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The Relationship between Early and Intermediate Level Spatial Vision During Typical Development and in Autism Spectrum Disorder

par
Audrey Perreault

Département de psychologie
Faculté des arts et des sciences

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Résumé

Certaines recherches ont investigué le traitement visuel de bas et de plus hauts niveaux chez des personnes neurotypiques et chez des personnes ayant un trouble du spectre de l'autisme (TSA). Cependant, l'interaction développementale entre chacun de ces niveaux du traitement visuel n'est toujours pas bien comprise. La présente thèse a donc deux objectifs principaux. Le premier objectif (Étude 1) est d'évaluer l'interaction développementale entre l'analyse visuelle de bas niveaux et de niveaux intermédiaires à travers différentes périodes développementales (âge scolaire, adolescence et âge adulte). Le second objectif (Étude 2) est d'évaluer la relation fonctionnelle entre le traitement visuel de bas niveaux et de niveaux intermédiaires chez des adolescents et des adultes ayant un TSA. Ces deux objectifs ont été évalué en utilisant les mêmes stimuli et procédures. Plus précisément, la sensibilité de formes circulaires complexes (Formes de Fréquences Radiales ou FFR), définies par de la luminance ou par de la texture, a été mesurée avec une procédure à choix forcés à deux alternatives.

Les résultats de la première étude ont illustré que l'information locale des FFR sous-jacents aux processus visuels de niveaux intermédiaires, affecte différemment la sensibilité à travers des périodes développementales distinctes. Plus précisément, lorsque le contour est défini par de la luminance, la performance des enfants est plus faible comparativement à celle des adolescents et des adultes pour les FFR sollicitant la perception globale. Lorsque les FFR sont définies par la texture, la sensibilité des enfants est plus faible comparativement à celle des adolescents et des adultes pour les conditions locales et globales. Par conséquent, le type d'information locale, qui définit les éléments locaux de la forme globale, influence la période à laquelle la sensibilité visuelle atteint un niveau développemental similaire à celle identifiée chez les adultes. Il est possible qu'une faible intégration visuelle entre les mécanismes de bas et de niveaux intermédiaires explique la sensibilité réduite des FFR chez les enfants. Ceci peut être attribué à des connexions descendantes et horizontales immatures ainsi qu'au sous-développement de certaines aires cérébrales du système visuel.

Les résultats de la deuxième étude ont démontré que la sensibilité visuelle en autisme est influencée par la manipulation de l'information locale. Plus précisément, en présence de luminance, la sensibilité est seulement affectée pour les conditions sollicitant un traitement local chez les personnes avec un TSA. Cependant, en présence de texture, la sensibilité est réduite pour le traitement visuel global et local. Ces résultats suggèrent que la perception de formes en autisme est reliée à l'efficacité à laquelle les éléments locaux (luminance versus texture) sont traités. Les connexions latérales et ascendantes / descendantes des aires visuelles primaires sont possiblement tributaires d'un déséquilibre entre les signaux excitateurs et inhibiteurs, influençant ainsi l'efficacité à laquelle l'information visuelle de luminance et de texture est traitée en autisme. Ces résultats supportent l'hypothèse selon laquelle les altérations de la perception visuelle de bas niveaux (local) sont à l'origine des atypies de plus hauts niveaux chez les personnes avec un TSA.

Mots-clés : trouble du spectre de l'autisme (TSA), développement, perception visuospatiale, traitement de bas niveaux, traitement de niveaux intermédiaires, luminance (premier ordre), texture (deuxième ordre).

Abstract

Most studies investigating visual perception in typically developing populations and in Autism Spectrum Disorder (ASD) have assessed lower- (local) and higher-levels (global) of processing in isolation. However, much less is known about the developmental interactions between mechanisms mediating early- and intermediate-level vision in both typically developing populations and in ASD. Based on such premise, the present thesis had two main objectives. The first objective (Study 1) was to evaluate the developmental interplay between low- and intermediate-levels of visual analysis at different periods of typical development (school-age, adolescence and adulthood). The second objective (Study 2) was to evaluate the functional relationship between low- and intermediate-levels of visual analysis in adolescents and adults diagnosed with ASD. Common methodologies were used to assess both objectives. Specifically, sensitivity to slightly curved circles (Radial Frequency Patterns or RFP), defined by luminance or texture information, was measured using a two alternative temporal forced choice procedure.

Results obtained in Study 1 demonstrated that local information defining a RFP (mediated by intermediate visual mechanisms) differentially affected sensitivity at different periods of development. Specifically, when the contour was luminance-defined, children performed worse when compared to adolescents and adults only when RFPs targeted a global processing style (few deformations along the RFP's contour). When RFPs were texture-defined, children's sensitivity was worse compared to that of adolescents and adults for *both* local and global conditions. Therefore, timing of adult-like sensitivity to RFPs is dependent on the type of local physical elements defining its global shape. Poor visual integration between low and intermediate visual mechanisms, which could be attributed to immature feedback and horizontal connections as well as under-developed visual cortical areas, may account for such reduced sensitivity in children.

Results obtained from Study 2 demonstrated that manipulating the local physical elements of RFPs impacts visual sensitivity in ASD. Specifically, sensitivity to RFPs is unaffected in ASD only when visual analysis is dependent on local deformations of luminance-defined contours. However, sensitivity is reduced for both local and global visual analysis when shapes are texture-defined. Such results suggest that intermediate-level, shape perception in ASD is functionally related to the efficacy with which local physical elements (luminance versus texture) are processed. It is possible that abnormal lateral or feed-forward / feedback connectivity within primary visual areas in ASD, which possibly arise from excitatory / inhibitory signalling imbalance, accounts for differential efficacy with which luminance and texture information is processed in ASD. These results support the hypothesis that atypical higher-level perception in ASD, when present, may have early (local) visual origins.

Keywords : Autism Spectrum Disorder (ASD), development, visuo-spatial perception, low-level vision, intermediate level vision, luminance-defined (first-order) information, texture-defined (second-order) information.

