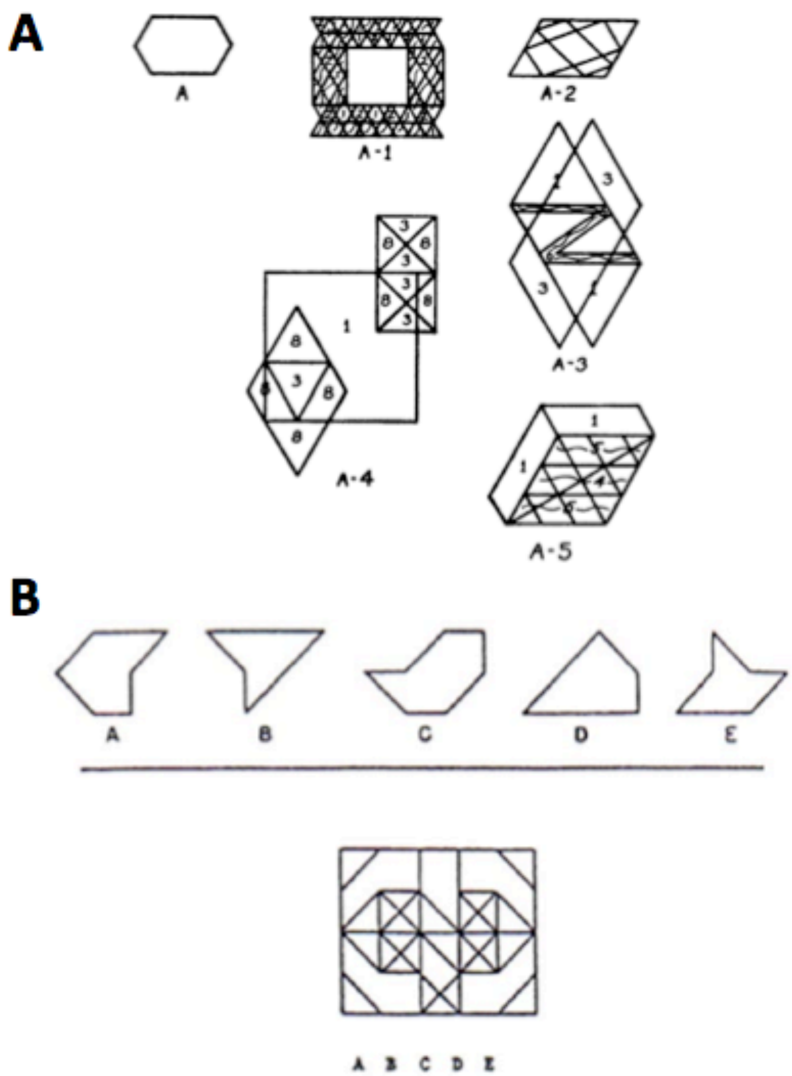

Figure 14. Examples of EFT and HFT stimuli. A) An example of the original EFT stimuli used by Witkin (1950). The numbers, which were not present in the actual stimuli, are used to denote different colors of the shapes. Observers reported which complex figure contained the simple shape (‘A’). B) An example of the HFT stimuli used by Ekstrom et al. (1976). Observers reported which simple shape (A-E) was contained in the complex figure.

Superior performance on the EFT in individuals with ASD has been proposed to be due to a disproportionate reliance on local and global visual cues, with imbalances driven by either a heightened reliance on low-level visual cues (i.e., enhanced perceptual functioning, Mottron, Dawson, Soulieres, Hubert, & Burack, 2006), an attenuated reliance on global contextual cues (i.e., weak central coherence, Happe & Frith, 2006), or some combination of the two. Accordingly, in the EFT, it is thought that a heightened sensitivity to the local features that define the target and/or an attenuated susceptibility to the contextual interference produced by the extraneous contours in the complex image may facilitate the process of disembedding the target shape from the complex array and result in superior performance.

Although local (i.e., featural) and global (i.e., contextual) perceptual biases may not be completely orthogonal, there have been attempts to dissociate the contributions of these mechanisms to EFT performance. For instance, Jarrold and colleagues (2005) found that EFT performance in an ASD sample was correlated with search time in a feature search task but was unrelated to search time in a conjunctive search task (in which features had to be contextually integrated at a higher level of processing). Likewise, Mottron and colleagues (2003) found that individuals with ASD, compared to matched controls, had superior performance on a disembedding task, but had similar performance on hierarchical and configural processing tasks (i.e., failed to exhibit any global impairments). This could suggest that a featural or locally-oriented processing bias underlies superior performance on the EFT. Indeed, activations in primary visual cortex have been found to be enhanced in individuals with ASD during search tasks compared to NT controls (Manjaly et al., 2007). However, in addition to enhanced recruitment of low-level perceptual processes, there is evidence that individuals with ASD may engage higher-level processes (e.g., contextual integration) to a lesser extent than NT controls.

For example, neuroimaging studies have found reduced cortical involvement (e.g., in temporal regions, Malisza, Clancy, Shiloff, Foreman, Holden, Jones, Paulson, Summers, Yu, & Chudley, 2011; Lee et al., 2007; in parietal regions, Malisza et al., 2011; Lee et al., 2007, and in prefrontal regions, Ring et al., 1999; Lee et al., 2007) during EFT performance in individuals with ASD compared to NT controls, and activations in parietal regions, in particular, have been associated with processing the contextual elements of an array (Walter & Dassonville, 2008; Walter & Dassonville, 2011). Therefore, it may be the case that both heightened sensitivity to local cues and attenuated susceptibility to global cues contribute to superior performance on the EFT.

Not all investigations have found superior EFT performance in ASD samples, though. For instance, White and Saldana (2011) found that individuals with ASD performed similar to NT controls on both accuracy and reaction time measures of EFT performance. Likewise, Kaland, Mortensen, and Smith (2007) found that EFT performance in individuals with high-functioning autism was slower (but not statistically different) compared to NT controls. A possible source for these inconsistent findings across studies is the variability in ASD severity (i.e., use of different subgroups across the autism spectrum) and the heterogeneity in symptoms displayed, particularly when small sample sizes are used to compare clinical and NT groups. Accordingly, variability in specific traits (i.e., symptoms) across the autism spectrum may modulate the magnitude of observed differences in EFT performance across group comparison studies. Indeed, there are a great deal of individual differences in EFT performance even in NT populations (Witkin, 1950; Hock, Gordon, & Marcus, 1974; Glicksohn & Kinberg, 2009), and the traits that drive these individual differences may be important variables to account for when assessing EFT performance in ASD.

An alternative methodological approach to studying the relationship between ASD and EFT performance while avoiding the difficulties associated with group comparisons between ASD and NT populations is to examine how variability in autistic tendencies that form a continuum in the general population can account for EFT performance. For example, NT individuals who score high on the Autism Quotient (AQ, Baron-Cohen et al., 2001) – a self-report questionnaire designed to measure tendencies related to autistic symptomology in the general population – have been found to be significantly faster and more accurate on the EFT compared to individuals who score low on the AQ (Grinter et al., 2009). Surprisingly, Russell-Smith and colleagues (2012) found that superior EFT performance in NT individuals was most strongly associated with high scores on the 'social skills' subscale of the AQ, and was not related to the 'attention to detail' subscale.

While the AQ provides a measure of general autistic tendencies, the specific trait of systemizing, or the tendency to think of things in a very analytical, mechanical way, has also been found to predict perceptual biases similar to those observed in ASD populations. For example, Walter, Dassonville, and Bochsler (2009) found that higher scores on the Systemizing Quotient (a self-report questionnaire developed by Baron-Cohen et al., 2003) negatively covaried with susceptibility to visual illusions driven by contextually-induced distortions of an observer's reference frame, suggesting that systemizing tendencies, which are known to be hyper-expressed in ASD (Baron-Cohen et al., 2003), are related to the relative balance in the use of local and global visual cues.

More recently, work from our lab (Chapter II) has found a two-factor structure to the Systemizing Quotient-Revised (SQ-R, Wheelwright et al., 2006) that is differentially predictive of a heightened sensitivity to local cues and an attenuated susceptibility to global contextual cues. Specifically, we found that higher scores on an Analytical Tendencies factor were associated with decreased susceptibility to the global visuovestibular effects of the rod-and-frame illusion, while higher scores on an Insistence on Sameness factor were associated with increased susceptibility to the low-level orientation contrast effects that contribute to the illusion.

In the current study, we therefore sought to examine how variability in these systemizing factors is predictive of EFT performance in the general population. If EFT performance is facilitated by a heightened sensitivity to the local features of the target (i.e., a local processing bias), we expect performance to correlate with scores on the Insistence on Sameness factor of the SQ-R, since this factor has previously been associated with heightened sensitivity to local cues. If EFT performance is facilitated by an attenuated susceptibility to the extraneous context of the search array (i.e., decreased global processing), we expect performance to correlate with scores on the Analytical Tendencies factor, since this factor has previously been associated with decreased susceptibility to the global effects of the RFI.

Experiment 1: Embedded Figures Test and Systemizing Factors

Methods

Participants. One hundred and nine participants (48 males, 61 females) were recruited from the University of Oregon human subjects pool. Participants received course credit for their participation. The average age of the sample was 19.9 years (*SD* = 2.4), and all participants had normal or corrected-to-normal vision and no known neurological deficits or disorders. All participants provided informed consent in accordance with the guidelines of the University of Oregon Institutional Review Board.

Systemizing Questionnaire. Participants completed a computer-based version of the Systemizing Quotient-Revised (SQ-R, Wheelwright et al., 2006). The SQ-R consists of 75 self-report questions that assess an individual's cognitive tendency to think in a very mechanical, systematic way, such as the proclivity to analyze, integrate, and systematically derive the order, variables, and operations within complex systems (e.g., "In maths, I am intrigued by the rules and patterns governing numbers", "When I learn about a new category, I like to go into detail to understand the small differences between different members of that category"). On the SQ-R, half of the items are worded so that a high score is based on agreement with an item, and the other half so that a high score is based on disagreement with an item. After recoding reverse-scored items, higher scores on the SQ-R are indicative of higher systemizing tendencies. The Analytical Tendencies factor of the SQ-R contains 26 items, while the Insistence on Sameness factor contains 12 items (Tables 2 and 3, Chapter II), with total scores on each factor calculated in the same way as overall SQ-R scores. The questionnaire was completed on a Macintosh computer (Apple Computers, Cupertino, CA) and took 10-15 min. for participants to complete.

Embedded Figures Test Procedure. Participants were seated with the head stabilized in chin and forehead rests and the eyes 42 cm away from a screen measuring 31 by 49.5 cm in a darkened room. Participants performed a variant of the EFT in which they had to locate one of two potential target objects embedded within a complex array

(Fig. 15). The EFT arrays were either square (8.5 by 8.5 cm; 11.4° per side) or rectangular (6.5 by 10.5 cm; 8.8° by 14°) in shape. All EFT line segments were white presented against a black background. Before performing the task participants were shown an instruction screen that consisted of the two target shapes – a 'left pointing' or 'right pointing' arrow – and a sample array in which the target was outlined in red (in actual trials, the target was never outlined). Participants were instructed to press the 'f' key on the keyboard in front of them if the array contained the left pointing arrow and to press the 'j' key if the array contained the right pointing arrow. Participants were told that the targets would always appear in the same orientation and configuration as shown on the instruction screen (i.e., targets would never appear rotated or inverted). The isolated targeted shapes (Figure 15A) only appeared on the instruction screen; on the actual trials, only the search array was shown (Figure 15B).

At the onset of each trial, the search array appeared on the screen and participants were instructed to press the corresponding target key ('f' or 'j') as soon as they located the target (i.e., they were instructed to perform as quickly and accurately as possible). The keypress terminated the trial, and following a 1-second delay, the next trial began with the onset of another array. On each trial, participants had a maximum of 10 s to search for the target; if no response was made within those 10 s, the search array was extinguished and participants were cued to make a response. Every trial contained either the left or right target (i.e., there were no 'target absent' trials), with target orientation equally balanced across all trials. Participants completed 1 practice trial and 91 experimental trials. Accuracy was computed as the percentage of correct responses across experimental trials, and mean reaction time was computed for correct trials only. The order of tasks (EFT, SQ-R) was counterbalanced across participants.

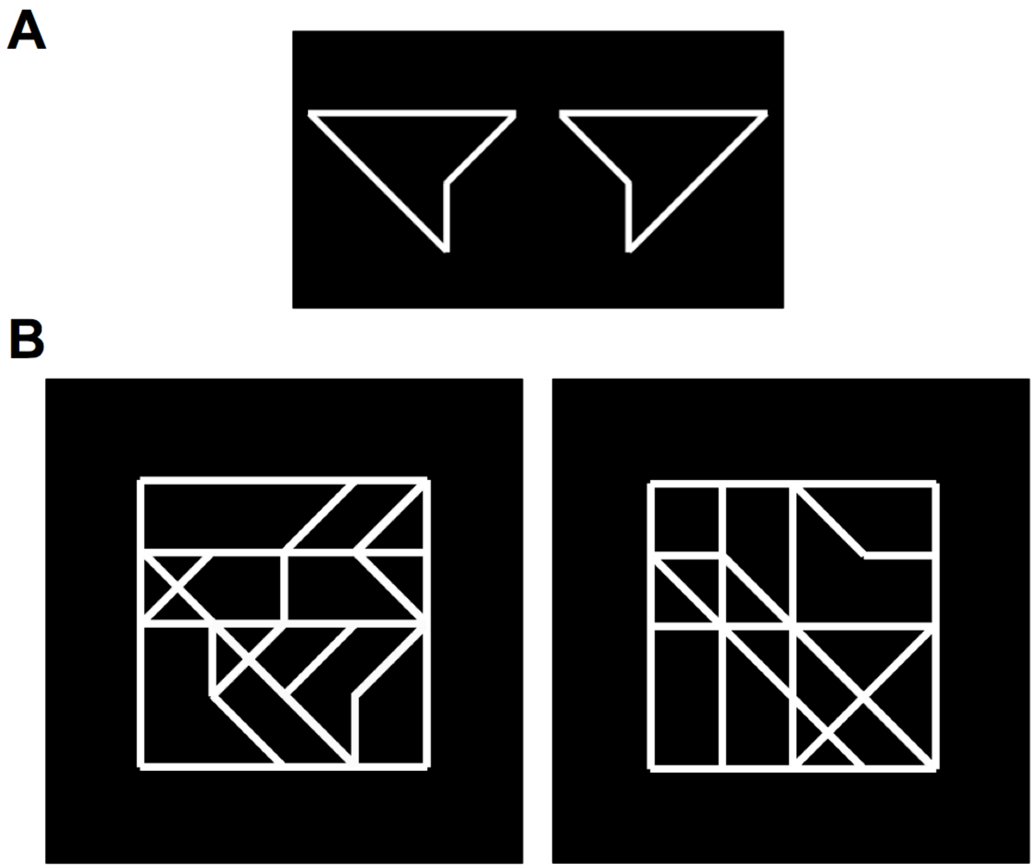

Figure 15. Sample stimuli used for the EFT. A) The two targets (‘left pointing’ and ‘right pointing’ arrows) of the EFT that could appear within the complex array. B) Two sample EFT search arrays. The array on the left contains the ‘left-pointing’ target and the array on the right contains the ‘right-pointing’ target. On experimental trials, only one search array was shown, and participants had to report whether the array contained the ‘left pointing’ target or the ‘right pointing’ target.

Results

Scores on the Systemizing Quotient-Revised (SQ-R) were normally distributed and ranged from 19 to 113 (M = 58.7, SD = 19.5). On the EFT, mean accuracy (70.50%, SD = 13.54%) was significantly above chance performance (i.e., 50%, $t(108) = 15.81$, $p < .001$). The mean reaction time (for correct trials) was 5056 ms (*SD* = 1459 ms).

Bivariate correlations were conducted comparing total SQ-R scores to EFT accuracy and reaction time. A significant correlation was found between the SQ-R and EFT accuracy ($r(107) = .229$, $p < .02$) in that higher SQ-R scores were associated with greater accuracy on the EFT (Fig. 16). No correlation was found between the SQ-R and reaction time on the EFT ($r(107) = -.143$).