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List of Abbreviations

2-IFC: two-interval forced choice

ADI-R: Autism Interview Revised – General

ADOS-G: Autism Diagnostic Observational Schedule – General

APA: American Psychiatric Association

AS: Autism Spectrum

ASD: Autism Spectrum Disorder

CETED: Clinique d’évaluation des troubles envahissants du développement

DSM-IV-TR: Diagnostic Manual for Mental Disorders – 4th ed. Text rev.

DSM-V: Diagnostic Manual for Mental Disorders – 5th ed.

EPF: Enhanced Perceptual Functioning

FFR: Formes de fréquences radiales

fMRI: functional Magnetic Resonance Imaging

FRF: Filter – Rectify – Filter

HIPPEA: High, Inflexible Precision of Prediction Errors in Autism

LGN: Lateral Geniculate Nucleus

RF: Radial Frequencies

RFP: Radial Frequency Patterns

TSA: Trouble du spectre de l’autisme

TTT: Trigger-Threshold-Target

WCC: Weak Central Coherence

"Start by doing what's necessary;

then do what's possible;

and suddenly you are doing the impossible."

Francis of Assisi

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Chapter 1: Thesis Overview

Most research investigating the development of visual mechanisms has assessed lower- (local) and higher-levels (global) of processing in isolation. Consequently less is known about the developmental interactions between mechanisms mediating early- and intermediate-level vision. This is true for both typically developing children, and individuals diagnosed with Autism Spectrum Disorder (ASD). Within this context, the objective of this thesis was twofold. The first objective (Study 1) was to evaluate the development of intermediate-level vision by assessing the ability to discriminate circular shapes (global) whose contour was defined by different local physical elements (luminance and texture) at different periods of typical development (school-ages, adolescence and adulthood). Using the same methodology, a second goal (Study 2) was to assess the relationship between early and intermediate level visual processing in adolescents and adults diagnosed with ASD. By better understanding how early and intermediate levels of visual processing are related in ASD, the origins of perceptual particularities in ASD and their impact on higher-level cognitive functioning can better be understood. Such knowledge may have major clinical and heuristic consequences by defining the origin of both cognitive and higher-level, socially related perceptual anomalies (face perception) that defines both the cognitive and perceptual phenotypes of ASD.

This thesis is presented as a series of seven chapters, which incorporates the present chapter (Chapter 1). Chapter 2 contains a brief overview of the visual system, including a description of its different pathways and their characteristic functions. The relationship residing between low- and intermediate levels of spatial vision is then introduced. Visual processing involved when analyzing visual stimuli used in the studies presented in this thesis is then summarized and followed by a description of developmental trajectories for different visual abilities. Chapter 2 concludes with the rational for Study 1, which aimed at assessing the development of the interplay between low and intermediate levels of processing. Chapter 3 is the exact reproduction of the first published article (Study 1) included in the thesis, entitled "Investigating the interaction between low and intermediate levels of spatial vision at different periods of development", authored by Perreault, Habak, Lepore, & Bertone (2013).

Chapter 4 provides an overview of ASD by first defining its diagnostic criteria, followed by a brief sections regarding its prevalence and possible origins. Subsequence sections define differential visual perception in ASD followed by a presentation of perception-relevant neurocognitive theories. Chapter 4 concludes with a rational for Study 2, which aimed at assessing the functional link between low- and mid-level visuo-spatial perception in ASD. Chapter 5 is an exact reproduction of the second published article (Study 2) included in the thesis, entitled, "Behavioral evidence for a functional link between low- and mid-level visual perception in the Autism Spectrum", authored by Perreault, Habak, Lepore, Mottron, & Bertone (2015).

Chapter 6 provides a general conclusion of the work presented in this thesis. Research objectives and hypotheses are reviewed, followed by a brief summary of the results obtained in Studies 1 and 2 followed by interpretations of the findings. Theoretical and clinical implications are then discussed, concluding with limitations to both studies and suggestions for future research directions. Finally, Chapter 7 provides a brief conclusion summarizing main findings presented in this thesis.

Chapter 2: Organization of the Visual System: Hierarchy and Specialization

2.1 Luminance- vs texture-defined information processing

The visual system is a very complex and organized system that is designed in a hierarchical manner (de Haan & Cowey, 2011; Zhuo, Cai, Fu, & Zhang, 2011). Retinal ganglion cells transform light into electrical signals through the optic nerve to the lateral geniculate nucleus (LGN) of the thalamus and the primary visual cortex (V1). These visual areas have 'simple cells' which are tuned for specific stimulus characteristics such as orientation and spatial frequency that are luminance-defined, also known as first-order information (Baker & Mareschal, 2001; Ferster & Miller, 2000; Hubel & Wiesel, 1962). The tuning of simple cells for such stimulus attributes is due to the occurrence of both excitatory and inhibitory discharge, surrounding the sub-regions of these simple cells' receptive fields. The pattern of the discharge further depends on the simple cell's preference for various stimulus attributes, such as the local orientation of gratings (Baker & Mareschal, 2001; DeValois & De Valois, 1988; Hubel & Wiesel, 1962). Although 'simple cells' are known to be tuned for luminance-defined stimuli, they are not sufficiently specialized to process more complex stimuli attributes, such as direction, disparity, and texture, also referred to as second-order information (Baker, 1999; Baker & Mareschal, 2001; Ferster & Miller, 2000; Nassi & Callaway, 2009). To process such attributes, more specialized neurons, located within V1 and in extra-striate areas (i.e., V2) are solicited (Baker, 1999; Baker & Mareschal, 2001; Ferster & Miller, 2000; McGraw, Levi, & Whitaker, 1999; Nassi & Callaway, 2009). Signals from the LGN, V1, and V2 are integrated within extra-striate visual areas in order to perceive texture-defined information coherently (Badcock, Clifford, & Khuu, 2005). Furthermore, research investigating luminance- and texture-defined visual processing suggests that each type of stimuli targets separate mechanisms (Landy & Oruc, 2002; Larsson, Landy, & Heeger, 2006; Morgan, Mason, & Baldassi, 2000; Reynaud, Tang, Zhou, & Hess, 2014). In fact, Larsson et al. (2006) suggest that there are two different types of neurons located in most visual areas for the processing of luminance- and texture-defined information.