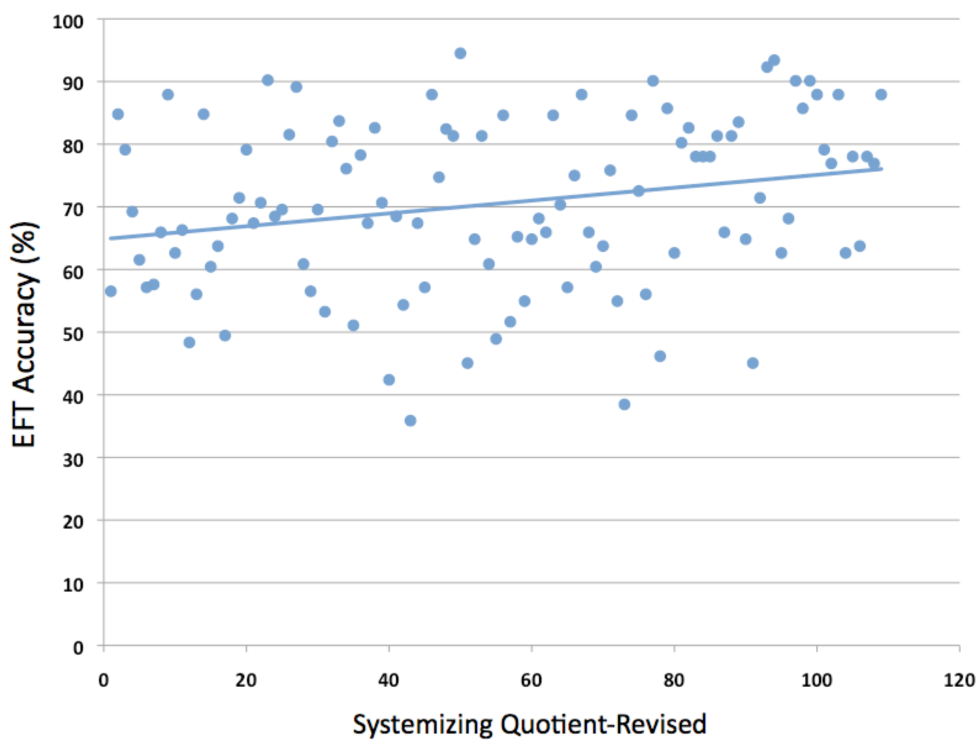

Figure 16. Scatterplot of the relationship between SQ-R scores and accuracy on the EFT. Higher systemizing scores were significantly predictive of greater accuracy on the EFT, $r(107) = .229$, $p < .02$.

Bivariate correlations were then conducted comparing EFT performance and the Analytical Tendencies and Insistence on Sameness SQ-R factors. For the Analytical Tendencies factor, a significant correlation was found with accuracy ($r(107) = .282$, $p <$

.01) in that higher factor scores were associated with more accurate performance on the EFT (Fig. 17A). Analytical Tendencies scores were unrelated to reaction time ($r(107) = -.155$). For the Insistence on Sameness factor, no significant correlations were found with either accuracy ($r(107) = -.008$; Fig. 17B) or reaction time ($r(107) = -.025$) on the EFT.

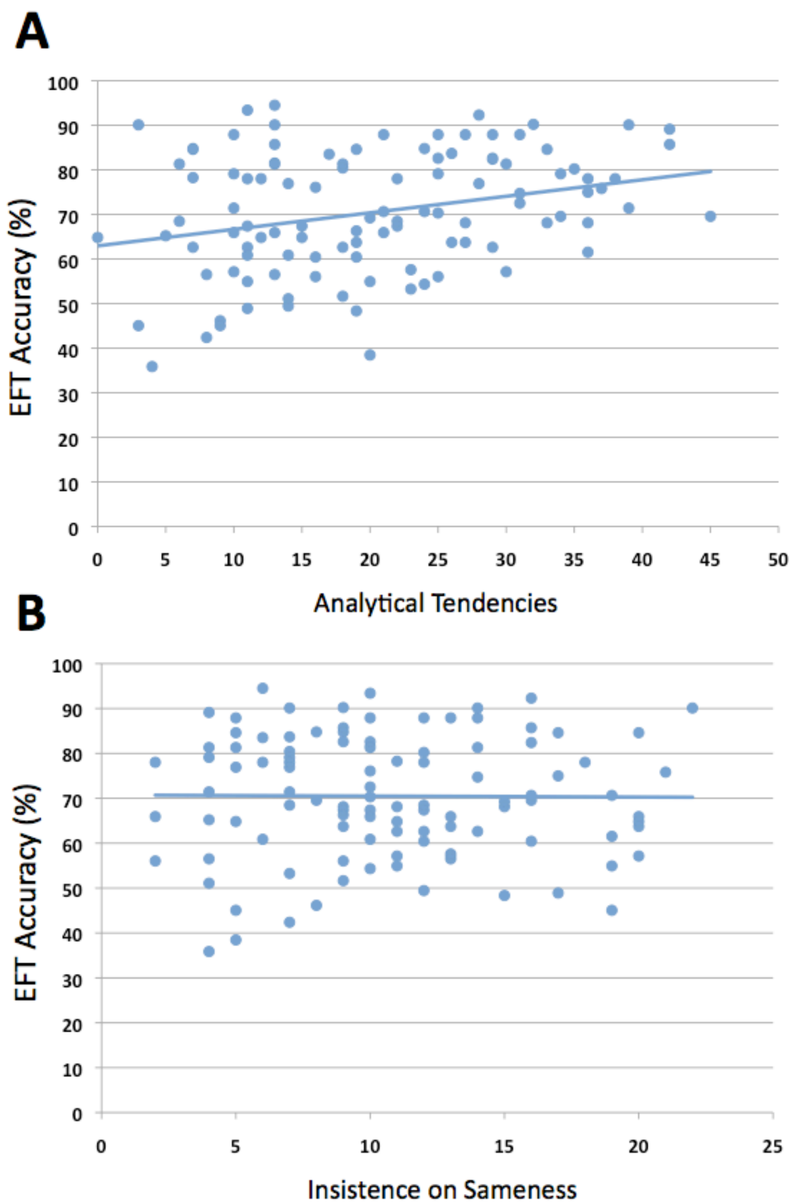

Figure 17. Scatterplots of the relationship between Systemizing Factors and accuracy on the EFT. A) Higher scores on the Analytical Tendencies factor were significantly associated with greater accuracy on the EFT, $r(107) = .282$, $p < .01$. B) Insistence on Sameness scores were unrelated to EFT accuracy, $r(107) = -.008$.

Discussion

Enhanced performance on the EFT in individuals with Autism Spectrum Disorders (Jolliffe & Baron-Cohen, 1997), or healthy individuals with high levels of autistic tendencies (Baron-Cohen et al., 2001), has often been attributed to perceptual biases associated with either weak central coherence (e.g., reduced tendencies to integrate the contextual elements of the search array), enhanced perceptual functioning (e.g., heightened sensitivity to the local features of the target), or some combination of the two. In the current study, we compared scores on the SQ-R, and on the two factors of the SQ-R (Analytical Tendencies and Insistence on Sameness), to performance on the EFT in order to examine how these cognitive tendencies may account for superior performance. While systemizing scores in general were associated with enhanced accuracy on the EFT, this relationship seemed to rely most heavily on the Analytical Tendencies factor, which was able to account for more variance in EFT performance, with higher scores predictive of greater accuracy. Scores on the Insistence on Sameness factor were unrelated to EFT accuracy, and neither factor (nor the SQ-R overall) was predictive of reaction time.

Higher analytical tendencies in the general population have previously been associated with decreased susceptibility to the global visuovestibular effects of the Rod-and-Frame illusion (Chapter II), which suggests that this cognitive tendency may be related to decreased susceptibility to global contextual cues. If so, the current association between the Analytical Tendencies factor and EFT accuracy suggests that superior EFT accuracy may be due to decreased sensitivity to the global contextual elements of the search array (which may facilitate the process of disembedding the target from the extraneous context of the array), as opposed to a heightened sensitivity to the local features of the target. While decreased interference from the extraneous context of the array may facilitate the accurate identification of the target, the current results indicate that this process may not necessarily benefit search time, as no correlations with reaction time were found. In any case, the current results suggest that a common cognitive disposition (i.e., analytical tendencies) may be related to both enhanced performance on the EFT and decreased sensitivity to the global effects of the rod-and-frame illusion, which implicates a common perceptual bias associated with this trait that may underlie performance on both tasks. However, a direct comparison of rod-and-frame susceptibility and EFT performance was not made in Experiment 1. Therefore, in Experiment 2, we compared susceptibility to the local and global mechanisms that underlie the rod-and-frame illusion to EFT performance in order to more directly assess which perceptual mechanisms, if any, may underlie performance on both tasks.

Experiment 2: Embedded Figures Test and the Rod-and-Frame Illusion

While both the Weak Central Coherence (Happe & Frith, 2006) and Enhanced Perceptual Functioning (Mottron et al., 2006) theories predict that individuals with autism should succumb less to visual illusions due to a locally-oriented processing bias that results in attenuated susceptibility to the context of the visual inducer, findings on reduced illusion susceptibility in autism have been mixed. Specifically, while some studies have indeed found that individuals with autism are less susceptible to certain types of visual illusions compared to healthy controls (Happe, 1996; Bolte, Holtmann, Poustka, Scheurich, & Schmidt, 2007), others have found no differences in susceptibility (Ropar & Mitchell, 1999, 2001). Using an individual differences approach, however, Walter and colleagues (2009) found that higher systemizing scores in the general population were predictive of decreased susceptibility to illusions driven by distortions in an observer's egocentric frame of reference. Similarly, the experiments presented in Chapter II found that the Analytical Tendencies factor of the SQ-R, in particular, was associated with decreased susceptibility to the global visuovestibular effects of the rod-and-frame illusion (RFI).

Given the findings from Experiment 1, demonstrating that greater analytical tendencies were associated with enhanced performance on the EFT, decreased susceptibility to the rod-and-frame illusion may therefore also be associated with enhanced performance on the EFT. Indeed, Witkin and colleagues (1954), in their early studies on space orientation, used performance on both the EFT and RFI to characterize different cognitive styles. Individuals who were 'field independent' were found to perform well on the EFT while also succumbing less to the RFI. Conversely, individuals who were 'field dependent' had lower levels of performance on the EFT and were more susceptible to the RFI. It was presumed that the concept of field dependence-independence – a cognitive style thought to be relatively stable – measured one's ability to separate, or disembed, an element from the context of the visual field (Witkin, Dyk, Faterson, Goodenough, & Karp, 1962). While such an ability is presumed to underlie performance on both the EFT and RFI, these tasks may not necessarily be equivalent measures of field dependence-independence (Bergman & Engelbrektson, 1973). However, conceptualization of field dependence-independence using the RFI has classically entailed an overall measure of susceptibility to the illusion that is then compared to EFT performance. The RFI, however, is driven by two separate visual processing mechanisms that disproportionately contribute to the illusion as a function of the size of the surrounding frame. When the illusion is driven by a large inducing frame, the tilt of the frame produces a visuovestibular distortion in the observer's frame of reference, such that the perception of vertical is tilted in the same direction as the frame (Ebenholtz & Benzschawel, 1977; Sigman, Goodenough, & Flanagan, 1979; Cian, Esquivie, Barraud, & Raphel, 1995). This global visuovestibular distortion in the observer's frame of reference causes the rod within the frame to appear tilted in the opposite direction (Ebenholtz & Benzschawel, 1977; Spinelli, Antonucci, Goodenough, Pizzamiglio, & Zoccolotti, 1991; Zoccolotti, Antonucci, Goodenough, Pizzamiglio, & Spinelli, 1992).

In contrast to this global distortion of the observer's egocentric reference frame, a different mechanism contributes to a qualitatively similar effect (i.e., a misperception of the rod's tilt in the direction opposite the tilt of the frame) when a small inducing frame is used. This second mechanism involves low-level orientation contrast effects (Goodenough, Oltman, Sigman, Rosso, & Mertz, 1979; Wenderoth & Johnstone, 1987; Cian et al., 1995; Spinelli, Antonucci, Daini, & Zoccolotti, 1995) brought about by the mutual inhibition of neurons that encode the orientations of the rod and frame in early visual areas (Blakemore, Carpenter, & Georgeson, 1970; Carpenter & Blakemore, 1973; Spinelli et al., 1995; Poom, 2000; Chen, 2005). Smaller frame sizes tend to produce greater orientation contrast effects due to the increased proximity of the rod and frame (Coren & Hoy, 1986; Zoccolotti et al., 1993). It has been suggested that the local orientation contrast effects typically outweigh the global visuovestibular distortions in perceived vertical when the size of the frame has a visual angle of 10° or less (Spinelli et al., 1991), but small contrast effects may still be present for larger frames (Goodenough et al., 1979), and small distortions in perceived vertical may still occur for smaller frames (Gogel & Newton, 1975, Zoccolotti et al., 1993; Cian et al., 1995).

In order to better understand the visual processing mechanisms, or abilities, that underlie performance on both the RFI and EFT, we isolated and independently measured the local and global mechanisms that contribute to the RFI and compared susceptibility on each to EFT performance. Based on the findings from Experiment 1, we predict that greater accuracy on the EFT will be associated with decreased susceptibility to the global visuovestibular effect of the RFI with a large-inducing frame, but will be unrelated to the local orientation contrast effects with a small-inducing frame.

Methods

Participants. An additional 109 participants (46 male, 63 female) participated in Experiment 2. The mean age of the sample was 19.5 (*SD* = 1.9). Participation criteria and ethical protocols were the same as that described in Experiment 1.

Measures of Autistic Tendencies. In addition to the SQ-R, participants completed a computer-based version of the Autism Quotient (AQ, Baron-Cohen et al., 2001). The AQ is a self-report measure of general autistic tendencies (e.g., "I prefer to do things the same way over and over again") that have been found to form a continuum in the general population. The AQ was included in Experiment 2 to examine whether the relationship between systemizing tendencies and EFT performance is driven by general autistic tendencies or the specific trait of systemizing, independent of other autistic tendencies that are measured by the AQ. Specifically, the AQ contains 50 items that provide an overall measure of autistic tendencies (with higher scores indicative of greater autistic tendencies) related to five symptomatic domains: attention switching, attention to detail, social skills, communication and imagination. Each subscale contains 10 questions, with some items reverse coded so that higher scores (on each subscale and on the AQ overall) are indicative of higher levels of autistic tendencies. Both the AQ and SQ-R questionnaires were completed on a Macintosh computer (Apple Computers, Cupertino, CA) and took a total of 20-25 min. for to complete.

Embedded Figures Test Procedure. The stimuli and procedure for the EFT was the same as that described in Experiment 1.

Rod-and-Frame Procedure. An eye tracker (Eyelink 2000: SensoMotoric Instruments, Needham, Massachusetts, United States) was used to monitor gaze and eye movement during performance on all RFI tasks. Before each task, participants were calibrated on the eye tracker, which consisted of a grid of 13 visual targets. If the average error in fixation across the 13 targets was greater than 1°, the calibration was rejected and begun again. If the calibration began to slip mid-task, the experimenter stopped the task, recalibrated, and when calibration was again successfully achieved, the participant continued where they had left off.

Participants were seated with the head stabilized in chin and forehead rests, and the eyes 86.4 cm from a screen (Da-Lite Polacoat Ultra projection screen with a DA-100 diffusion coating) measuring 101.6 cm by 135.9 cm. Stimuli were back-projected (Electrohome Marquee 8500, with custom-fit HD145 lenses) onto the screen in a completely darkened room. The RFI stimuli were red in color and consisted of a circular fixation point (0.5° of visual angle) surrounded by a red circle (the response circle) measuring 13.7° in diameter with a width of 0.1°. The fixation point was intersected by a rod measuring 6.9° of visual angle in length and 0.2° in width. Surrounding the rod was either a small frame (8.6° for each side) or a large frame (35.9° for each side) that had a stroke width of 1.0° and a rotational tilt of either –15° or 15° from vertical (Fig. 2).

All participants completed the three RFI variants that were previously described in Chapter II (Fig. 1): a Perception task to measure the combined global visuovestibular and local orientation contrast effects of the illusion, a Saccade-to-Vertical task to isolate the global visuovestibular effects, and a Saccade-to-Rod task to isolate the local orientation contrast effects. For each task, following successful calibration on the eye tracker, participants first completed a practice session that only included the fixation point, the outer circle, and the rod (with the exception of the Saccade-to-Vertical task in which no rod was presented). No frame was present on the practice trials in order to allow participants to gain experience in each of the tasks without being exposed to the illusion itself. During the experimental trials when the frame was present, both frame sizes (8.6° or 35.9°) and tilts (–15° or 15°) were used in all tasks described below. The order of the tasks were counterbalanced across participants and took around 60 min to complete.

Perception Task. The Perception task measured the additive sum of the local orientation contrast and global visuovestibular effects that drive the RFI (Fig. 1). On each trial, participants were instructed to make a judgment about the perceived orientation of the rod. At the onset of each trial, the fixation point, response circle, and the tilted frame (– 15° or 15°) appeared on screen. (While the inclusion of the response circle was necessary to measure the local and global effects in the Saccade-to-Rod and Saccade-to-Vertical tasks, respectively, note that it does not provide any orientation cues and was only included in the Perception Task to provide consistency in stimulus parameters across tasks. Participants were instructed to direct their gaze to the fixation point before starting a trial and to maintain this gaze location throughout the task (a trial was aborted if fixation deviated by more than 1° from the fixation point, or if a blink occurred). While fixating on the central fixation point, a button press on a gamepad controller (under the left thumb) initiated the onset of the trial. After 200 ms, a rod that was tilted either – 6°, – 4°, – 2°, – 1°, 0°, 1°, 2°, 4°, or 6° from vertical (and centered on the fixation point) would appear on screen for 300ms, after which both the rod was extinguished (500 ms from trial onset). Participants then judged whether they perceived the rod to be tilted to the "left" (counterclockwise) or "right" (clockwise) and indicated their response by pressing the left or right trigger on the gamepad controller. There were 10 trials for each combination of frame tilt (– 15° or 15°), frame size (small or large), and rod orientation (9 tilts), with 360 trials total (10 blocks, 36 trials per block).