Different perceptual models have been proposed to explain how luminance- and texture-defined information is processed by the visual system. Specifically, the linear filter model has been put forward to explain how changes in local luminance, which can be identified everywhere in our environment, are perceived (Baker & Mareschal, 2001). According to the model, linear summation of excitatory and inhibitory discharge of simple cells, located in primary visual area V1, allows for the detection of first-order information (Baker & Mareschal, 2001). The linear filter model cannot explain processing of texture-defined information. Specifically, processing of texture information by V1 simple cells would result in the cancellation of inputs instead of proper linear summation of excitatory and inhibitory discharge given that simple cells in V1 receive the same amount of luminance in the presence of texture (Baker & Mareschal, 2001; Kingdom, Prins, & Hayes, 2003). As a consequence, processing of second-order information requires an extra step, as proposed by the Filter-Rectify-Filter (FRF) model (Baker & Mareschal, 2001; Chubb & Sperling, 1988; Dakin, Williams, & Hess, 1999; Kingdom et al., 2003; Landy & Graham, 2004). According to this model, the rectification stage converts all responses to a positive discharge so as to ensure that there is no cancellation during the second stage of filtering. The resulting percept of texture information is achieved when neurons at the second-stage of filtering, which have larger receptive fields as compared to those responsible for first-stage filtering, sum the activation of transformed filters as converted from the rectification stage (Kingdom et al., 2003). Although the FRF model is thought to correctly represent processing of second-order information, Hallum, Landy, and Heeger (2011) propose that the FRF model cannot account for the processing of all types of second-order information and suggest that a normalization stage (i.e. surround suppression) be necessary. They therefore propose that a model based on Filter-Rectify-Normalization-Filter would best account for how second-order information is perceived. More research is needed to assess whether this model can be used to replace the FRF model.

The FRF model is supported by both behavioural and imaging data that suggests that luminance- and texture-defined information (static and dynamic) is processed by different cortical mechanisms within the visual hierarchy (see Baker, 1999; Baker & Mareschal, 2001 for review). For example, psychophysical studies have demonstrated that visual adaptation to luminance-defined stimuli does not have an impact on sensitivity to texture-defined stimuli (Nishida, Ledgeway, & Edwards, 1997; Whitaker, McGraw, & Levi, 1997). Furthermore, perception of luminance-defined stimuli appears to be improved in the presence of a luminance-defined background, which does not facilitate the perception of texture-defined stimuli. The same is true for texture-defined stimuli, whereby a texture-defined background only improves sensitivity to texture-defined stimuli (Schofield & Georgeson, 1999). Imaging studies also point to different mechanisms for the perception of luminance- versus texture-defined information. For example, research has shown that specific lesions to different extra-striate visual areas differently affect sensitivity to luminance-defined information as compared to texture-defined information and vice versa (Greenlee & Smith, 1997; Vaina & Cowey, 1996; Vaina, Cowey, & Kennedy, 1999; Vaina, Makris, Kennedy, & Cowey, 1998). Overall, such results point to the solicitation of different visual mechanisms (i.e., striate vs extra-striate) depending on the type of visual information perceived.

2.2 Stream-specific processing: magno (dorsal-stream) vs parvocellular (ventral-stream) processing

In addition to multiple visual areas responsible for the processing of different types of visual information (i.e., luminance and texture), the visual system also consists of larger cortical pathways or streams that are differentially activated by stimuli characteristics. For example, connections between the LGN and neurons located in primary visual areas form connections organized within the magnocellular (or dorsal-stream) and parvocellular (ventral-stream) pathways. The magnocellular pathway plays a role in processing of motion and depth, whereas the parvocellular pathway is primarily involved in processing of form and colour information (Nassi & Callaway, 2009). From the primary visual areas, other projections to extra-striate cortical areas are created and are known as the dorsal and ventral pathways. The dorsal pathway, connecting primary visual areas to parietal regions, is involved in perception of motion and visual guidance when reaching for an object (Goodale & Milner, 1992; Nassi & Callaway, 2009). On the other hand, the ventral pathway, which projects to inferior temporal areas, is responsible for the recognition of shapes, objects, and faces (Goodale & Milner, 1992; Grill-Spector & Malach, 2004; Scherf, Behrmann, Humphreys, & Luna, 2007). For example, during object perception, elementary visual information is processed locally by mechanisms operating within early visual areas. Information is then integrated into meaningful forms or configurations, such as circularity, by specialized mechanisms operating in higher-level, extra-striate visual areas (i.e., V4) (Loffler, 2008; Wilson & Wilkinson, 1998; Wilson, Wilkinson, & Asaad, 1997).

Connections within the different visual pathways follow different trajectories, with signals being sent both up- and down-stream. Signals sent upstream through dorsal and ventral pathways are guided by feed-forward connections. Such connections send local computations from V1 and V2 to higher order cortical areas so that a coherent percept can be obtained (Bullier, 2001). This visual processing is performed pre-attentively and unconsciously (Lamme & Roelfsema, 2000). Although these connections are necessary for a comprehensive visual analysis, they cannot interpret visual information in the presence of ambiguity, such as in the presence of shadows or occlusion. In such circumstances, other connections are necessary, such as feedback and horizontal or lateral connections. Feedback projections send signals downstream from higher order cortical areas to V1 and the LGN (Bullier, 2001). Computations performed by higher order cortical areas will therefore influence responses of V1 and V2 neurons in order to obtain an accurate analysis of the perceived information. For feedback connections to have an influence on early level areas, downward projections must be sent very quickly, slightly delaying the information sent from feed-forward connections. Feedback connections allow for global representations to be sent to primary visual areas. The interplay between feed-forward and feedback connections typically allows for global representations to be perceived first (Bullier, 2001). However, under some circumstances (e.g. visual search), feedback connections take longer to reach low-level visual areas given that attentional resources and visual awareness are required (Lamme & Roelfsema, 2000). Finally, there are also horizontal or lateral connections. Such projections send signals within particular cortical areas, between laminar columns. Research has shown that horizontal connections play a role in grouping perceptual information and contour integration (Choe & Miikkulainen, 2004; Lamme & Roelfsema, 2000).