Perceptual reports for each frame tilt were quantified by fitting a psychometric function to the proportion of "clockwise" responses in order to derive the point of subjective equality (PSE) – the orientation of the rod that the participant reported as being rotated clockwise and counterclockwise with equal likelihood – using the equation:

$$\text{proportion “clockwise” responses} = e^{((\text{rodtilt}-\text{PSE})/\text{tau})}/(1+e^{((\text{rodtilt}-\text{PSE})/\text{tau})})$$

where *rodtilt* was the orientation of the rod, *PSE* was the point of subjective equality, and *tau* was the space constant of the psychometric function. RFI susceptibility was operationalized as the difference in the PSEs for the clockwise and counterclockwise frame tilts, calculated separately for small and large frames, where higher values indicate greater susceptibility to the illusion and lower values indicate reduced susceptibility to the illusion.

Saccade-to-Vertical Task. The Saccade-to-Vertical task isolated the global visuovestibular effect of the RFI (Fig. 1). The task consisted of the same stimulus parameters as in the Perception task, except that no rod was presented (and therefore, no local orientation contrast effects could occur). In this task, participants were instructed to make a saccade (cued by the offset of the fixation point 500 ms after the button press) from the fixation point to the top of the circle (i.e., where they believed a vertical line passing through the fixation point would intersect with the circle. There were 44 trials total (11 trials for each frame size and frame tilt), and trials were aborted if blinks occurred, or if participants looked away from the fixation point before the offset of the fixation point (aborted trials were rerun later in the experiment).

Performance in the Saccade-to-Vertical task was operationalized by calculating the difference in the mean rotational errors (the mean difference between the saccade vector, plotted from the fixation point to the final eye position, and true vertical) for left- and right-tilted frames, where higher values indicate larger errors in perceived vertical, or greater susceptibility to the global visuovestibular effects of the frame. Susceptibility was calculated for both small- and large-frame versions of the task. Here, large-frame susceptibility is expected to provide a more sensitive measure of global processing than small frames due to greater visuovestibular distortions in perceived vertical that occur with a large inducing frame (Ebenholtz & Benzschawel, 1977).

Saccade-to-Rod Task. The Saccade-to-Rod task (Fig. 1) is designed to isolate the local orientation contrast effects of the RFI (the task is immune to the global visuovestibular effects of the illusion since the saccade is made within the same distorted reference frame that is used to encode rod orientation; Dassonville & Bala, 2004; Dassonville, Bridgeman, Bala, Thiem, & Sampanes, 2004; Dassonville, Sanders, & Capp, 2009). The task consisted of the same stimulus parameters and presentation time course as in the Perception task, with the exception of different rod orientations (– 5°, – 3°, – 1°, 0°, 1°, 3°, 5°). In this task, the offset of the fixation point (500ms from trial onset) cued participants to make a saccade to the point on the outer circle that would be intersected by the rod if it were extended upward (Fig. 1). After the saccade, a button press (on the gamepad controller) prompted the computer to record the saccade vector and terminate the trial.

The Saccade-to-Rod task consisted of 140 trials (5 blocks with 28 trials per block). On each trial, the angle of rotation of a vector plotted from the fixation point to the final eye position on the circle (where the participant perceived the rod to intersect the circle) was calculated. Performance in the Saccade-to-Rod task was operationalized by calculating the difference between the mean rotational errors (the mean difference between the saccade vector and the rod vector) for left- and right-tilted frames, where higher values indicate larger orientation contrast effects, or greater susceptibility to the local effects of the RFI. Susceptibility was calculated for both small- and large-frame versions of the task, where small frames are expected to provide a more sensitive measure of the orientation contrast effects than large frames due to the closer proximity of the rod to the frame (Zoccolotti, Antonucci, & Spinelli, 1993).

The order of tasks (AQ, SQ-R, EFT, RFI Perception, Saccade-to-Vertical, and Saccade-to-Rod) was counterbalanced across participants and took around 90-120 min. to complete. On the RFI perception task, three participants were excluded from the analyses due to psychometric fits that failed to cross 50% on the y-axis, which prevented the calculation of the PSE.

Results

Scores on the Autism Quotient (AQ) ranged from 3 to 35 (M = 15.9, SD = 5.4), while scores on the Systemizing Quotient-Revised (SQ-R) ranged from 16 to 108 (M = 58.6, SD = 18.8). On the EFT, mean accuracy (73%, SD = 12.8%) was significantly above chance performance (i.e., 50%, $t(108) = 18.73$, $p < .001$). The mean reaction time (for correct trials) was 4936 ms (SD = 1482 ms).

The RFI Perception task was able to induce a significant distortion in the perceived orientation of the rod with both a small (mean difference in PSEs = 4.5º, SD = 1.8º, $t(105) = 25.95$, $p < .001$) and large (M = 3.2º, SD = 1.6º, $t(105) = 20.60$, $p < .001$) inducing frame. On the Saccade-to-Vertical task, the tilted frame induced a significant shift in perceived vertical with both small (mean difference in rotational errors = 3.3º, SD = 2.3º, $t(108) = 10.64$, $p < .001$) and large (M = 1.8º, SD = 2.4º, $t(108) = 18.73$, $p < .001$) inducing frames. Similarly, on the Saccade-to-Rod task, the tilted frame significantly biased saccades aimed in the direction of the rod with both small (mean difference in rotational errors = 2.3º, SD = 2.1º, $t(108) = 11.29$, $p < .001$) and large (M = .9º, SD = 1.7º, $t(108) = 5.31$, $p < .001$) inducing frames.

Bivariate correlations were first conducted comparing AQ and SQ-R scores to EFT performance. Scores on the AQ were unrelated to EFT accuracy ($r(106) = .09$) or reaction time ($r(106) = -.07$), and no significant correlations were found between EFT performance and any of the AQ subscales ($r(106) < .15$). Similarly, scores on the SQ-R were not significantly associated with EFT accuracy ($r(106) = .14$) or reaction time ($r(106) = -.13$). Higher scores on the Analytical Tendencies factor of the SQ-R, however, were significantly associated with greater EFT accuracy ($r(106) = .22$, $p < .03$; Fig. 18A), replicating the results from Experiment 1. Analytical Tendencies were not associated with EFT reaction time ($r(106) = -.10$), and Insistence on Sameness scores were unrelated to either EFT accuracy ($r(106) = -.10$; Fig. 18B) or reaction time ($r(106) = -.13$).

Bivariate correlations were then conducted comparing measures of RFI susceptibility to EFT performance. On the Perception task, small and large frame susceptibility was unrelated to EFT accuracy ($r(107) = -.11$ and $r(107) = -.12$, respectively). On the Saccade-to-Vertical task, however, reduced susceptibility to the large frame was significantly associated with greater accuracy on the EFT ($r(107) = -.213$, $p < .03$; Fig. 19A). For small frame performance on the Saccade-to-Vertical task, a marginally significant association was found in that, similar to large frames, reduced susceptibility was predictive of greater EFT accuracy ($r(107) = -.186$, $p = .051$). In the Saccade-to-Rod task however, small and large frame performance was unrelated to accuracy on the EFT (small frames: ($r(107) = -.156$, Fig. 19B; large frames: $r(107) = -.115$).

For EFT reaction time, marginally significant associations were found, wherein decreased susceptibility to small and large frame versions of the RFI perception task were predictive of faster reaction times on the EFT ($r(107) = .19$, $p = .051$ and $r(107) = .18$, p

= .061, respectively). A direct comparison of EFT reaction time and the global visuovestibular component in the large frame Saccade-to-Vertical task was also of marginal significance ($r(107) = .17$, $p = .077$), with larger distortions of subjective vertical associated with slower EFT reaction times. However, performance in the small frame Saccade-to-Vertical task was not related to EFT reaction time ($r(107) = -.12$, $p = .23$), nor were performances in either the small or large frame versions of the Saccade-to-Rod task ($r(107) = .14$, $p = .13$ and $r(107) = .15$, $p = .11$, respectively).

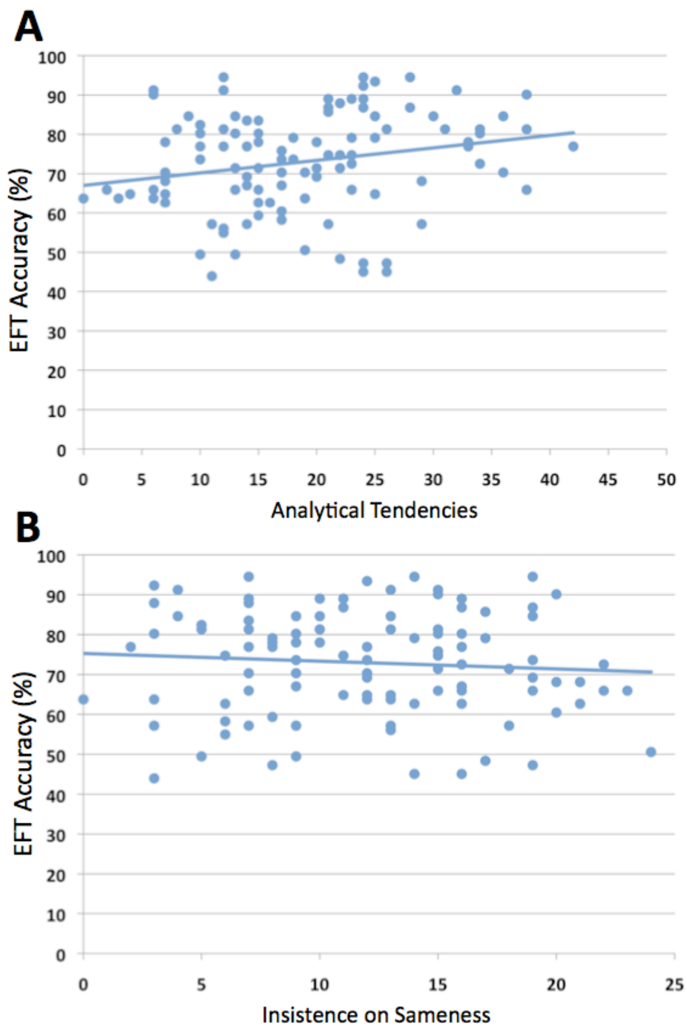

Figure 18. Scatterplots of the relationship between Systemizing factors and accuracy on the EFT in Experiment 2. A) Higher scores on the Analytical Tendencies factor were associated with greater accuracy on the EFT, $r(106) = .22$, $p < .03$. B) Insistence on Sameness scores were unrelated to EFT accuracy, $r(106) = -.10$.

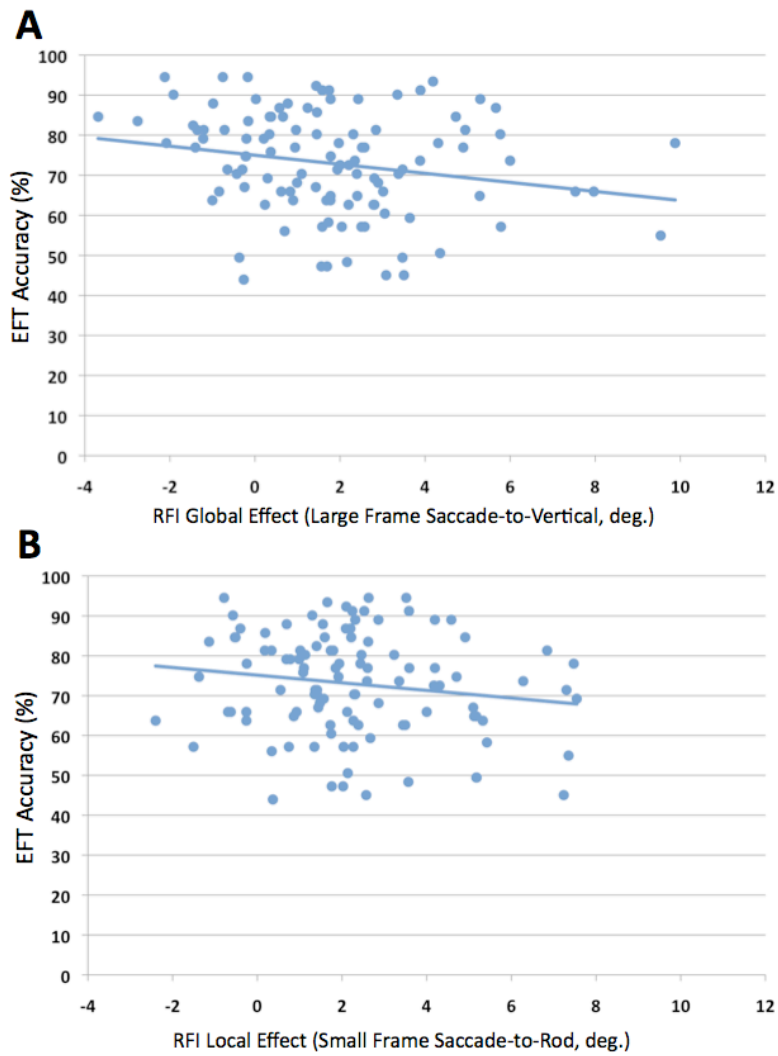

Figure 19. Scatterplots of the relationship between accuracy on the EFT and susceptibility to the local and global effects of the RFI. A) Reduced susceptibility to the global visuovestibular effect was significantly associated with greater EFT accuracy, $r(107) = -.213$, $p < .03$. B) Local orientation contrast effects were unrelated to EFT accuracy, $r(107) = -.156$.

Discussion

Superior performance on the EFT in individuals with ASD (Jolliffe & Baron-Cohen, 1997) has been attributed to reduced tendencies to perceptually integrate the contextual configurations of the search array (i.e., attenuated global processing), heightened sensitivity to the local cues of the target (i.e., enhanced low-level perceptual functioning), or some combination of the two. In a large sample of participants from the general population, we compared EFT performance to the local and global mechanisms that contribute to the RFI in order to examine the perceptual mechanisms that underlie enhanced performance on the EFT. While Witkin and colleagues (1954) initially found a relationship between RFI susceptibility and EFT performance (i.e., reduced susceptibility was associated with enhanced EFT accuracy), we failed to replicate this relationship. In our variant of the EFT, however, observers had a more limited viewing time of the EFT stimuli (10 s), which may have induced an added time pressure during the search process. Consequently, while we failed to find a relationship between EFT accuracy and RFI susceptibility, we did find marginally significant associations between EFT reaction time and RFI susceptibility (on both small- and large-frame versions) in that faster search times were associated with reduced susceptibility.

However, when the isolated measures of the mechanisms that drive the RFI were examined (Saccade-to-Vertical and Saccade-to-Rod tasks), we found that reduced susceptibility to the global visuovestibular effects (i.e., distortions in perceived vertical induced by the tilt of the surrounding frame), but not local orientation contrast effects, did significantly predict enhanced accuracy on the EFT. While these results are therefore consistent with those of Witkin and colleagues (1954) who found an association between EFT accuracy and perceptual susceptibility to the RFI, we extend these findings by showing that susceptibility to the global visuovestibular effects of the RFI in particular are associated with EFT performance, and that the low-level orientation contrast effects that contribute to the RFI are unrelated to EFT performance. Accordingly, these findings suggest that EFT performance is facilitated by a reduced susceptibility to the contextual gestalt of the search array, and implicate a common underlying neural mechanism for contextual processing in both EFT and RFI tasks.

While a wide range of cortical regions and networks are active during EFT performance (Malisza et al., 2011; Walter & Dassonville, 2011; Lee et al., 2007; Manjaly et al., 2007; Ring et al., 1999), there is evidence that some of these same regions are active during contextual processing of illusions. Specifically, Walter and Dassonville (2008) found bilateral activations in superior parietal cortex during the contextual processing associated with the illusion known as the induced Roelofs effect, in which a visible frame offset from the observer's midline causes biased perceptions of object locations by distorting the egocentric reference frame and the subjective midline (Roelofs, 1935; Dassonville & Bala, 2004; Dassonville et al., 2004). Since both the induced Roelofs effect and the RFI are driven by a distortion in an observer's egocentric reference frame, it is likely that a common neural region underlies contextual processing of the visual inducer in both tasks. Indeed, Lester and Dassonville (2014) recently found that the use of slow repetitive transcranial magnetic stimulation to deactivate right superior parietal cortex – the same region involved in processing the context of the Roelofs-inducing frame – significantly decreased susceptibility to the RFI. Moreover, this same parietal regions has been found to be active during EFT performance (Walter & Dassonville, 2011). The existence of a cortical site that is involved in processing the contextual cues involved in both illusory distortions of the egocentric reference frame and performance of the EFT makes the findings of a relationship between individual differences in EFT performance and susceptibility to the visuovestibular effects of the EFT unsurprising. In addition, the lack of a relationship between EFT performance and the local orientation contrast effects of the RFI is also unsurprising, given that orientation contrast effects are thought to rely on processes within a different cortical structure, namely, primary visual cortex, with mutual inhibition among orientation-selective cells driving the distortion in the perceived tilt of the rod (Blakemore, Carpenter, & Georgeson, 1970; Carpenter & Blakemore, 1973; Spinelli et al., 1995; Poom, 2000; Chen, 2005).

General Discussion

While performance on the EFT is often found to be superior in individuals with autism (de Jonge, Kemner, & van Engeland, 2006; Mottron, Burack, Iarocci, Belleville, & Enns, 2003; Jolliffe & Baron-Cohen, 1997; Shah & Frith, 1983), studies have been mixed, with some reports suggesting individuals with autism perform similar to healthy controls (White & Saldana, 2011; Kaland, Mortensen, & Smith, 2007). Accordingly, alternative methodological approaches that avoid the potential confounds of the group comparison design (e.g., small sample sizes, unmatched variables, heterogeneity in types and severity of autistic symptomology) have examined how variance in autistic tendencies that are known to form continua across the general population can account for EFT performance. In the current study, we found that the cognitive trait of systemizing (Wheelwright et al., 2006) is predictive of performance on the EFT. Specifically, based on the previous finding of a two-factor structure to the SQ-R (Chapter II), we found that a form of systemizing related to analytical tendencies was predictive of EFT performance, with higher trait levels associated with more accurate performance. In contrast, a different form of systemizing – insistence on sameness – was unrelated to EFT performance.

Interestingly, we found that general autistic tendencies, as measured by scores on the AQ (Baron-Cohen et al., 2001), were unrelated to EFT performance, suggesting that the specific trait of systemizing, as opposed to other attentional, social, and communicative tendencies as measured by the AQ, modulates performance on this task. While the lack of an association between the AQ and EFT performance conflicts with previous findings of more efficient performance in high AQ individuals (e.g., Grinter et al., 2009), this association may be driven by the underlying systemizing component that the AQ is thought, in part, to measure (Baron-Cohen et al., 2001). While we failed to find associations between the attention subscales of the AQ, which do consist of systemizing-based items, the dispersion of systemizing questions across multiple subscales may account for these null associations. In any case, if previous associations between EFT performance and AQ scores are driven by the systemizing components of the AQ, the fewer number of questions on the AQ that tap into systemizing (particularly those related to analytical tendencies) may result in unreliable measurements and accordingly, variability in findings across studies.

In addition, the current findings suggest that higher scores on the Analytical Tendencies factor of the SQ-R predict enhanced accuracy on the EFT. In accounting for this relationship, one possibility is that cognitive factors (e.g., strategies) may directly modulate EFT performance. For instance, Glicksohn and Kinberg (2009) found that cognitive style was strongly predictive of individual differences in EFT performance. Another possibility, however, is that cognitive tendencies may be associated with specific attentional and/or perceptual biases, and that these biases are what modulate EFT performance. Indeed, scores on the Analytical Tendencies factor of the SQ-R have previously been found to predict decreased susceptibility to the global contextual cues of the RFI (Chapter II), and in the current study, we found that decreased susceptibility to the global visuovestibular cues of the RFI, but not local orientation contrast effects, were associated with enhanced EFT performance. This is consistent with the notion that weaker levels of central coherence (i.e., as observed in ASD populations, Happe & Frith, 2006) may lead to reduced tendencies to integrate the contextual gestalt of the search array, and accordingly, result in more accurate identification of the embedded target.

In addition, however, enhanced perceptual functioning has also been implicated as a possible mechanism to account for superior EFT performance in individuals with autism (e.g., Manjaly et al. 2007). While we found no relationship between the orientation contrast effects of the RFI and performance on the EFT, this does not rule out the possibility that additional low-level perceptual processes, which may be affected in ASD, also modulate EFT performance. For example, according to Happe and Frith (2006), weak central coherence (i.e., attenuated susceptibility to global gestalt cues) may result in a local or detailed-oriented processing style. Therefore, decreased susceptibility to gestalt contextual cues may shift attention to a local level, and this global-to-local shift in perceptual processing (i.e., as opposed to heightened local processing alone), in particular, may subsequently underlie enhanced performance on the EFT. Consequently, while the current results suggest that reduced susceptibility to global contextual cues facilitate accurate performance on the EFT, we cannot rule out the possibility that this relationship is modulated by an attentional enhancement in local processing that may accompany a perceptual shift away from reliance on global contextual cues. If such a locally-oriented attentional bias is beneficial to EFT performance, it may be that this bias occurs due to neural processes that are functionally distinct from those implicated in the local orientation contrast effects of the RFI (i.e., lateral inhibition in primary visual cortex), as no relationship was found between EFT performance and local RFI effects. Future research is therefore needed to further dissociate the local and global perceptual processes that underlie performance on the EFT, and how these processes may be affected by both attentional biases (i.e., distinct from perceptual mechanisms) and ASD symptomology.

CHAPTER IV

SYSTEMIZING AND SUSCEPTIBILITY TO GLOBAL VISUAL CUES: DEFICIT OR BIAS?

While Autism Spectrum Disorders (ASD) are typically characterized by qualitative deficits in social, communicative, and motor domains (DSM-IV, American Psychiatric Association, 1994), there is increasing evidence that perceptual and attentional processes may also be affected. Visual processing in ASD, for instance, is typically characterized by a disproportionate reliance on low-level featural information (Mottron et al., 2006) with a subsequent diminished reliance on higher-level contextual information (Frith, 1989). For example, individuals with ASD are less likely to use gestalt grouping principles such as proximity and similarity (Brosnan et al., 2004), and perform better (i.e., faster) in impossible figure-copying tasks, presumably because they are less affected by the impossible gestalt configuration of the stimulus (Mottron et al., 1999), and demonstrate impairments in discriminating global configurations of radial frequency patterns relative to neurotypical (NT) controls (Grinter et al., 2010). Even NT individuals who exhibit high levels of autistic tendencies (i.e., who score high on the Autism Quotient, Baron-Cohen et al., 2001) have increased thresholds in global motion and global form tasks (Grinter et al., 2009). At the same time, individuals with ASD exhibit a heightened reliance on low-level visual information. For instance, local processing biases have been observed during processing of hierarchical stimuli (O'Riordan et al., 2001; Plaisted et al., 1999) and in drawing tasks (Mottron et al., 1999), and have been proposed to underlie their intact or even superior performance on search tasks, as evidenced by increased activations in early visual areas (Manjaly et al., 2007). In addition, enhanced discrimination abilities for novel stimuli (Plaisted et al., 1998) and local melody manipulations (Mottron et al., 2000), and intact performance in discriminating local manipulations in radial frequency patterns (Grinter et al., 2010), has provided further evidence that local processing is intact, or even enhanced, in ASD. Therefore, an attenuated tendency to process and integrate higher-level contextual information, in conjunction with an overreliance on low-level information, is thought to characterize the perceptual processing style of individuals with ASD.

The Enhanced Perceptual Functioning (EPF) theory of autism (Mottron et al., 2006) has been proposed to account for, in part, this disproportionate reliance on local and global visual cues. Specifically, the EPF theory proposes that low-level visual processing is enhanced in individuals with ASD, and that this enhancement results in a prioritization of, and predisposition to rely on, low-level featural information. Accordingly, the EPF theory proposes that a local processing bias is the 'default' setting in autistic perception, and that higher-level contextual processing is optional in ASD. Importantly, in this view, the local processing bias in ASD is thought to arise from superior low-level visual processing that is orthogonal to the underutilization of higher-level contextual cues. That is, while individuals with ASD may be able to process higher-level contextual cues, the EPF theory proposes that such cues will be disregarded in favor of low-level information, particularly when performance in a task can be accomplished using low-level information alone (Mottron et al., 2006).

Another theory that has attempted to account for the disproportionate reliance on local and global information among individuals with ASD is the Weak Central Coherence

(WCC) theory of autism (Frith, 1989; Happe & Frith, 2006). In its original conception, the WCC theory of autism proposed that a core deficit in ASD was the failure to use and integrate global contextual form, information, and meaning, resulting in a variety of impairments across perceptual, cognitive, and social domains (Frith, 1989). More recent revisions to the theory have emphasized that this failure to use global information may be the result of a detail-focused processing style which places priority on local visual details and information at the cost of global contextual processing, and that this processing bias may be orthogonal to, rather than explain, the social deficits exhibited in ASD (Happe & Frith, 2006). In addition, the WCC theory has been revised to propose that the failure to use global information may be the result of a bias to ignore global context, rather than a deficit in the ability to use global context *per se* (Happe & Frith, 2006). In either case, the WCC theory suggests that attenuated use of global information results in, rather than occurs alongside, a local processing bias, and therefore, that both local and global processing are affected in ASD.

Indeed, in Chapter II we found evidence that in the general population, higher levels of the autistic trait of systemizing were related to both local and global processing biases. Specifically, we found that two distinct types of systemizing factors differentially predicted this global-to-local shift, with an Analytical Tendencies factor associated with decreased use of global contextual cues (i.e., the visuovestibular effects of the rod-and-frame illusion) and an Insistence on Sameness factor associated with heightened susceptibility to local cues (i.e., the orientation contrast effects of the rod-and-frame illusion). However, no association was found between susceptibility to these local and global cues, suggesting that in contrast to the predictions of the WCC theory, local processing biases do not result from an attenuated use of global contextual processing. It is still unclear, however, whether the relationship found between the Analytical Tendencies factor of the SQ-R and reduced susceptibility to the global contextual cues of the rod-and-frame illusion reflect an impairment in global processing, or rather result from a bias to attend to low-level information, where global processing may otherwise be intact.

While the original WCC theory regarded the underutilization of higher-level contextual processing as indicative of a deficit in ASD, some studies have failed to find evidence of global processing impairments. For example, in perceptual grouping tasks in which observers must match two shapes based on either local or global configurations, no performance differences have been found between individuals with ASD and NT controls (Plaisted et al., 2006), particularly when explicitly instructed to prioritize the global configuration (Koldewyn, Jiang, Weigelt, & Kanwisher, 2013). In addition, in studies using Navon tasks (Navon, 1977), ASD samples have been found to perform similar to NT controls in exhibiting faster response times to global shapes relative to local shapes (i.e., global precedence, Mottron et al., 2003; Mottron et al., 1999), and in showing global interference during local reports (Koldewyn et al., 2013). Likewise, in other tasks that have been used to assess global processing (e.g., fragmented letters, silhouette identification, and grouping tasks), individuals with ASD were found to perform similar to NT controls (Mottron et al., 2003). Individuals with ASD have also been found to exhibit normal contextual cueing effects (i.e., faster search times for repeated search arrays, Barnes, Howard, Howard, Gilotty, Kenworthy, Gaillard, & Vaidya, 2008). Evidence for intact global processing in ASD has also been found in non-visual tasks. For example, individuals with ASD have similar levels of performance in change detection of global melody manipulations compared to NT controls (Mottron et al., 2000).

In light of inconsistent findings on impaired processing of global, higher-level contextual cues in ASD, we sought to examine whether decreased use of contextual information as a function of the systemizing trait of autism is indicative of a processing *deficit* (i.e., an impairment in the ability to integrate higher-level contextual cues), or is instead indicative of a processing style that is reflected in a bias or preference to attend to local, low-level visual information, even though higher-level perceptual processes may otherwise be intact. Importantly, previous findings of attenuated use of global information in ASD (Happe, 1996; Bolte et al., 2007), or as a function of autistic tendencies (Walter et al., 2009), have come, in part, from evidence assessing susceptibility to visual illusions. For example, in Chapter II, the association between higher systemizing tendencies in the general population and attenuated use of global information was based on reduced susceptibility to the rod-and-frame illusion (RFI), in which the orientation of a rod is mislocalized in the direction opposite the tilt of a surrounding frame. This illusion, in particular, is thought to occur due to the brain's reliance on visual orientation cues in the establishment of the observer's egocentric reference frame, in addition to vestibular and proprioceptive cues. For example, in the real world, the brain relies on salient cues in the environment (e.g., doors, walls, window frames) to help establish the horizontal and vertical coordinates of the observer's spatial reference frame. In the case of the RFI, where the only environmental cue present is the tilted frame, the brain's reliance on the frame for establishing the egocentric reference frame results in a distortion in perceived vertical, with a distortion occurring in the same direction as the tilt of the surrounding frame (Ebenholtz & Benzschawel, 1977).

In the current study, we therefore speculated that the presence of an upright frame, where the lateral segments of the frame are aligned with gravitational vertical, would provide a beneficial contextual cue that may facilitate, rather than hinder, an accurate representation of the observer's egocentric reference frame. In two tasks (Fig. 22) that required observers to either report the orientation of a line or make a saccadic eye movement to the top of a circle (a sensorimotor report of perceived vertical), we indeed found that the presence of an upright frame significantly increased the precision of responses, compared to frame-absent conditions. We then compared scores on the Systemizing Quotient-Revised (SQ-R: Wheelwright et al., 2006), and the Analytical Tendencies and Insistence on Sameness factors of the SQ-R (Chapter II), to the magnitude of the benefit in the frame-present condition in order to assess whether the previously-reported relationship between systemizing and attenuated susceptibility to contextual cues in the rod-and-frame illusion reflects a deficit in the ability to process the global contextual cue provided by the frame, or is instead a mere bias against using contextual cues when the task can be solved without their use, or when the context is misleading (as in the case of visual illusions). If high systemizers have a deficit in the ability to process contextual cues, this should be reflected in a diminished use of even the beneficial cues provided by upright frames. Alternatively, if high systemizers are merely biased against the use of contextual cues, this bias could potentially be overcome so that performance could be improved by the beneficial cues of the upright frame. In order to maximize the likelihood that participants would use the contextual cues of the upright frame if they are able to do so, they were explicitly instructed that the frame would provide useful cues that would facilitate their performance in the task. In addition to scores on the SQ-R, we also measured scores on the Autism Quotient (AQ: Baron-Cohen et al., 2001), which like the SQ-R are known to form a continuum in the general population (Baron-Cohen et al., 2003; Wheelwright et al., 2006), in order to assess whether any observed associations were due specifically to systemizing tendencies or could instead be accounted for by general autistic tendencies (as measured by the AQ).

Experiment 1: Visuovestibular and Perception Tasks

Methods

Participants. Eighty-two participants (52 female) were recruited from the University of Oregon human subjects pool. Participants received either course credit or monetary compensation for their participation. The average age of the sample was 21.5 years (*SD* = 4.2), and all participants had normal vision (without correction) and no known neurological deficits or disorders. All participants provided informed consent in accordance with the guidelines of the University of Oregon Institutional Review Board.

Apparatus. An eye tracker (Eyelink 2000: SensoMotoric Instruments, Needham, Massachusetts, United States) was used to monitor fixation and eye movements during all tasks. Before each task, the eye tracker was calibrated for each participant using a grid of 13 calibration targets. If the average error in fixation across the 13 targets was greater than 1°, the calibration was rejected and begun again. If the calibration began to slip mid-task, the experimenter stopped the task, recalibrated, and when calibration was again successfully achieved, the participant continued where they had left off.

Stimuli. Participants were seated with the head stabilized in chin and forehead rests with the eyes 86 cm away from a screen (Da-Lite Polacoat Ultra projection screen with a DA-100 diffusion coating) measuring 101.6 cm tall by 135.9 cm wide. Stimuli were back-projected (Electrohome Marquee 8500, with custom-fit HD145 lenses) onto the screen in a darkened room. The stimuli (Fig. 20) were red and included a circular fixation point (0.5° of visual angle) surrounded by a response circle (measuring 13.7° in diameter with a stroke width of 0.1°) and an upright square frame (35.9° for each side, with a stroke width of 1°). All stimuli were centered on the screen at eye level. The fixation point was intersected by a rod (a central line measuring 6.9° with a width of .2°) that was tilted either –4°, –3°, –2°, –1°, 0°, 1°, 2°, 3°, 4° from vertical.

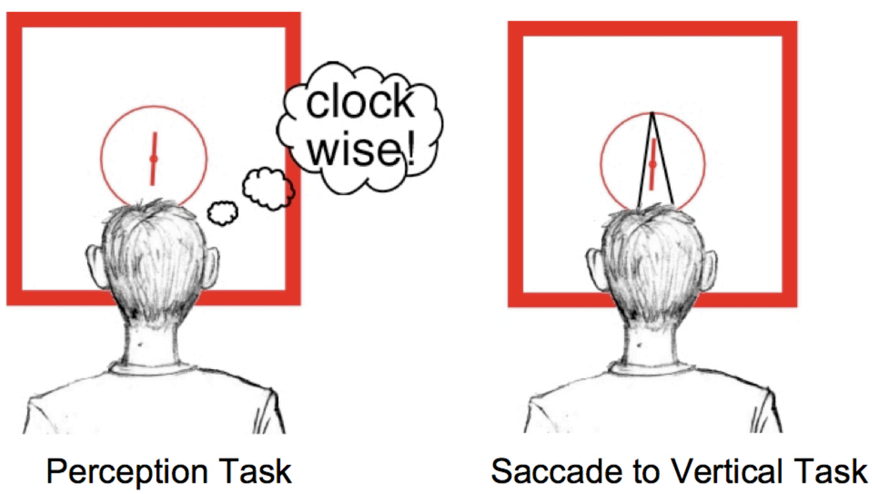

Figure 20. Perception and Saccade-to-Vertical tasks for Experiment 1. Participants judged the orientation of a rod (Perception task) or made a saccade to the top of the response circle while ignoring the rod (Saccade-to-Vertical task) in the presence (shown) or absence of an upright frame. Solid black lines in the Saccade-to-Vertical task represent the line-of-sight for the two eyes after the saccade to the top of the response circle.