2.3 Interplay between low- and intermediate levels of spatial vision

Over the years, much research has been conducted to assess how the visual system integrates contours into coherent shapes. This is especially important considering that perception of shapes is the basis for object and face perception. Several review articles have in fact been written to discuss how the visual system integrates visual information into a coherent percept (see Loffler, 2008, 2015; Wilson & Wilkinson, 2015 for review). To achieve this, multiple computations with increasing complexity are performed throughout the visual hierarchy (Loffler, 2015). As was described above, neurons located in V1 detect local contour orientation and such information is then integrated by long-range lateral interactions between V1 cells that are situated close to one another at a given retinotopic location (Loffler, 2008, 2015). Excitatory discharges are combined since they provide input signalling that the discharge belongs to the same object. On the contrary, inhibitory discharge signals that the neuronal activity belongs to other types of visual information (Loffler, 2008). Excitatory connections between neurons as well as their local interactions are therefore the building blocks of contour integration as they are the first steps to extracting object contours (Loffler, 2008, 2015). The interaction between excitatory connections allows for subsequent stages of visual perception to further bind neuronal responses in order to eventually obtain a final perception of a coherent contour. Once local orientation information has been extracted by neurons located in V1, extra striate cortical areas residing in V2 will perform more complex computations so as to combine outputs coming from orientation-selective neurons in V1 (Loffler, 2015).

However, a problem remains. Excitatory connections are unable to detect whether different signals originate from the same object or from a different object in the presence of abrupt changes in the shape's contour or in the presence of occlusion (Loffler, 2008, 2015). In this case, the visual system must be able to identify which aspects of an object should be combined and which ones should be kept apart. Research has demonstrated that the visual system has global mechanisms whose role is to assist neighbouring cells when combining information. Intermediate visual area V4 appears to be a likely candidate for such a task, as demonstrated by physiological and imaging research (Dumoulin & Hess, 2007; Gallant, Braun, & Van Essen, 1993; Wilkinson et al., 2000). In fact, a population of neurons tuned for the processing of curved shapes has been identified in V4 (Pasupathy & Connor, 1999, 2001, 2002). Consequently, the role of mechanisms within V4 appears to be the pooling of information from signals at lower processing stages. Moreover, research is showing that V4 neurons play an important role in face perception in that integration at this level of the visual system appears to precede the accurate processing of faces (Wilkinson et al., 2000; Wilson, Wilkinson, Lin, & Castillo, 2000). Overall, processing of shapes requires input and interaction from both low and intermediate levels of visual processing, as these stages are crucial for accurate perception of contours. In fact, detrimental effects on the perception of shapes can result from either damage to early level visual mechanisms or from damage to intermediate level visual areas (see Loffler, 2015 for examples of such negative consequences).

2.4 Radial Frequency Patterns (RFP)

Given that the goal of this thesis is to investigate how low- and intermediate levels of visual analysis interact during typical development and in the Autism Spectrum (AS), we will now turn to a description of the stimuli used (i.e. Radial Frequency Patterns) in all experimental studies to assess the relationship of interest. Radial Frequency Patterns (RFP, see Figure 1) are complex circular shapes whose contour can be manipulated by adding deformations deviating from a perfect geometric circle (Wilkinson, Wilson, & Habak, 1998).

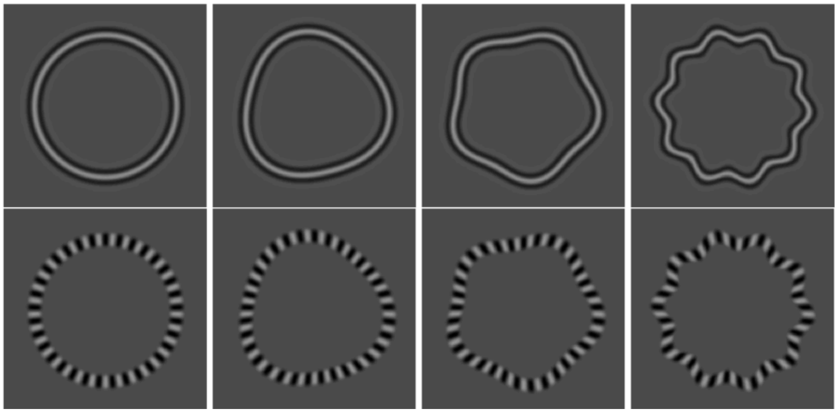

Figure 1. RFP of varying radial frequencies (zero, two, three, five, and 10). The top row depicts luminance-defined RFP, whereas the bottom row depicts texture-defined RFP.

In order to perceive RFPs, the visual system first processes local information ("bumps") around its contour via a local analysis by oriented spatial filters or neurons. At a second-stage of analysis, the local deformations (i.e., bumps) are spatially integrated and detected by cortical mechanisms operating in extra-striate visual areas that are responsible for the detection of forms (Poirier & Wilson, 2006). Such shapes are processed by intermediate-level visual mechanisms that integrate local deformations or curvatures (local elements or features) into a complete global representation (global pooling) of its shape (Gallant, Shoup, & Mazer, 2000; Loffler, 2008; Pasupathy & Connor, 1999, 2001, 2002; Wilkinson et al., 2000). In fact, imaging research has demonstrated that these stimuli activate both intermediate and higher-level brain areas within the ventral visual stream, which is responsible for both form (area V4) and face processing (fusiform face area) (Kanwisher, Stanley, & Harris, 1999; Wilson, Krupa, & Wilkinson, 2000).