Procedure. All participants completed two separate tasks that required them to either judge the orientation of the rod (Perception task) or to make a saccade to the top of the response circle (Saccade-to-Vertical task) in either the presence or absence of a surrounding upright frame (Fig. 20). In both tasks, the frame was present on 50% of trials, with frame-present and frame-absent conditions randomized across trials. Prior to performing each task, participants completed a practice session that only included the fixation point, response circle, and the rod (i.e., no frame was present). For the actual trials, participants were instructed that the tasks would be the same but that on some trials an upright frame would be present, and that they could "use the context of the frame to benefit their performance." Participants also completed the AQ and SQ-R questionnaires, with the order of all tasks counterbalanced across participants. The completion of all tasks approximately 60 min.

Perception Task. In the Perception task, participants were required to report the tilt of a line in the presence or absence of a large upright frame. Contrary to the rod-and-frame illusion in which a tilted frame is expected to have an illusory effect on orientation judgments, the upright frame here is expected to have a beneficial effect on performance. At the onset of each trial, a central fixation point and response circle were visible at the center of the screen. Although the response circle served no purpose in the Perception task, it was included to provide consistency with the stimuli presented in the Saccade-to-Vertical task (described below), and it should be noted that the circle provided no orientation cues that would systematically affect performance. Participants first directed their eyes to the central fixation point and were instructed to maintain their gaze on the fixation point throughout the trial. After fixation was achieved, the onset of the trial was initiated with a button press (under the left thumb) on a gamepad controller. At the onset of the trial, a large frame (or no frame) appeared on the screen, followed 200 ms later by a rod that was tilted either –4°, –3°, –2°, –1°, 0, 1°, 2°, 3°, or 4° from vertical. After 500 ms, the rod and fixation point were extinguished, which cued participants to make a judgment (by pressing the left or right trigger button on the gamepad controller) as to whether they perceived the rod to be tilted "left" (counterclockwise) or "right" (clockwise). Participants completed 20 trials for each combination of frame condition (frame-absent or frame-present) and rod tilt (9 tilts), with 360 trials total (10 blocks, 36 trials per block).

Performance in the Perception task was calculated by fitting a psychometric curve to the proportion of "clockwise" responses to derive the space constant (i.e., slope) and point of subjective equality (PSE) of the psychometric function using the following equation:

$$\text{proportion "clockwise" responses} = e^{((\text{rodtilt}-\text{PSE})/\text{tau})}/(1+e^{((\text{rodtilt}-\text{PSE})/\text{tau})})$$

where *rodtilt* was the orientation of the rod, *PSE* was the point of subjective equality, and *tau* was the space constant of the psychometric function. Since the presence or absence of the frame is not expected to produce a systematic bias in perceived rod orientation, the primary variable of interest is the space constant of the psychometric function, as this provides an index of the precision of the orientation judgments, with smaller values indicative of steeper slopes or greater precision in the judgments. Performance was operationalized as the difference in the space constants of the psychometric functions for the frame-present and frame-absent conditions, with negative values indicative of a performance benefit in the frame-present condition.

Saccade-to-Vertical Task. In the Saccade-to-Vertical task, participants were instructed to make a saccade from a central fixation point to the top of the response circle (i.e., the location directly above the fixation point; Fig. 20). For each trial, participants were instructed to direct their gaze to the fixation and began the trial by pressing a button on the gamepad controller. The time-course for the onset and offset of the stimulus components was the same as that described in the Perception task (note that the presence of the rod was irrelevant to the Saccade-to-Vertical task but was included to provide consistency with the stimuli of the Perception task). In the Saccade-to-Vertical task, the offset of the rod and fixation point (after 500 ms) cued participants to make a saccade to what they perceived to be the top, or most vertical point, on the response circle. Participants then pressed a button on the gamepad controller (under their left thumb) to prompt the computer to record the eye position and terminate the trial. Trials were aborted if the participant blinked during the trial, or looked away from an invisible window (1°) around the central fixation point before its offset, with these aborted trials rerun later in the experiment. Participants completed 44 trials, with 22 each of the frame-present and frame-absent conditions.

Performance in the Saccade-to-Vertical task was measured by calculating the angle of rotation of a vector plotted from the fixation point to the final eye position. The standard deviation for the mean rotational error provided a metric for the precision of responses and was calculated separately for the frame-absent and frame-present conditions. Performance was then operationalized as the difference in standard deviations between frame-present and frame-absent conditions, with negative values indicative of better performance (smaller standard deviations) in the frame-present condition.

Measures of Autistic Tendencies. Participants completed computer-based versions of the Autism Quotient (AQ) and Systemizing Quotient-Revised (SQ-R). The AQ contains 50 items that provide a general measure of autistic tendencies (with higher scores indicative of greater autistic tendencies) based on the sum of scores from five subscales: attention switching, attention to detail, social skills, communication and imagination. The SQ-R consists of 75 items that measure an individual's tendency to analyze the structure, rules, and operations in rule-based systems, with higher scores indicative of greater systemizing tendencies. The Analytical Tendencies factor of the SQ-R contains 26 items that specifically measure analytical forms of systemizing (Table 2, Chapter II), while the Insistence on Sameness factor of the SQ-R contains 12 items that measure environmental forms of systemizing (e.g., need for order, routine, and sameness; Table 3, Chapter II). Scores on both factors were computed based on the sum of item responses (Chapter II). The questionnaires were completed on a Macintosh computer (Apple Computers, Cupertino, CA) and took 20-25 min. for participants to complete.

Results

Across all participants, the mean score for the AQ was 16.5 (*SD* = 6.4; range = 6-36), which closely matches the previously reported mean of 16.3 (*SD* = 5.9) by Wheelwright and colleagues (2006). The mean score for the SQ-R was 59.6 (*SD* = 21.2; range = 14-112), which approximates the mean of 55.6 (*SD* = 19.2) previously reported by Wheelwright and colleagues (2006).

For the Perception task, the space constants of the psychometric functions for the frame-absent (*M* = .47°, *SD* = .27°) and frame-present conditions (*M* = .35°, *SD* = .28°) were compared in order to assess the precision of orientation judgments for each condition. A paired-samples t-test indicated a significant difference between space constants ($t(79) = 4.36$, $p < .001$) in that the presence of the upright frame had a significant effect in increasing the precision (i.e., decreasing the space constant) of the orientation judgments (Fig. 21A). In addition, the presence of the upright frame had a significant effect ($t(79) = 5.84$, $p < .001$) in reducing the bias (i.e., the PSE) in orientation judgments ($PSE_{frame\text{-}absent} = .57°$, $SD = .51°$; $PSE_{frame\text{-}present} = .29°$, $SD = .30$; Fig. 22A). However, the magnitude of the benefit of the frame on the precision ($tau_{frame\text{-}presesnt} - tau_{frame\text{-}absent}$) and bias ($PSE_{frame\text{-}present} - PSE_{frame\text{-}absent}$) of the orientation judgments was not correlated with scores on the SQ-R (tau_{diff}: $r(76) = -.083$, $p =.470$, Fig. 21B; PSE_{diff}: $r(76) = .093$, $p =.416$, Figure 22B), nor with scores on the Analytical Tendencies (tau_{diff}: $r(76) = –.12$, $p =.28$; PSE_{diff}: $r(76) = .11$, $p =.36$) or Insistence on Sameness (tau_{diff}: $r(76) = .09$, $p =.44$; PSE_{diff}: $r(76) = –.04$, $p =.74$) factors of the SQ-R. Similarly, the magnitude of the benefit of the frame was unrelated to scores on the AQ (tau_{diff}: $r(77)= .038$, $p = .743$; PSE_{diff}: $r(77) = .069$, $p =.548$) or any of the AQ subscales ($r(77) < .13$).

For the Saccade-to-Vertical task, the standard deviation of saccade vectors (made to the top of the circle) was compared across frame-absent conditions ($M = 4.44°$, $SD = 1.85°$) and frame-present conditions ($M = 4.35°$, $SD = 1.72°$) in order to assess the precision of visuovestibular judgments of perceived vertical. No significant difference was found in the mean standard deviations across the two frame conditions ($t(79) = 1.03$, $p = .308$). Similarly, analysis of the absolute value of the mean rotational error of the saccade vector showed no significant difference ($t(79) = – 1.61$, $p = .111$) between the frame-absent ($M = 3.27°$, $SD = 2.39°$) and frame-present ($M = 3.66°$, $SD = 2.73°$) conditions, indicating that the presence of the frame had no impact on the size of the constant bias in the direction of these saccades. In addition, the magnitude of the difference in performance between frame-present and frame-absent conditions was not correlated with the SQ-R (SD_{diff}: $r(76) = -.161$, $p = .159$; $bias_{diff}$: $r(76) = .072$, $p = .530$), nor with the Analytical Tendencies (SD_{diff}: $r(76) = -.13$, $p = .27$; $bias_{diff}$: $r(76) = .02$, $p = .87$) or Insistence on Sameness (SD_{diff}: $r(76) = -.12$, $p = .31$; $bias_{diff}$: $r(76) = .21$, $p = .07$) factors of the SQ-R. Similarly, the magnitude of the difference in performance was unrelated to AQ scores (SD_{diff}: $r(77) = .007$, $p = .948$; $bias_{diff}$: $r(77) = .044$, $p = .700$) or any of the AQ subscales ($r(77) < .12$).

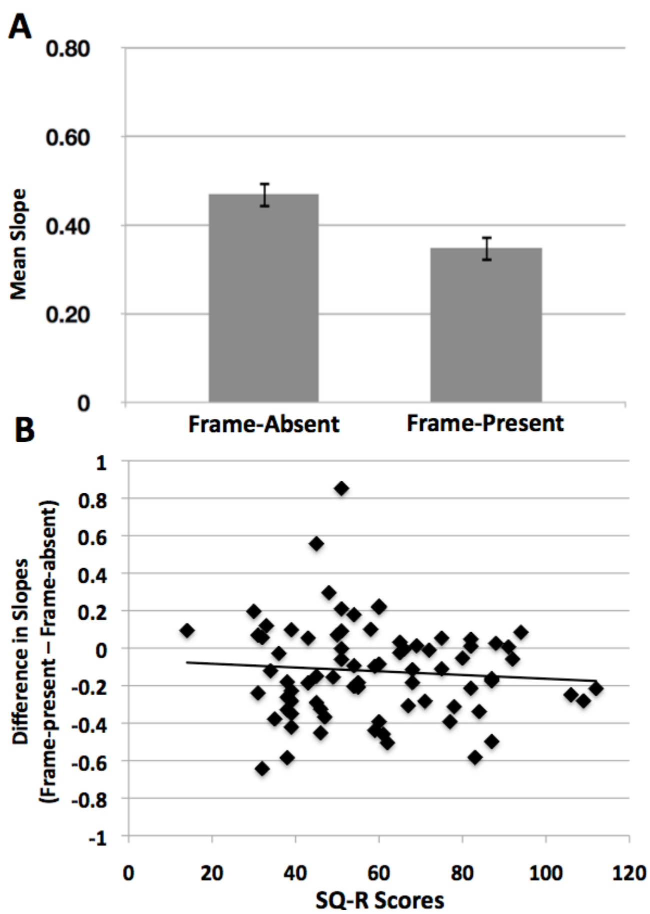

Figure 21. The effect of an upright frame on the slope of the psychometric function for orientation judgments (Perception task). A) The upright frame significantly ($p < .001$) increased the precision (space constant tau, y-axis) of responses. B) The magnitude of this benefit (difference in space constants between frame-present and frame-absent conditions) was unrelated to SQ-R scores.

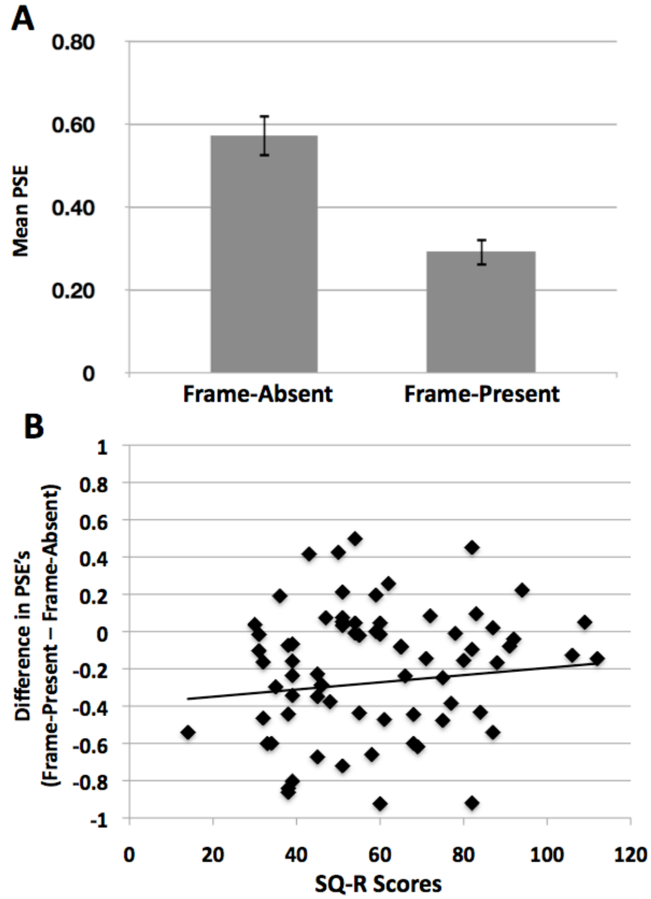

Figure 22. The effect of an upright frame on the point of subjective equality (PSE) of the psychometric function for orientation judgments (Perception task). A) The upright frame significantly ($p < .001$) reduced the mean orientation error (PSE, y-axis) for orientation judgments. B) The magnitude of this benefit (difference in PSE's) was unrelated to SQ-R scores.

Discussion

In previous findings of reduced illusion susceptibility in ASD (Happe, 1996; Bolte et al., 1997), or as a function of autistic tendencies (e.g., SQ-R) in the general population (Walter et al., 2009), the presence of visuospatial context (e.g., the tilted frame in the rod-and-frame illusion) is expected to have a detrimental effect on performance. In the current study, we examined whether heightened autistic tendencies in the general population would be associated with a similar reduction in the use of contextual cues under conditions in which the context is *beneficial* to performance. Indeed, we confirmed in the Perception trials of Experiment 1 that the presence of an upright frame is beneficial, significantly increasing the mean precision of the orientation judgments (as measured by a decrease in the space constant of the psychometric functions), and decreasing the bias in the judgments (as measured by a decrease in the PSE of the psychometric functions). However, the magnitude of these benefits were uncorrelated with all assessed measures of the autistic traits exhibited by the participants (SQ-R, the Analytical Tendencies and Insistence on Sameness factors of SQ-R, AQ, and all subcomponents of AQ). Thus, it appears that high systemizers are just as capable of benefitting from helpful visuospatial cues (i.e., upright frames) as are low systemizers, even though high systemizers are less susceptible to the similar but misleading cues (i.e., tilted frames) that drive the rod-and-frame illusion (Walter et al., 2009; Chapter II). These findings indicate that high systemizers experience no deficit in processing this contextual information, but instead have the flexibility to use the context when it is helpful but ignore it when it is misleading.

Given that previous studies have shown that tilted frames of the size used in the present study tended to drive the rod-and-frame illusion predominantly by causing a visuovestibular distortion in the observer's egocentric reference frame (Ebenholtz & Benzschawel, 1977; Chapter II), it was our assumption that the upright frames of Experiment 1 would serve as useful cues for stabilizing the egocentric reference frame, allowing for an increase in precision and a decrease in the bias of saccades made to the top of the response circle in the Saccade-to-Vertical task. However, there were no significant differences in performance between the frame-present and frame-absent conditions. One possible explanation for this null effect is that the magnitude of any frame-related improvement in the egocentric reference frame may have been too small to be measured with the methods employed. That is, the precision of the eye tracker may have been insufficient to allow for measurements of the saccade vectors with enough accuracy to observe a small frame-related improvement. If this is the case, it should be possible to increase the sensitivity of our measurements by using a larger response circle – and larger response circle will require a longer saccade, resulting in larger horizontal deviations of the endpoints of saccades with different vectors. Therefore, in Experiment 2 we altered the Saccade-to-Vertical task to include a larger response circle in order to more precisely examine whether the presence of beneficial contextual cues can facilitate visuovestibular stabilization of the egocentric reference frame.

Experiment 2: Test of a More Sensitive Visuovestibular Task

Methods

Participants. An additional 76 participants (53 female) participated in Experiment 2. The mean age of the sample was 19.8 (*SD* = 3.5). Participation criteria and ethical protocols were the same as that described for Experiment 1.

Apparatus. The apparatus was the same as that described in Experiment 1.

Stimuli. All stimulus parameters and trial sequences were identical to those described in Experiment 1 for the Saccade-to-Vertical task, with the exception that the size of the response circle was larger in Experiment 2 (34.2° in diameter, with a stroke width of 0.1°), allowing for a more sensitive measurement saccade vector (Fig. 23).

Procedure. The procedure was identical to that for Experiment 1, with the exception that participants only completed the SQ-R and the modified version of the Saccade-to-Vertical task.