Although the processing of RFP predominately requires visual integration, the processing can shift from local to global integration depending on the number of deformations along the circumference of the shape (Bell & Badcock, 2008; Jeffrey, Wang, & Birch, 2002; Loffler, 2008; Poirier & Wilson, 2006). Deformation detection of a circular shape relies on local curvature, with integration over only a limited portion of the contour for a high number of curvatures (≥ 10). For example, with greater numbers of curvatures surrounding the contour of the shape, a sequential analysis is performed, whereby information along the contour of the shape is added sequentially, resulting in what is known as probability summation (Loffler, Wilson, & Wilkinson, 2003; Schmidtmann, Kennedy, Orbach, & Loffler, 2012; Wilkinson et al., 1998). On the other hand, for fewer than five to eight deformations, integration is global over the entire shape (Jeffrey et al., 2002; Loffler et al., 2003). In this case, an object-centered approach is used, whereby information surrounding the contour of the shape is integrated in reference to the center, an approach known as global pooling (Loffler et al., 2003; Wilkinson et al., 1998). The type of visual processing (i.e. local or global) can also be influenced by the characteristics defining the contour of the shape. For example, research has demonstrated that chromatic shapes or RFP at low contrast are processed predominately by local shape cues no matter the number of curvatures surrounding the contour of the shape (Ivanov & Mullen, 2012; Mullen & Beaudot, 2002; Mullen, Beaudot, & Ivanov, 2011).

In addition to manipulating the number of curvatures surrounding the contour of the RFP, the physical attributes defining the shape can be manipulated by having RFPs defined by either luminance (first-order) or texture (second-order) information (Bell & Badcock, 2008; Loffler et al., 2003). As described above, the processing of texture information is more complex than for the processing of luminance information since an extra processing stage is necessary (Habak, Wilkinson, & Wilson, 2009; Lin & Wilson, 1996). By assessing the detection of RFPs with contours defined by either luminance and texture information, it is possible to assess whether manipulating the complexity of the shape differently influences intermediate level perception in typically developing individuals and in individuals on the Autism Spectrum (AS). Analysing the perception of circular shapes is especially important in Autism Spectrum Disorder (ASD) given their relevance to face perception, which is atypical in ASD. In addition, RFPs have been used successfully to assess form perception in both typically aging (Habak et al., 2009) and ASD (children) populations (Grinter, Maybery, Pellicano, Badcock, & Badcock, 2010). Therefore, RFP are ideal for effectively measuring the functional relationship between early and intermediate-level cortical mechanisms.

2.5 Development of Visual Abilities

A large body of research has been conducted in the aim of enhancing our current understanding of how the visual system functions throughout development (Braddick & Atkinson, 2011). Obtaining a better understanding of how the visual system develops is important, since abnormal transduction of visual information throughout the visual system can affect social and cognitive development such as in various neurodevelopmental disorders (Braddick & Atkinson, 2011; van den Boomen, van der Smagt, & Kemner, 2012). This being said, previous studies have assessed visual development for mechanisms operating at different levels within the visual hierarchy (e.g., local versus global information), recently summarized in two review articles (Braddick & Atkinson, 2011; van den Boomen et al., 2012). Interestingly, the developmental trajectories for different visual abilities are often contingent on the nature of the information being assessed (Bertone, Hanck, Guy, & Cornish, 2010; Braddick & Atkinson, 2011; Lewis & Maurer, 2005; van den Boomen et al., 2012).

At early levels of processing, such as that mediating visual acuity, contrast sensitivity, orientation selectivity, and tuning of spatial frequency, development begins during infancy (Braddick & Atkinson, 2011). However, maturity for such visual input occurs later during childhood. For example, adult-like sensitivity for contrast sensitivity occurs later in development, as depicted by behavioural studies (Benedek, Benedek, Keri, & Janaky, 2003; Ellemberg, Lewis, Liu, & Maurer, 1999). However, timing of adult-like sensitivity seems to be influenced by the type of spatial frequency presented. For example, development for contrast sensitivity depicted by high spatial frequencies occurs earlier in life at approximately 4-5 years of age as compared to those depicted by low spatial frequencies occurring at approximately 10-11 years of age (Adams & Courage, 2002; Benedek et al., 2003).

Differential developmental trajectories were also identified for other stimulus attributes, such as whether visual information is defined by either simple, luminance-defined (first-order) or more neurally-complex, texture-defined (second-order) information (Armstrong, Maurer, & Lewis, 2009; Bertone, Hanck, Cornish, & Faubert, 2008). An example of such differential development was demonstrated by Bertone et al. (2010), who found that adult-like sensitivity to Landolt-C patterns defined by luminance occurs at approximately 10-12 years of age but goes beyond 12 years of age for those defined by texture, as does the ability to identify a global contour embedded in noise (Hadad, Maurer, & Lewis, 2010; Kovacs, Kozma, Fehér, & Benedek, 1999). In general, the visual mechanisms responsible for processing simple, luminance-defined information seems to mature earlier than mechanisms underlying the integration of visual information into coherent forms.

When the analysis of visual information becomes progressively more complex, such as for the processing of shapes, maturation of mechanisms underlying visual processes takes longer. For example, the ability to identify a contour embedded in noise continuously improves until adolescence (Bertone, Hanck, Guy, & Cornish, 2010; Kovacs, 2000; Parrish, Giaschi, Boden, & Dougherty, 2005). Differences between age groups are not only identified in terms of sensitivity to such forms but also in terms of the task characteristics. For example, when detecting shapes, children seem to be affected to a greater extent by the spacing between local visual information compared to adults, who are more affected by the signal-to-noise ratio (Hadad et al., 2010; Kovacs et al., 1999). Furthermore, unlike adults, children do not seem to be facilitated by collinearity, which is the presence of continuation along a contour of a shape and is thought to assist in the detection of contours especially when there is greater spacing in between local cues (Kovacs et al., 1999).

Varying the stimulus attributes further seems to influence the age at which adult-like levels of performance, or maturity, is reached. Adult-like sensitivity to luminance- (i.e. 11-12 years old) and motion-defined (i.e. 7 years old) shapes occurs earlier in development than texture-defined shapes (i.e. after 12 years of age) (Hadad et al., 2010). The delayed maturation for texture-defined shapes (i.e., Landolt-C patterns) appears to contradict research findings demonstrating earlier maturation for the processing of simple texture-defined gratings (Bertone et al., 2010; Parrish et al., 2005). It is possible that timing of maturation be dependent on the type of stimuli presented. Specifically, earlier maturation seems to occur for simple features, whereas delayed maturation seems to appear for more complex visual information, such as for the processing of stimuli requiring the integration of visual information across space so as to perceive a pattern coherently (Armstrong et al., 2009; Bertone et al., 2008).

2.6 Rational for Study 1. The development of the interplay between low and intermediate levels of processing

Although much research is being conducted to assess development of different visual processes, much less is known about how differential development of different levels of visual analysis impacts the development of subsequent visual mechanisms. Therefore, Study 1 assessed the development of the interplay between low- and intermediate levels of processing, so as to evaluate whether differential development of mechanisms at one level effects visual processing at another level. This was done using RFP with varying amounts of deformations surrounding the contour (three, five, and 10 curvatures) targeting both local and global visual processing. Local contour elements were also manipulated by adding luminance- and texture-defined information to the contour of the shape. Forty-seven individuals participated in this first study and were placed into three age groups: 7 to 12, 13 to 17, and 18 to 26 years old. All participants were asked to identify which of two stimuli presentations was the RFP. The other stimulus was a perfect circle, with no curvatures surrounding the contour. Shapes had a radius of 1.5 degrees. Six different levels of amplitude modulations (0.001, 0.002, 0.004, 0.008, 0.016, and 0.032), representing the depth of the deformations and dips as a proportion change in radius (Wilkinson et al., 1998), were chosen for each RFP condition based on pilot testing. Threshold, estimated at 75% correct responses, was measured using a method of constant stimuli with a two-interval forced choice paradigm.

Since past research has demonstrated that visual processing underlying the perception of shapes takes longer to develop than the visual processing underlying local physical elements (Bertone et al., 2010; Kovacs, 2000; Parrish et al., 2005), it was predicted that sensitivity to RFP with fewer deformations around the contour (i.e. three and five radial frequencies) would take longer to reach adult-like sensitivity as compared to when there are greater numbers of deformations (i.e. 10 radial frequencies). Furthermore, it was predicted that visual development would take longer for shapes defined by texture information as compared to shapes defined by luminance information, since texture information is more complex to process visually (see Vandenbroucke, Scholte, van Engeland, Lamme, & Kemner, 2008 for review).

Chapter 3: Article 1

This is an exact reproduction of the following published article:

Investigating the Interaction between Low and Intermediate Levels of Spatial Vision at Different Periods of Development

Audrey Perreault (1,2), Claudine Habak (3), Franco Lepore (2), & Armando Bertone (1,4)

(1) Perceptual Neuroscience Lab for Autism and Development (PNLab), Rivière-des-Prairies Hospital, Montreal, Canada
(2) Centre de Recherche en Neuropsychologie et Cognition (CERNEC), Department of Psychology, Université de Montréal, Montreal, Canada
(3) Centre de Recherche, Institut Universitaire de Gériatrie and Visual Perception and Psychophysics Lab, Université de Montréal, Montreal, Canada
(4) School /Applied Child Psychology, Department of Education and Counselling Psychology, McGill University, Montreal, Canada

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3.1 Abstract

Although much research has investigated the visual development of lower- (local) and higher-levels (global) of processing in isolation, less is known about the developmental interactions between mechanisms mediating early- and intermediate-level vision. The objective of this study was to evaluate the development of intermediate-level vision by assessing the ability to discriminate circular shapes (global) whose contour was defined by different local attributes; luminance and texture. School-aged children, adolescents, and adults were asked to discriminate a deformed circle (radial frequency patterns or RFP) from a circle. RFPs varied as a function of (1) - number of bumps or curvatures (radial frequency of three, five, and ten) and (2) – the physical attribute (luminance or texture) that defined the contour. Deformation thresholds were measured for each radial frequency and attribute condition. In general, results indicated that when compared to adolescents and adults children performed worse only when luminance-defined shapes had fewer curvatures (i.e. three and five), but for texture-defined shapes, children performed worse across all types of radial frequencies (three, five, and ten). This suggests that sensitivity to global shapes mediated by intermediate level vision is differentially affected to the type of local information defining the global shape at different periods of development.

Keywords: Spatial vision, typical development, low-level vision, intermediate vision

3.2 Introduction

Visual object perception is the result of numerous levels of cortical processing that increase in complexity. For example, intermediate-level visual mechanisms underlying shape perception constitute a crucial step in the representation of complex visual objects, such as faces (van den Boomen, van der Smagt, & Kemner, 2012). The developmental trajectories of simple percepts or local attributes (e.g. lines) mediated by lower-level visual cortical mechanisms, along with those of complex or global representations (e.g. faces or objects) mediated by higher-level processes, are relatively well documented (Braddick & Atkinson, 2011; van den Boomen, van der Smagt, & Kemner, 2012). However, the relationship between lower and intermediate levels of perception has yet to be systematically assessed within a developmental context. This represents an important void in the literature since visual mechanisms operating at different levels within the visual hierarchy develop at different rates (Braddick & Atkinson, 2011), contingent on the type of the information each mechanism is most sensitive to (Lewis & Maurer, 2005; Braddick & Atkinson, 2011; van den Boomen, van der Smagt, & Kemner, 2012).

Visual mechanisms operating in V1, the earliest level of cortical processing, mediate simple information that is defined by changes in luminance (a first order characteristic; Ferster & Miller, 2000; Baker, 1999; Baker, & Mareschal, 2001). When visual information is defined by non-luminance information, such as texture (second-order attributes, mediated by V2; Nassi & Callaway, 2009; Ferster & Miller, 2000; Baker, 1999; Baker & Mareschal, 2001) sensitivity is relatively decreased during local orientation (Lin & Wilson, 1996), local curvature (Wilson & Richards, 1992), and global shape (Bell & Badcock, 2008; Hess, Achtman, & Wang, 2001) perception tasks. This differential sensitivity is also reflected during development. For example, adult-like sensitivity to Landolt-C patterns defined by luminance occurs at approximately 10-12 years of age but goes beyond 12 years of age for those defined by texture (Bertone, Hanck, Guy, & Cornish, 2010), as does the ability to identify a global contour embedded in noise (Kovács, Kozma, Fhér, & Benedek, 1999; Hadad, Maurer, & Lewis, 2010). In general, the visual mechanisms responsible for processing simple, luminance-defined information seems to mature earlier than mechanisms underlying the integration of visual information into coherent forms (Kovács, 2000; Parrish, Giaschi, Boden, & Dougherty, 2005; Bertone et al., 2010).