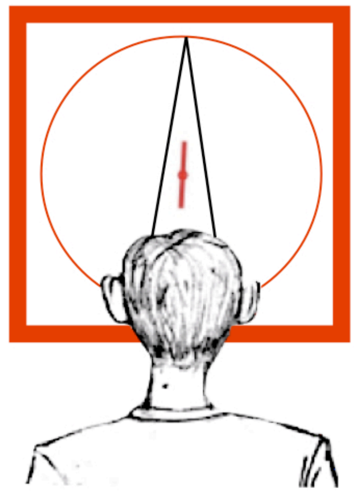

Figure 23. The Saccade-to-Vertical task for Experiment 2. The stimuli and task were identical to Experiment 1 with the exception of a larger response circle (34.2° diameter). Solid black lines represent the line-of-sight for the two eyes after the saccade to the top of the response circle.

Results

In Experiment 2, the mean score for the SQ-R was 59.7 (*SD* = 17.4 ; range = 25-105).

For the Saccade-to-Vertical Task, a significant difference was found between the mean standard deviations of saccades directed to the top of the response circle in frame-absent (*M* = 2.64°, *SD* = 1.25°) and frame-present (*M* = 2.35°, *SD* = 1.11°) conditions, with the presence of the upright frame significantly reducing variability in performance ($t(73) = 4.52$, $p < .001$; Figure 24A). The magnitude of this benefit ($SD_{frame\text{-}present} - SD_{frame\text{-}absent}$), however, was not related to scores on the SQ-R ($r(69) = .144$, $p = .231$;

Figure 24B), nor the Analytical Tendencies ($r(69) = .16$, $p = .17$) and Insistence on Sameness ($r(69) = –.06$, $p = .60$) factors of the SQ-R. No significant difference ($t(73) = –.13$, $p = .895$) was found in the absolute saccade errors between frame-absent ($M = 1.81°$, $SD = 1.80°$) and frame-present ($M = 1.82°$, $SD = 1.77°$) conditions, and across individuals, the difference in absolute errors between frame conditions was unrelated to SQ-R scores ($r(69) = .09$, $p = .45$), as well as the Analytical Tendencies ($r(69) = .15$, $p = .20$) and Insistence on Sameness ($r(69) = –.09$, $p = .48$) factors of the SQ-R.

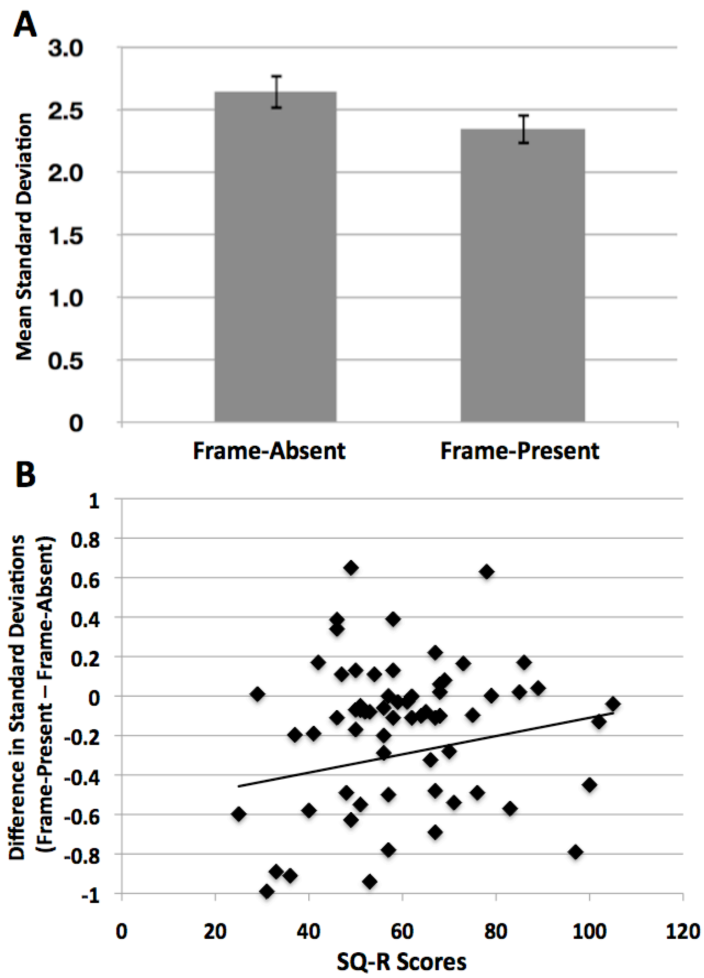

Figure 24. The effect of an upright frame on saccades to perceived vertical (Saccade-to-Vertical task in Experiment 2). A) The upright frame significantly ($p < .001$) increased the precision (standard deviation, y-axis) of saccades made to the top of the response circle. B) The magnitude of this benefit (difference in SD's between frame-present and frame-absent conditions) was unrelated to SQ-R scores.

Discussion

In Experiment 2, in order to more precisely measure saccadic vectors to perceived vertical in the presence and absence of a veridical contextual cue, we increased the size of the response circle in the Saccade-to-Vertical task. Consistent with the findings from Experiment 1 on orientation judgments (Perception task), the presence of the upright frame was now found to have a significant effect in increasing the precision (i.e., reducing the variability) of the participant's response. Importantly, though, the magnitude of this contextual benefit was unrelated to SQ-R scores in the general population, just as it was in Experiment 1. Thus, it appears that high systemizers exhibit no deficit in the use of contextual cues when they provide a benefit to performance.

General Discussion

While previous investigations of perceptual processes in ASD have generally supported the notion of a detail-oriented processing bias (Happe & Frith, 2006; Mottron et al., 2006), it is unclear whether this bias results from, or is orthogonal to, a subsequent deficit in processing higher-level global contextual cues, or whether higher-level contextual processes remain intact but are utilized less due to prioritized preference for low-level visual information. Although previous studies have indicated that the autistic trait of systemizing is associated with a diminished use of visuospatial contextual cues that cause the visuovestibular distortions that underlie the rod-and-frame illusion (Walter et al., 2009; Chapter II), the results from the present study clearly indicate that similar but non-illusory cues can benefit the performance of even high systemizers in tasks involving perceptual judgments (Experiment 1) and goal-directed movements (Experiment 2).

Furthermore, the current findings suggest that even the heightened levels of systemizing tendencies that exist in ASD populations (Baron-Cohen et al., 2003; Wheelwright et al., 2006) may reflect intact abilities to process visuospatial contextual cues (i.e., with no deficits or impairments), but also a tendency to underutilize these cues (compared to an NT population) due to a preference for low-level visual information. Of course, the presence of additional neurophysiological aberrancies in clinical ASD populations may compromise other aspects of higher-level processing (e.g., of social stimuli).

Although we found that the presence of a veridical contextual cue facilitated precision of both perceptual judgments and goal-directed actions, it is unclear as to *how* the information provided by the contextual cue facilitated performance. One possibility is that the frame provided a visual cue to gravitational vertical that was used to stabilize the participant's egocentric reference frame. Alternatively, however, the presence of the frame may have provided an *allocentric* cue that facilitated performance. Specifically, in the Perception task, judgments as to whether the central rod was tilted clockwise or counterclockwise from vertical could have been made based on a direct comparison of the rod's orientation to the vertical line segments of the frame. Similarly, enhanced performance in the Saccade-to-Vertical task in the presence of an upright frame could have been achieved through recognition that the midpoint of the upper horizontal line segment of the frame was an indicator of true veridical (since the frame was centered with respect to both the response circle and the observer's field of view). The midpoint of the frame would thereby provide an allocentric cue – relative to the top of the response circle – that may have contributed to the performance benefit in this task.

The notion that autistic perception can be characterized not by a deficit in contextual processing, but rather by a *bias* to ignore higher-level contextual cues in favor of low-level information is generally consistent with past findings that the extent to which contextual cues are utilized during performance may be modulated by the attentional demands of the task. For example, in Navon tasks, when individuals with ASD must respond to a target at a pre-specified level (i.e., when selective attention is directed to the pre-specified level of the target shape), global precedence is observed. However, when individuals with ASD must identify a target that could appear at *either* the local or global level (i.e., when attention must be divided across both levels of the stimulus), then local precedence is observed (Plaisted et al., 1999). Therefore, the magnitude and consistency of global precedence (i.e., and, therefore, higher-level contextual processing) in ASD may be contingent on whether tasks across studies employ selective or divided attention in assessing hierarchical processing. This modulatory effect of attention on perceptual processing suggests that utilization of higher-level contextual cues is not obligatorily impaired in ASD, but rather that such processes can be flexibly allocated to different levels of a stimulus depending on task demands. Therefore, consistent with the predictions of the EPF theory, the disproportionate reliance on low-level information in ASD may only be manifest as a 'default' perceptual setting (Mottron et al., 2006), with higher-level contextual processes being optional, and otherwise intact, with the balance of local and global processing used to solve a task dependent on the cognitive and attentional demands of the task. It is unclear, however, what precise parameters in a given task are needed to elicit the use of optional higher-level processes in ASD. Indeed, there are many instances in which individuals with ASD may use low-level information to achieve performance levels comparable to NT controls, despite the tendency of NT controls to use higher-level processes when performing the task (e.g., the embedded figures task, Lee et al., 2007; Manjaly et al., 2007). However, in tasks that provide explicit instructions to attend to global cues, individuals with ASD seem to be able to overcome this bias and flexibly allocate resources to global levels of processing.

In addition, an important question for future research is to assess whether enhanced low-level functioning and atypical top-down functioning are orthogonal, yet comorbid, phenotypes of ASD, or whether direct covariance between these neurophysiological processes is present, possibly due to some common underlying etiology. For example, if these phenotypes are orthogonal, this could indicate that the neural substrates that subserve these processes are affected by different underlying factors (e.g., genes), and that treatment of one symptom may have no effect on the other. Conversely, if these phenotypes covary, it may be the case that both arise from a common epigenetic source, or that one is only manifest due to aberrancies in the other. For example, if atypical top-down functioning arises due to heightened low-level functioning, with the neural substrates that subserve these top-down processes otherwise intact, it may be possible to compensate for top-down aberrancies by manipulating other factors (e.g., attention, explicit task instructions) that are known to affect these same processes. Importantly, identifying such compensatory mechanisms may be useful in informing current interventions and treatment approaches for helping individuals with ASD.

CHAPTER V

CONCLUSIONS

While Autism Spectrum Disorders (ASD) are characterized by deficits and abnormalities across a broad range of social and cognitive domains, remarkably, performance in attentional and perceptual domains, while sometimes atypical, is often preserved. While variability in ASD severity across small sample sizes, use of heterogeneous tasks and stimulus parameters across studies, and the methodological limitations of quasi-experimental comparisons have often resulted in inconsistent findings in the literature, there are common themes that have emerged which offer clues as to how these visuospatial processes may be affected in ASD. The most consistent finding is that individuals with ASD exhibit a locally-oriented bias in how they process sensory information (Dakin & Frith, 2005). This processing style has been proposed to explain a diverse range of ASD behaviors, from superior performance in disembedding on visual search tasks (Jolliffe & Baron-Cohen, 1997), to local interference during hierarchical visual processing (Wang et al., 2007), to reduced configural interference on face processing tasks (Teunisse & de Gelder, 2003).

Nevertheless, it is important to consider alternative methodological approaches to studying ASD that may help minimize the inconsistent findings (or at least the sizes of the error bars) across studies that are so prevalent in ASD literature. One such methodological approach has been informed by the findings that some aspects of ASD can be characterized by extreme manifestations of neurotypical traits that form continua across the general population (Baron-Cohen et al., 2001; Baron-Cohen et al., 2003, Baron-Cohen & Wheelwright, 2004). Specifically, the traits of empathizing and systemizing have been found to be disproportionately expressed in ASD populations, with an attenuated drive to empathize and a heightened drive to systemize (relative to NT populations) characterizing the cognitive style of individuals with ASD (Baron-Cohen et al., 2003; Baron-Cohen & Wheelwright, 2004). Importantly, these traits have been found to exist along a continuum in the general population, with ASD populations often occupying the extreme ends of the distributions (Baron-Cohen et al., 2003; Baron-Cohen & Wheelwright, 2004). These findings qualify the use of an alternative methodological approach to studying autism in which the variability in specific traits in the *general* population can be used to explain the variance and expression of key behaviors that are related to ASD. In other words, by taking an individual differences approach in examining the association between trait variability (e.g., in empathizing and systemizing) and specific phenotypical outcomes in the general population, trait variability can be used as a *tool* (or signal) for explaining ASD symptomology rather than a *confound* (or noise) in traditional quasi-experimental group comparisons.

A useful example of the benefit of this individual differences approach to investigating differences in visuospatial processing in ASD comes from examining the literature on the extent to which individuals with autism are susceptible to visual illusions. Specifically, while previous research produced inconsistent findings as to whether or not individuals with ASD were susceptible or immune to visual illusions (Happe, 1996; Ropar & Mitchell, 1999, 2001; Bolte et al., 2007), Walter et al. (2009) used an individual differences approach to examine how autistic traits in the general population (which in extreme levels characterize some of the cognitive biases in ASD) predict illusion susceptibility. As discussed in the preceding chapters, they found that the trait of systemizing (which is hyper-expressed in ASD) negatively covaries with susceptibility to a specific class of visual illusions (i.e., those driven by distortions in an observer's spatial reference frame), with higher systemizing tendencies associated with decreased illusion susceptibility. In Chapter II, we extended these findings by showing that systemizing tendencies are also predictive of illusions driven low-level mechanisms (i.e., orientation contrast effect), but in the opposite direction, with higher systemizing tendencies associated with *increased* illusion susceptibility. This helps reconcile previous disparate findings on illusion susceptibility in ASD by showing that susceptibility is contingent on the magnitude in which systemizing tendencies are expressed, as well as the types of illusions that are tested. Accordingly, the magnitude of group differences in illusion susceptibility may only manifest as a function of systemizing tendencies across groups. For example, given that systemizing tendencies are hyper-expressed in ASD, an NT-matched control group who happens to be low on systemizing may result in significant group differences, while an NT-matched control group who happens to be high on systemizing may result in null differences. The individual differences approach is therefore beneficial not only in identifying the shared variance between traits and behaviors, but is also useful in that it can identify mediating variables that group comparison designs can utilize as a matched-variable (which otherwise may serve as confounds). Furthermore, a benefit of this approach is that it is not reliant on the use of small ASD samples in which such variability in unmatched traits is maximized.

It is still unclear, however, whether the relationship between illusion susceptibility and the systemizing trait of autism reflects a processing style characterized by weak central coherence (Happe & Frith, 2006) or superior sensory processing (Mottron et al., 2006). For instance, reduced susceptibility to visual illusions could be explained by an attenuated susceptibility to global contextual cues, a heightened sensitivity to local visual cues, or some combination of the two. In Chapter II, this was examined by isolating the local (i.e., orientation contrast effects) and global (i.e., visuovestibular effects) mechanisms that contribute to the rod-and-frame illusion (RFI), and comparing these susceptibilities to scores on the Systemizing Quotient-Revised (SQ-R, Wheelwright et al., 2006). High levels of systemizing were found to predict *both* increased susceptibility to the local orientation contrast effects of the RFI and decreased susceptibility to global visuovestibular effects. Importantly, however, these mechanisms were not correlated with each other, suggesting that these may be two orthogonal perceptual processes that are each associated which distinct components of systemizing (i.e., groups of items embedded in the SQ-R). Factor analysis resulted in the extraction of two SQ-R factors (Analytical Tendencies and Insistence on Sameness) that differentially accounted for these associations, with high levels of Analytical Tendencies predictive of decreased global effects and high levels of Insistence on Sameness predictive of increased local effects. In addition, scores on both factors were found to be significantly higher in a large ASD sample compared to neurotypical controls, suggesting that high trait levels in ASD may account for some of the perceptual biases observed in this population.

Indeed, in Chapter III, SQ-R factor levels in the general population were compared to performance on the Embedded Figures Test (EFT), a visual search task in which individuals with ASD are frequently found to excel (Jolliffe & Baron-Cohen, 1997). Higher scores on the Analytical Tendencies factor, but not the Insistence on

Sameness factor, were found to significantly account for superior performance (i.e., accuracy) on the EFT. In addition to providing further evidence as to the discriminant validity of the two-factor structure to the SQ-R, these findings demonstrate that superior search performance in ASD can, in part, be accounted for by heightened analytical tendencies that are characteristic of this population. Given that heightened analytical tendencies were found to predict decreased use of global information (in Chapter II), these findings suggest superior search performance in ASD may be due to decreased interference from the contextual gestalt of the search array which may subsequently facilitate disembedding and localization of the EFT target. This was confirmed by comparing EFT performance to the local orientation contrast and global visuovestibular effects of the rod-and-frame illusion, in which decreased susceptibility to the global, but not local, RFI effects significantly predicted greater accuracy on the EFT.