While attributes or characteristics (e.g. luminance or texture) can define a contour, features of the contour describe a global shape. Among other global stimuli, the human visual system displays exquisite (hyperacuity) sensitivity to radial frequency patterns (RFP). RFPs are complex circular shapes whose contour can be manipulated by adding deformations deviating from a perfect geometrical circle (Wilkinson, Wilson, & Habak, 1998). Such shapes are processed by intermediate-level visual mechanisms (most likely in V4) that integrate local deformations or curvatures (local elements or features) into a complete global representation (global pooling) of its shape (Pasupathy & Connor, 1999, 2001, 2002; Wilkinson, James, Wilson, Gati, Menon, & Goodale, 2000; Loffler, 2008; Gallant, Shoup, & Mazer, 2000).

However, when the number of deformations along the circumference varies, processing can shift towards local or global integration (Jeffrey, Wang & Birch, 2002; Bell & Badcock, 2008; Loffler, 2008; Poirier & Wilson, 2006). Deformation detection of a circular shape relies on local curvature, with integration over only a limited portion of the contour for a high number of curvatures (≥ 10). Precisely, with greater numbers of curvatures surrounding the contour of the shape, a sequential analysis is performed, whereby information along the contour of the shape is added sequentially, resulting in what is known as probability summation (Wilkinson et al, 1998; Loffler, Wilson, & Wilkinson, 2003; Schmidtmann, Kennedy, Orbach, & Loffler, 2012). On the other hand, for fewer than five-eight deformations, integration is global over the entire shape (Jeffrey, Wang & Birch, 2002; Loffler, Wilson, & Wilkinson, 2003). In this case, an object-centered approach is used, whereby information surrounding the contour of the shape is integrated in reference to the center, an approach known as global pooling (Wilkinson et al, 1998; Loffler, Wilson, & Wilkinson, 2003).

In addition to manipulating the number of curvatures surrounding the contour of the RFP, the physical attributes defining the shape can be manipulated by having RFPs defined by either luminance- (first-order) or texture-defined (second-order) information (Loffler, Wilson, & Wilkinson, 2003; Bell & Badcock, 2008). The processing of texture information is more complex than for the processing of luminance information since larger receptive fields of neurons tuned for local orientation need to be integrated, a process that takes longer than for luminance information. Therefore, an extra processing stage is involved when processing this physical attribute as compared to when luminance information defines the shape (Lin & Wilson, 1996; Habak, Wilson, & Wilkinson, 2009). By assessing the detection of RFPs defined by luminance and texture information, it is possible to assess whether manipulating the complexity of the shape differently influence intermediate level perception in children compared to adolescents and adults, which to our knowledge has never been conducted before.

In sum, the aim of the present study was to assess development of the interplay between low and intermediate levels of processing, by manipulating the attributes defining the contour (luminance - texture) and the amount of deformation surrounding the shape (local - global). To accomplish this, we used radial frequency patterns (RFP) defined by either luminance or texture that varied in the number of deformations about the contour.

3.3 Methods

3.3.1 Participants

Forty-seven participants in total participated in the study and were placed into three age groups (i) 7-12 years, n = 16, 7 girls and 9 boys, mean chronological age (CA) = 9.93; (ii) 13-17 years, n = 15, 3 girls and 12 boys, mean CA = 15.87; (iii) 18-26 years, n = 16, 2 women and 14 men, mean CA = 22.18. Forty-three of these participants were recruited from the Clinique d'Évaluation des Troubles Envahissants du Développement (CETED), at Rivière-des-Prairies Hospital. The remaining participants were recruited from outside the hospital setting. A semi-structured interview was used to exclude participants with a history of psychiatric treatment or learning disabilities, a familial history (1st degree) of mood disorders, autism or schizophrenia, defective vision or audition and who are taking medication. All participants had Wechsler IQ (i.e. WISC-III or WASI) of 80 or higher and had normal or corrected-to-normal far and near vision, which was assessed using both near and far acuity charts (i.e. near point directional –E- and –C-cards, Snellen letter sequence-A-new Logmar).

3.3.2 Apparatus and Stimuli

Stimulus construction, presentation, and data recordings were controlled using custom Matlab software, incorporating routines from the Psychophysics and Video Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on a gamma-corrected, 19-inch Viewsonic CRT G90fb monitor, driven by a MACBOOK PRO laptop, and a CS-100 Minolta Chromameter was used for luminance/color reading and monitor gamma-correction. Mean luminance of the monitor was 30.00 cd/m^2 (u' = 0.1912, v' = 0.4456 in CIE color space) with minimum and maximum luminance levels of 0.5 and 59.5 cd/m^2, respectively.