While EFT performance may covary with susceptibility to global, but not local, visual cues, atypical ASD performance on other attentional and perceptual tasks may nevertheless result from a specific bias to process local information, independent of global processing tendencies. Indeed, findings from Chapter II suggest that the fact that individuals with ASD tend to have heightened levels of both analytical tendencies and an insistence on sameness predicts a global-to-local shift in perceptual processing, but attenuated global susceptibility did *not* predict enhanced local processing. While both the Intense World (Markram & Markram, 2010) and Enhanced Perceptual Functioning (Mottron et al., 2006) theories predict that a local processing bias in ASD is due to superior low-level functioning in primary sensory areas, it is therefore unclear whether such a bias necessitates impairment in global contextual processing, as suggested by the

Weak Central Coherence theory (Happe & Frith, 2006), or is a comorbid perceptual phenotype that is orthogonal to global processing. In other words, while global processing has been found to be attenuated in ASD (e.g., reduced sensitivity to gestalt configurations, Brosnan et al., 2004; visual illusions, Happe, 1996; and motion coherence, Simmons et al., 2009), it is unclear whether this reflects a deficit in global processing that is *orthogonal* to enhanced low-level functioning, a deficit that is *due* to enhanced low-level functioning, or simply a *bias* not to use global cues (due to over-reliance on local cues) even though global processing may be otherwise intact.

In order to examine this, in Chapter IV, scores on the SQ-R were compared to performance on two tasks in which contextual cues were *beneficial* to performance (unlike the RFI and EFT, in which reliance on contextual cues results in biased or non-optimal performance). Specifically, perceptual reports (orientation judgments) and goal-directed movements (saccades to perceived vertical) were measured in conditions with and without a contextual cue (i.e., an upright frame) that was found to significantly benefit performance. Importantly, the performance benefits derived from the presence of the contextual cue did not depend on levels of systemizing, suggesting that high systemizers can in fact recruit global processing when it is beneficial or explicitly elicited for performance. These findings therefore suggest that in ASD, at least as a function of heightened systemizing tendencies, attenuated use of global information reflects a bias to ignore such information, and not a deficit in processing. These findings are also consistent with reports of normal global precedence (in hierarchical selective attention tasks, Mottron et al., 1999) and face inversion effects (Lahaie et al., 2006; Teunisse et al., 2003) in ASD, which further suggest that some aspects of global processing may indeed be intact. Indeed, the Weak Central Coherence theory – which has been the most influential theory in suggesting deficits in global processing – has recently been revised (Happe & Frith, 2006) to account for the possibility of attenuated global processing reflecting a bias, rather than a deficit, that predominantly emergences due to ASD individuals' preference for local information.

If global contextual processing is indeed intact in ASD, yet attenuated due to a bias for local information, an important question ensues: under what circumstances will, or can, individuals with ASD recruit global processing? This question is important in that while global processing may be intact, if a local bias in ASD always precludes use of global information, even at the cost of performance, then such a bias may have the same consequence as a deficit. In research on hierarchical processing in ASD, local biases are more commonly observed when the target in a Navon stimulus can appear at either the local or global level (i.e., divided-attention tasks, Plaisted et al., 1999), which suggests that, as predicted by the Enhanced Perceptual Functioning theory, the *default* setting for autistic perception is locally-oriented. However, in tasks that provide explicit instructions to attend to global cues (e.g., selective attention tasks using congruent Navon stimuli), individuals with ASD may be able to overcome this bias and flexibly allocate resources to global levels of processing (and perhaps even implicitly as well, as is the case for normal contextual cueing effects observed in ASD samples, Barnes et al., 2008).

It is important to clarify that if global processing is preserved in ASD, this does not imply that top-down processing in higher-level areas are necessarily intact. For example, it is likely that parietal regions are strongly associated with global perceptual (e.g., Walter & Dassonville, 2008) and attentional (e.g., Robertson et al., 1988) processes, and while similar performance in global-based tasks is sometimes observed between ASD and NT groups, activation in these regions may still be atypical. In addition, many top-down processes recruit prefrontal regions (e.g., verbal working memory tasks, Koshino et al., 2005), and under-connectivity between primary sensory and prefrontal regions (Simmons et al., 2009) may result in top-down impairments in ASD that could compromise some aspects of higher-level contextual processing. In addition, performance on complex tasks related to social functioning is likely to involve prefrontal (and FFA) recruitment, and although these tasks may similarly recruit parietal areas involved in global contextual processes, impairment in these higher-level areas may result in severe deficits in social and communicative domains.

Therefore, while some aspects of global processing may be spared, or compensated for, in ASD, higher-level top-down processes are likely affected and may account for a wide range of impairments. An important question for future research is to assess whether enhanced low-level functioning and atypical top-down functioning are orthogonal, yet comorbid, phenotypes of ASD, or whether direct covariance between these processes is present due to some common underlying neurophysiological etiology (e.g., hyper-active microcircuits that overwhelm higher-level neural integration). Whatever the case, while many theories in ASD tend to emphasize abnormalities in either low-level (bottom-up) or higher-level (top-down) functioning, it is likely that both are applicable in explaining ASD symptomology and atypical performance across a wide range of tasks. Theories that account for ASD symptomology at both of these levels (such as the Intense World theory) are likely to be beneficial in reconciling the overwhelming number of theories on ASD that currently exist.

Although the current findings may offer empirical insight as to how the tenets of these theories can be evaluated, it is likely that other sources of variability that are unique to ASD populations (e.g., differential developmental trajectories for different core symptoms, Seltzer, Krauss, Shattuck, Orsmond, Swe, & Lord, 2003) cannot be fully reconciled by examining traits in the general population, and that non-linear thresholds of ASD pathology may result in extreme outcomes that can only be identified by directly studying clinical populations. A next step, then, for future research, is to test these illusion effects (i.e., the visuovestibular and orientation contrasts effects of the RFI) in a clinical ASD sample. Specifically, confirming that individuals with ASD are differentially susceptible to different types of illusions (i.e., showing decreased susceptibility to some types of illusions, but *increased* susceptibility to other types of illusions) can offer important clues as to the underlying neurophysiological systems that may be affected. Indeed, of greatest relevance for future research is the examination of how structural and functional neurophysiological phenotypes associated with ASD can manifest into clinical symptomology, and such work will certainly require study of individuals with ASD diagnoses. The use of alternative methodological approaches to studying ASD, however, is still a crucial aspect for advancement in understanding this disorder. Specifically, refinement of traditional methodological approaches through identification of mediating variables that, when controlled for, can significantly strengthen the validity and certainty of the conclusions that are made within and across studies on ASD will greatly advance scientific knowledge within this field of research. With a combination of both approaches, we can hopefully gain a more sound understanding as to the etiology and underlying neurophysiology that characterize the often mysterious nature of autism.

REFERENCES CITED

American Psychiatric Association, (1994). Diagnostic and statistical manual of mental disorders (4^{th} Ed.). Washington, DC: Author.

Angst, J., Gamma, A., Endrass, J., Goodwin, R., Ajdacic, V., Eich, D., & Rossler, W. (2004). Obsessive-compulsive severity spectrum in the community: prevalence, comorbidity, and course. *Eur Arch Psychiatry Clin Neuroscience, 254*, 156-164.

Auyeung, B., Baron-Cohen, S., Chapman, E., Knickmeyer, R., Taylor, K., & Hackett, G. (2006). Foetal testosterone and the child systemizing quotient. *European Journal of Endocrinology, 155,* 123-130.

Auyeung, B., Baron-Cohen, S., Ashwin, E., Knickmeyer, R., Taylor, K., & Hackett, G. (2009). Fetal testosterone and autistic traits. *British Journal of Psychology, 100(1*), 1-22

Auyeung, B., Taylor, K., Hackett, G., & Baron-Cohen, S. (2010). Foetal testosterone and autistic traits in 18 to 24-month-old children. *Molecular Autism, 1(1),* 1-11.

Barbeau, E.B., Mendrek, A., & Mottron, L. (2009). Are autistic traits autistic? *British Journal of Psychology, 100,* 23-28.

Barnes, K.A., Howard, J.H., Howard, D.V., Gilotty, L., Kenworthy, L., Gaillard, W.D., & Vaidya, C.J. (2008). Intact implicit learning of spatial context and temporal sequences in childhood autism spectrum disorder. *Neuropsychology, 22(5),* 563-570.

Baron-Cohen, S. (2002). The extreme male brain theory of autism. *Trends in Cognitive Science, 6,* 248-254.

Baron-Cohen, S. (2006). The hyper-systemizing, assortative mating theory of autism. *Progress in Neuro-Psychopharmacology & Biological Psychiatry, 30*, 865-872.

Baron-Cohen, S. (2008). Autism, hypersystemizing, and truth. *The Quarterly Journal of Experimental Psychology, 61(1),* 64-75.

Baron-Cohen, S. (2009). Autism: The empathizing-systemizing (E-S) theory. *The Year in Cognitive Neuroscience, 1156*, 68-80.

Baron-Cohen, S., & Hammer, J. (1997) Parents of children with Asperger syndrome: what is the cognitive phenotype? *Journal of Cognitive Neuroscience, 9*, 548-554.

Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: An investigation of adults with Asperger syndrome or high-functioning autism, and normal sex differences. *Journal of Autism and Developmental Disorders, 34*, 163-175.

Baron-Cohen, S., Leslie, A.M., & Frith, U. (1986). Mechanical, behavioral and intentional understanding of picture stories in autistic children. *British Journal of Developmental Psychology, 4*, 113-125.

Baron-Cohen, S., Wheelwright, S., & Jolliffe, T. (1997). Is there a "language of the eyes"? Evidence from normal adults, and adults with autism or Asperger syndrome. *Visual Cognition, 4,* 311-331.

Baron-Cohen, S. Ashwin, E., Ashwin, C., Tavassoli, T., & Chakrabarti, B. (2009). Talent in autism: hyper-systemizing, hyper-attention to detail and sensory hypersensitivity. *Philosophical Transactions of the Royal Society, 364,* 1377-1383.

Baron-Cohen, S., Richler, J., Bisarya, D., Gurunathan, N., & Wheelwright, S. (2003). The systemizing quotient: An investigation of adults with Asperger syndrome or high-functioning autism, and normal sex differences. *Proceedings of the Royal Society of London, B, 358*, 361-374.

Baron-Cohen, S., Wheelwright, S., Stott, C., Bolton, P., Goodyer, I. (1997). Is there a link between engineering and autism? *Autism, 1*, 153-163.

Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The "Reading the Mind in the Eyes" test revised version: A study with normal adults, and adults with Asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry and Allied Disciplines, 42,* 241-251.

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The autism-spectrum quotient (AQ): Evidence from Apserger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders, 31*, 5-17.

Bergman, H., & Engelbrektson, K. (1973). An examination of factor structure of rod-and-frame and embedded-figures test. *Perceptual and Motor Skills, 37,* 939-947.

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

Billington, J., Baron-Cohen, S., & Bor, D. (2008). Systemizing influences attentional processes during the Navon task: An fMRI study. *Neuropsychologia, 46,* 511-520.

Blakemore, C.B., Carpenter, R.H.S., & Georgeson, M.A. (1970). Lateral inhibition between orientation detectors in the human visual system. *Nature, 228*, 37–39.

Bolte, S., Holtmann, M., Poustka, F., Scheurich, A., & Schmidt, L. (2007). Gestalt perception and local-global processing in high-functioning autism. *Journal of Autism and Developmental Disorders, 37*, 1493-1504.

Bridgeman, B., Peery, S., & Anand, S. (1997). Interaction of cognitive and sensorimotor maps of visual space. *Perception & Psychophysics, 59(3),* 456-469.

Brosnan, M.J., Scott, F.J., Fox, S., & Pye, J. (2004). Gestalt processing in autism: Failure to process perceptual relationships and the implications for contextual understanding. *Journal of Child Psychology and Psychiatry, and Allied Disciplines, 45,* 459-469.

Carpenter, R.H.S., & Blakemore, C. (1973). Interactions between orientations in human vision. *Experimental Brain Research, 18*, 287–303.

Centers for Disease Control and Prevention (2007). Prevalence of autism spectrum disorders. Retrieved from: http://www.cdc.gov/mmwr/preview/mmwrhtml/ss5601a1.htm

Chen, L. (2005). The topological approach to perceptual organization. *Visual Cognition, 12(4),* 553-637.

Cian, C., Esquivie, D., Barraud, P.A., & Raphel, C. (1995). Respective contribution of orientation contrast and illusion of self-tilt to the rod-and-frame effect. *Perception, 24*, 623–630.

Coren, S., & Hoy, V.S. (1986). An orientation illusion analog to the rod and frames: Relational effects in the magnitude of the distortion. *Perception & Psychophysics, 39*, 159–163.

Coren, S., & Porac, C. (1987). Individual differences in visual-geometric illusions: Predictions from measures of spatial cognitive abilities. *Perception & Psychophysics, 41*, 211-219.

Coren, S., Girgus, J., Erlichman, H., & Hakstian, A.R. (1976). An empirical taxonomy of visual illusions. *Perception and Psychophysics, 20*, 129-137.

Dakin, S., & Frith, U. (2005). Vagaries of visual perception in autism. *Neuron, 48*, 497-507.

Dassonville, P. (2010). Dissociations of perception and action do not automatically imply independent visual processing streams. *Cognitive Neuroscience, 1(1)*, 62-63.

Dassonville, P., & Bala, J.K. (2004). Perception, action, and the Roelofs effect: a mere illusion of dissociation. *PLoS Biology, 2*, 1936-1945.

Dassonville, P., & Williamson, C. (2010). The systemizing trait of autism reflects a shift from reliance on global to local contextual cues. *Journal of Vision, 10 (7),* 458.

Dassonville, P., Sanders, T., & Capp, B. (2009). The rod-and-frame and simultaneous tilt illusions: Perception, action, and the two-wrongs hypothesis. *Journal of Vision, 9,* 845.

Dassonville, P., Walter, E., & Bochsler, T. (2007). A specific trait that modulates illusion susceptibility. Journal of Vision, 7(9), 918.

Dassonville, P., Bridgeman, B., Bala, J.K., Thiem, P., & Sampanes, A. (2004). The induced Roelofs effect: two visual systems or the shift of a single reference frame. *Vision Research, 44,* 603-611.

De Jonge, M.V., Kemner, C., & van Engeland, H. (2006). Superior disembedding performance of high-functioning individuals with autism spectrum disorders and their parents: The need for subtle measures. *Journal of Autism and Developmental Disorders, 36*, 677-683.

Dinstein, I., Pierce, K., Eyler, L., Solso, S., Malach, R., Behrmann, M., & Courchesne, E. (2011). Disrupted neural synchronization in toddlers with autism. *Neuron, 70*, 1218-1225.

Ebenholtz, S.M., & Benzschawel, T.L. (1977). The rod and frame effect and induced head tilt as a function of observed distance. *Perception & Psychophysics, 22(5),* 491-496.

Ekstrom, R.B., French, J.W., Harman, H.H., & Dermen, D. (1976). *Manual for kit of factor-referenced cognitive tests*. Princeton, New Jersey: Educational Testing Service.

Fink, G.R., Halligan, P.W., Marshall, J.C., Frith, C.D., Frackowiak, R.S.J., & Dolan, R.J. (1997). Neural mechanism involved in the processing of global and local aspects of hierarchically organized visual stimuli. *Brain: A Journal of Neurology, 120(10),* 1779-1791.

Fink, G.R., Halligan, P.W., Marshall, J.C., Frith, C.D., Frackowiak, R.S.J., & Dolan, R.J. (1996). Where in the brain does visual attention select the forest and the trees? *Nature, 382(6592),* 626-628.

Flevaris, A.V., Bentin, S., & Robertson, L.C. (2010a). Local or Global? Attentional selection of spatial frequencies binds shapes to hierarchical levels. *Psychological Science, 21(3),* 424-431.

Flevaris, A.V., Bentin, S., & Robertson, L.C. (2010b). Attention to hierarchical level influences attentional selection of spatial scale. *Journal of Experimental Psychology: Human Perception and Performance, 37(1),* 12-22.

Foa, E.B., Huppert, S.L., Langner, R., Kichic, R., Hajcak, G., & Salkovskis, P.M. (2002). The obsessive-compulsive inventory: Development and validation of a short version. *Psychological Assessment, 14(4),* 485-496.

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

Glicksohn, J., & Kinberg, Z. (2009). Performance on embedded figures tests: Profiling individual differences. *Journal of Individual Differences, 30(3),* 152-162.

Gogel, W.C., & Newton, R.E. (1975). Depth adjacency and the rod-and-frame illusion. *Perception and Psychophysics, 18(2),* 163-171.

Goodenough, D.R., Oltman, P.K., Sigman, E., Rosso, J., & Mertz, H. (1979). Orientation contrast effects in the rod-and-frame test. *Perception & Psychophysics, 25(5),* 419-424.

Grinter, E.J., Van Beek, P.L., Maybery, M.T., & Badcock, D.R. (2009). Brief report: Visuospatial analysis and self-rated autistic-like traits. *Journal of Autism and Developmental Disorders, 39*, 670-677.

Grinter, E.J., Maybery, M.T., Pellicano, E., Badcock, J.C., & Badcock, D.R. (2010). Perception of shapes targeting local and global processes in autism spectrum disorders. *Journal of Child Psychology and Psychiatry, 51(6),* 717-724.

Grinter, E.J., Maybery, M.T., Van Beek, P.L., Pellicano, E., Badcock, J.C., & Badcock, D.R. (2009). Global visual processing and self-rated autistic-like traits. *Journal of Autism and Developmental Disorders, 39*, 1278-1290.

Happe, F. (1996). Studying weak central coherence at low levels: Children with autism do not succumb to visual illusions. A research note. *Journal of Child Psychology and Psychiatry, 37(7)*, 873-877.

Happe, 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.

Hartley, S.L., & Sikora, D.M. (2009). Sex differences in autism spectrum disorder: An examination of developmental functioning, autistic symptoms, and coexisting behavior problems in toddlers. *Journal of Autism and Developmental Disorders, 39(12),* 1715-1722.

Hock, H.S., Gordon, G.P., & Marcus, N. (1974). Individual differences in the detection of embedded figures. *Perception & Psychophysics, 15(1),* 47-52.

Horowitz, T.S., & Wolfe, J.M. (1998).Visual search has no memory. *Nature, 394,* 575-577.

Howlin, P., Goode, S., Hutton, J., & Rutter, M. (2004). Adult outcome for children with autism. *Journal of Child Psychology and Psychiatry, 45,* 212-229.

Hubner, R., Volberg, G., & Studer, T. (2007). Hemispheric differences for global/local processing in divided attention tasks: Further evidence for the integration theory. *Perception & Psychophysics, 69*, 413-421.

Iarocci, G., Burack, J.A., Shore, D.I., Mottron, L., & Enns, J.T. (2006). Global-local visual processing in high functioning children with autism: Structural vs. implicit task biases. *Journal of Autism and Developmental Disorders, 36*, 117-129.

Ivarsson, T., & Melin, K. (2008). Autism spectrum traits in children and adolescents with obsessive-compulsive disorder (OCD). *Journal of Anxiety Disorders, 22*, 969-978.

Jarrold, C., Gilchrist, I.D., & Bender, A. (2005). Embedded figures detection in autism and typical development: preliminary evidence of a double dissociation in relationships with visual search. *Developmental Science, 8(4)*, 344-351.

Jolliffe, T., & Baron-Cohen, S. (1997). Are people with autism and Asperger syndrome faster than normal on the embedded figures test? *Journal of Child Psychology and Psychiatry, 38(5),* 527-534.

Kaland, N., Mortensen, E.L., & Smith, L. (2007). Disembedding performance in children and adolescents with Asperger syndrome or high-functioning autism. *Autism, 11(1),* 81-92.

Kaldy, Z., Kraper, C., Carter, A.S., & Blaser, E. (2011). Toddlers with autism spectrum disorders are more successful at visual search than typically developing toddlers. *Developmental Science, 14(5)*, 980-988.

Kanner, L. (1943). Autistic disturbances of affective contact. *Nervous Child, 2,* 217-250.

Knickmeyer, R., Baron-Cohen, S., Raggatt, P., & Taylor, K. (2005). Foetal testosterone, social relationships, and restricted interests in children. *Journal of Child Psychology and Psychiatry, 46(2),* 198-210.

Koldewyn, K., Jiang, Y.V., Weigelt, S., & Kanwisher, N. (2013). Global/local processing in autism: Not a disability but a disinclination. *Journal of Autism and Developmental Disorders*. DOI: 10.1007/s10803-013-1777-z.

Koshino, H., Carpenter, P.A., Minshew, N.J., Cherkassky, V.L., Keller, T.A., & Just, M.A. (2005). Functional connectivity in an fMRI working memory task in high-functioning autism. *NeuroImage, 24*, 810-821.

Labad, J., Menchon, J.M., Alonso, P., Segalas, C., Jimenez, S., Jaurrieta, N., Leckman, J.F., & Vallejo, J. (2008). Gender differences in obsessive-compulsive symptom dimensions. *Depression and Anxiety, 25*, 832-838.

Lahaie, A., Mottron, L., Arguin, M., Berthiaume, C., Jemel, B., & Saumier, D. (2006). Face perception in high-functioning autistic adults: Evidence for superior processing of face parts, not for a configural face-processing deficit. *Neuropsychology, 20(1)*, 30-41.

Lawson, J., Baron-Cohen, S., & Wheelwright, S. (2004). Empathising and systemizing in adults with and without Asperger syndrome. *Journal of Autism and Developmental Disorders, 34,* 301-310.

Lee, P.S., Foss-Feig, J., Henderson, J.G., Kenworthy, L.E., Gilotty, L., Gaillard, W.D., & Vaidya, C.J. (2007). Atypical neural substrates of Embedded Figures Task performance in children with autism spectrum disorder. *NeuroImage, 38*, 184-193.

Lester, B., & Dassonville, P. (2014). The role of the right superior parietal lobule in processing visual context for the establishment of the egocentric reference frame. *Journal of Cognitive Neuroscience*, 1-9.

Malisza, K.L., Clancy, C., Shiloff, D., Foreman, D., Holden, J., Jones, C., Paulson, K., Summers, R., Yu, C.T., & Chudley, A.E. (2011). Functional evaluation of hidden figures object analysis in children with autistic disorder. *Journal of Autism and Developmental Disorders, 41,* 13-22.

Manjaly, Z.M., Bruning, N., Neufang, S., Stephan, K.E., Brieber, S., Marshall, J.C., Kamp-Becker, I., Remschmidt, H., Herpertz-Dahlmann, B., Konrad, K., & Fink, G.R. (2007). Neurophysiological correlates of relatively enhanced local visual search in autistic adolescents. *NeuroImage, 35,* 283-291.

Markram, H., & Markram, K. (2010). The intense world theory – a unifying theory of the neurobiology of autism. *Frontiers in Human Neuroscience, 4,* 1-29.

Markram, H., Rinaldi, T., & Markram, K. (2007). The intense world syndrome – an alternative hypothesis for autism. *Frontiers in Neuroscience, 1(1),* 77-96.

Mitchell, P., Mottron, L., Soulieres, I., & Ropar, D. (2010). Susceptibility to the shepard illusion in participants with autism: Reduced top-down influences within perception? *Autism Research, 3,* 133-119.

Mottron, L., Belleville, S., & Menard, E. (1999). Local bias in autistic subjects as evidenced by graphic tasks: Perceptual hierarchization or working memory deficit? *Journal of Child Psychology and Psychiatry, 40*, 743-755.

Mottron, L., Peretz, I., & Menard, E. (2000). Local and global processing of music in high-functioning persons with autism: Beyond central coherence? *Journal of Child Psychology and Psychiatry, 41(8)*, 1057-1065.

Mottron, L., Burack, J.A., Stauder, J.E.A., & Robaey, P. (1999). Perceptual processing among high-functioning persons with autism. *Journal of Child Psychology and Psychiatry, 40(2)*, 203-211.

Mottron, L, Burack, J.A., Iarocci, G., Belleville, S., & Enns, J.T. (2003). Locally oriented perception with intact global processing among adolescents with high-functioning autism: Evidence from multiple paradigms. *Journal of Child Psychology and Psychiatry, 44(6)*, 904-913.

Mottron, L., Dawson, M., Soulieres, I., Hubert, B., & Burack, J. (2006). Enhanced perceptual functioning in autism: An update, and eight principles of autistic perception. *Journal of Autism and Developmental Disorders, 36(1)*, 27-43.

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology, 9*, 353-383.

O'Riordan, M.A., & Plaisted, K.C. (2001). Enhanced discrimination in autism. *Quarterly Journal of Experimental Psychology, 54(4)*, 961-979.

O'Riordan, M.A., Plaisted, K.C., Driver, J., & Baron-Cohen, S. (2001). Superior visual search in autism. *Journal of Experimental Psychology: Human Perception & Performance, 27,* 719-730.

Plaisted, K., O'Riordan, M., & Baron-Cohen, S. (1998). Enhanced visual search for a conjunctive target in autism: A research note. *Journal of Child Psychology and Psychiatry, 39*, 777-783.

Plaisted, K., O'Riordan, M., & Baron-Cohen, S. (1998). Enhanced discrimination of novel, highly similar stimuli by adults with autism during a perceptual learning task. *Journal of Child Psychology and Psychiatry, 39(5)*, 777-783.

Plaisted, K., Swettenham, J., & Rees, L. (1999). Children with autism show local precedence in a divided attention task and global precedence in a selective attention task. *Journal of Child Psychology and Psychiatry, 40*, 733-742.

Plaisted, K., Dobler, V., Bell, S., & Davis, G. (2006). The microgenesis of global perception in autism. *Journal of Autism and Developmental Disorders, 36(1),* 107-116.

Poom, L. (2000). Inter-attribute tilt effects and orientation analysis in the visual brain. *Vision Research, 40,* 2711–2722.

Prinzmetal, W., & Beck, D. (2001). The tilt-constancy theory of visual illusions. *Journal of Experimental Psychology: Human Perception and Performance, 27*, 206-217.

Rankins, D., Bradshaw, J.L., & Georgiou-Karistianis, N. (2005). Local-global processing in obsessive-compulsive disorder and comorbid Tourette's syndrome. *Brain and Cognition, 59*, 43-51.

Rinehart, N.J., Bradshaw, J.L., Moss, S.A., Brereton, A.V., & Tonge, B.J. (2000). Atypical interference of local detail on global processing in high-functioning autism and Asperger's disorder. *Journal of Child Psychology and Psychiatry, 41(6),* 769-778.

Ring, H.A., Baron-Cohen, B., Wheelwright, S., Williams, S.C.R., Brammer, M., Andrew, C., &Bullmore, E.T. (1999). Cerebral correlates of preserved cognitive skills in autism: A functional MRI study of embedded figures task performance. *Brain, 122,* 1305-1315.

Robertson, L.C. & Delis, D.C. (1986). "Part-whole" processing in unilateral brain damaged patients: Dysfunction of hierarchical organization. *Neuropsychology, 24*, 363-370.

Robertson, L.C., & Lamb, M.R. (1991). Neuropsychological contributions to theories of part/whole organization. *Cognitive Psychology, 23(2),* 299-330.

Robertson, L.C., Lamb, M.R., & Knight, R.T. (1988). Effects of lesions of temporal-parietal junction on perceptual and attentional processing in humans. *Journal of Neuroscience, 8,* 3757-3769.

Roelofs, C. (1935). Optische localization. *Archivesfür Augenheilkunde, 109*, 395–415.

Ropar, D., & Mitchell, P. (1999). Are individuals with autism and Asperger's syndrome susceptible to visual illusions? *Journal of Child Psychology and Psychiatry, 40*, 1283-1293.

Ropar, D., & Mitchell, P. (2001). Susceptibility to illusions and performance on visuospatial tasks in individuals with autism. *Journal of Child Psychology and Psychiatry, 42*, 539-549.

Russell, A.J., Mataix-Cols, D., Anson, M., & Murphy, D.G.M. (2005). Obsession and compulsions in Asperger syndrome and high-functioning autism. *British Journal of Psychiatry, 186*, 525-528

Russel-Smith, S.N., Maybery, M.T., Bayliss, D.M., & Sng, A.A.H. (2012). Support for a link between the local processing bias and social deficits in autism: An investigation of embedded figures test performance in non-clinical individuals. *Journal of Autism and Developmental Disorders.* DOI: 10.1007/s10803-012-1506-z.

Sarachana, S., Xu, M., Wu, R.C., & Hu, V.W. (2011). Sex hormones in autism: Androgens and estrogens differentially and reciprocally regulate RORA, a novel candidate gene for autism. *PLoS ONE, 6(2),* 1-9.

Schwarzkopf, D.S., Song, C., & Rees, G. (2011). The surface area of human V1 predicts subjective experience of object size. *Nature Neuroscience, 14,* 28-30.

Seltzer, M.M., Krauss, M.W., Shattuck, P.T., Orsmond, G., Swe, A., & Lord, C. (2003). The symptoms of autism spectrum disorders in adolescence and adulthood. *Journal of Autism and Developmental Disorders, 33,* 565-581.

Shah, A., & Frith, U. (1983). An islet of ability in autism: a research note. *Journal of Child Psychology and Psychiatry, 24,* 613-620.

Shah, A., & Frith, U. (1993). Why do autistic individuals show superior performance on the Block Design task? *Journal of Child Psychology and Psychiatry, 34*, 1351-1364.

Sigman, E., Goodenough, D.R., & Flanagan, M. (1979). Instructions, illusory self-tilt and the rod-and-frame test. *The Quarterly Journal of Experimental Psychology, 31(1),* 155-165.

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*, 2705-2739.

Spinelli, D., Antonucci, G., Daini, R., & Zoccolotti, P. (1995). Local and global visual mechanisms underlying individual differences in the rod-and-frame illusion. *Perception & Psychophysics, 57(6),* 915-920.

Spinelli, D., Antonucci, G., Goodenough, D.R., Pizzamiglio, L., & Zoccolotti, P. (1991). Psychophysiological mechanisms underlying the rod and frame illusion. In S. Wapner & J. Demick (Eds.), *Field dependence-independence: Cognitive style across the life span* (pp. 37-60). Hillsdale, N.J.: Erlbaum.

Sripati, A.P., & Olson, C.R. (2009). Representing the forest before the trees: A global advantage effect in monkey inferotemporal cortex. *Journal of Neuroscience, 29(24),* 7788-7796.

Sutherland, A., & Crewther, D.P. (2010). Magnocellular visual evoked potential delay with high autism spectrum quotient yields a neural mechanism for altered perception. *Brain, 133,* 2089-2093.

Teunisse, J.P., & Gelder, B. (2003). Face processing in adolescents with autistic disorder: The inversion and composite effects. *Brain and Cognition, 52,* 285-294.

Volkmar, F.R., & McPartland, J.C. (2014). From Kanner to DSM-5: Autism as an evolving diagnostic concept. *Annual Review of Clinical Psychology, 10,* 193-212.

Wakabayashi, A., Baron-Cohen, S., Uchiyama, T., Yoshida, Y., Kuroda, M., & Wheelwright, S. (2007). Empathizing and systemizing in adults with and without autism spectrum conditions: Cross-cultural stability. *Journal of Autism and Developmental Disorders, 37*, 1823-1832.

Walter, E., & Dassonville, P. (2008). Visuospatial contextual processing in the parietal cortex: An fMRI investigation of the induced Roelofs effect. *Neuroimage, 42*, 1686-1697.

Walter, E., Dassonville, P., & Bochsler, T.M. (2009). A specific autistic trait that modulates visuospatial illusion susceptibility. *Journal of Autism and Developmental Disorders, 39*, 339-349.

Walter, E., & Dassonville, P., (2011). Activation in a frontoparietal cortical network underlies individual differences in the performance of an embedded figures task. *PLoS ONE, 6(7):* e20742.

Wang, L., Mottron, L., Peng, D., Berthiaume, C., & Dawson, M. (2007). Local bias and local-to-global interference without global deficit: A robust finding in autism under various conditions of attention, exposure time, and visual angle. *Cognitive Neuropsychology, 24(5)*, 550-574.

Wenderoth, P., & Johnstone, S. (1987). Possible neural substrates for orientation analysis and perception. *Perception, 16*, 693–709.

Wheelwright, S., Baron-Cohen, S., Goldenfeld, N., Delaney, J., Fine, D., Smith, R., Weil, L., & Wakabayashi, A. (2006). Predicting autism spectrum quotient (AQ) from the systemizing quotient-revised (SQ-R) and empathy quotient (EQ). *Brain Research, 1079*, 47-56.

White, S.J., & Saldana, D. (2011). Performance of children with autism on the embedded figures test: A closer look at a popular task. *Journal of Autism and Developmental Disorders, 41*, 1565-1572.

Witkin, H.A. (1950). Individual differences in ease of perception of embedded figures. *Journal of Personality, 19*, 1-15.

Witkin, H.A., & Asch, S.E. (1948). Studies in space orientation. IV. Further experiments on perception of the upright with displaced visual fields. *Journal of Experimental Psychology, 38(6),* 762-782.

Witkin, H.A., Oltman, P.K., Raskin, E., & Karp, S.A. (1971). *Manual for the Embedded Figures Test, Children's Embedded Figures Test, and Group Embedded Figures Test.* Palo Alto, CA: Consulting Psychologists Press.

Witkin, H.A., Dyk, R.B., Faterson, H.F., Goodenough, D.R., & Karp, S.A. (1962). *Psychological Differentiation: Studies of Development.* New York, NY: Wiley.

Witkin, H.A., Lewis, H.B., Hertzmann, M., Machover, K., Meissner, P.B., et al. (1954). *Personality through perception*. Westport, CT: Greenwood Press.

Wolfe, J.M., Cave, K.R., Franzel, S.L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance, 15*419-433.

Woodman, G.F., Vogel, E.K., & Luck, S.J. (2001). Visual search remains efficient when visual working memory is full. *Psychological Science, 12*, 219-224.

Yovel, G., Yovel, I., & Levy, J. (2001). Hemispheric asymmetries for global and local visual perception: Effects of stimulus and task factors. *Journal of Experimental Psychology, 27(6),* 1369-1385.

Zoccolotti, P., Antonucci, G., & Spinelli, D. (1993). The gap between rod and frame influences the rod-and-frame effect with small and large inducing displays. *Perception & Psychophysics, 54(1),* 14-19.

Zoccolotti, P., Antonucci, G., Goodenough, D.R., Pizzamiglio, L., Spinelli, D. (1992). The role of frame size on vertical and horizontal observers in the rod-and-frame illusion. *Acta Psychologica, 79*, 171–187.