Stimuli consisted of radial frequency patterns (RFP), which resemble deformed circular contours and are defined by a sinusoidal modulation to a circle's radius according to the following equation:

$$r(\theta) = r_o(1+A \sin(\omega\theta + \phi))$$

where r and θ are the polar coordinates of the contour and r_o is the mean or average radius (that of the base circle). The shape's geometry is controlled by the remaining parameters: ω is the radial frequency, which represents the integer number of sinusoidal modulation cycles around the circumference (number of curvatures or bumps and dips), ϕ is the angular phase, which controls the overall orientation of the shape, and A is the amplitude of the modulation and represents the depth of the bumps and dips as a proportion change in radius (Wilkinson et al., 1998). In addition, stimuli were defined either by luminance (first-order) or texture (second-order) information. Luminance-defined RFPs (first-order; Figure 1, top) were constructed using a fourth derivative of a Gaussian (D4) with a peak spatial frequency of 4 cpd

[INSERT FIGURE 1 HERE]

(bandwidth = 1.24 cycles) and a luminance contrast of 90% (see Wilkinson, Wilson, & Habak, 1998). Texture-defined RFPs (second-order; Figure 1, bottom) were created by multiplying a radially modulated Gaussian Window by a radial carrier grating with a spatial frequency of 4 cpd and a luminance of 90% (see Habak, Wilkinson, & Wilson, 2004). For the pattern defined by second-order characteristics, we chose a texture that consisted of a sinusoidal carrier so that spatial frequency could be matched exactly to that of the first-order RFP, whereas a noise carrier (or other) would contain higher spatial frequencies and confound any differential effects of development on stimulus characteristics with spatial frequency sensitivity. In order to encourage participants to perceive the patterns globally, the position of all patterns was slightly jittered and presentation time was set at 200 ms. Radial frequencies of three, five, and ten cycles per circumference were presented in separate runs (see Figure 1). Based on pilot testing, six different levels of amplitude modulation were chosen (.001, .002, .004, .008, .016, and .032) for each RFP. Non-RFP (non-target) stimuli were perfect circular shapes (amplitude = 0).

3.3.3 Procedure

Thresholds for the minimal deformation (or amplitude) needed to detect the deformed circle (the RFP) were measured. The method of constant stimuli was used in a two-interval forced choice paradigm (2-IFC), where participants indicated which of the two intervals contained the deformed circle or RFP (amplitude > 0); the other interval contained a perfect circle (amplitude = 0). Each stimulus was presented for 200 ms with a 400 ms inter-stimulus interval, during which the mean-gray background was maintained. Thresholds were measured for RFPs of varying radial frequency (three, five, & ten RF) with contours defined by either luminance or texture, for a total of six experimental conditions. In each block, a single combination of radial frequency and contour-definition was shown. Within each block, six levels of deformation (amplitudes of .001, .002, .004, .008, .016, and .032) were presented 20 times in pseudo-random order, for a total of 120 trials per condition.

Prior to data collection, participants completed a brief practice session, with the same 2-IFC procedure as the experimental conditions. However, in order to facilitate comprehension of the task, radial frequency patterns were presented from easiest to hardest (amplitude of .062, .032, .016, .008, .004, .002, and .001). Throughout the entire testing session, participants were reminded to fixate the center of a uniform screen. In order to avoid participant fatigue, short breaks were provided after each condition. The experimenter entered the participants' response (first or second interval) by pressing a key on the computer's keyboard. Conditions were counterbalanced across all subjects. The entire testing session took approximately 1½ to 2 hours. This study was carried out in accordance with the Declaration of Helsinki as well as was approved by the ethics committee at Rivière-des-Prairies Hospital. All participants provided informed consent and were given financial compensation for their time.

3.3.4 Data Analysis

Data from each block were fit with a Weibull function (Weibull, 1951) using maximum likelihood estimation, and thresholds were estimated at 75% correct responses. Two separate mixed ANOVAs were conducted, one for first-order RFPs and the other for second-order RFPs. After analyzing the data for basic assumptions, two participants were identified as having extreme scores (i.e. two standard deviations above the mean) on all conditions. These participants (one child and one adult) were therefore removed from all analyses. The final sample size was 45, with 15 participants being included in each of the three age groups. All other basic assumptions were met except for that of sphericity. Since multiple analyses were performed and the basic assumption of sphericity was not met, the Greenhouse-Geisser estimated *F*-value and an alpha level of .01 were used (Tabachnick & Fidell, 2007). Finally, minimal deformation thresholds were logged transformed; all analyses were performed on log-transformed thresholds.

3.4 Results

The first analysis [Groups (between) X RFP (within)] was conducted to evaluate differences between age groups for luminance-defined RFPs of varying number of curvatures (three, five, ten RFs). From this analysis, a significant Group X RFP interaction was firstly identified, $F(2.76, 57.99) = 4.70$, $p = .006$, $\eta^2_{partial} = .18$ (see Figure 2). This interaction

[INSERT FIGURE 2 HERE]

indicated that age group differences vary for differing number of RFPs. Simple main effects tests, conducted to evaluate group differences for three, five, ten RFP, revealed group differences for RFPs of three [$F(2, 42) = 11.41$, $p < .001$, $\eta^2_{partial} = .35$] and five [$F(2, 42) = 5.60$, $p = .007$, $\eta^2_{partial} = .21$] radial frequencies. No group difference was noticed for RFPs of ten radial frequencies [$F(2, 42) = 3.43$, $p = .042$, $\eta^2_{partial} = .14$]. Tukey post hoc tests were performed to evaluate group differences for RFPs of three and five radial frequencies. For both types of RFPs, children performed worse compared to adolescents (three RFP: $p < .001$;

five RFP: $p = .004$) and adults (three RFP: $p < .001$; five RFP: $p = .01$); however, adolescents and adults performed similarly. These results are also evidenced when analyzing *Figure* 2, which demonstrates that thresholds decreased systematically as the number of curvatures surrounding the contour of the RFP increased suggesting that global processing (required for three or five radial frequencies – Jeffrey, Wang & Birch, 2002; Loffler, Wilson, & Wilkinson, 2003) is more difficult than local processing (required for ten radial frequencies – Jeffrey, Wang & Birch, 2002; Loffler, Wilson, & Wilkinson, 2003). The identified interaction revealed that children performed worse for first-order RFPs when a global processing strategy is required. Finally, a significant main effect of group was noted ($F(2, 42) = 12.44$, $p < .001$, $\eta^2_{partial} = .37$) with Tukey post hoc tests revealing that children performed overall worse compared to adolescents ($p < .001$) and adults ($p < .001$). No significant difference between adolescents and adults was evidenced. There was also a significant main effect of RFP ($F(1.38, 57.99) = 114.63$, $p < .001$, $\eta^2_{partial} = .73$). Tukey post hoc tests, calculated by hand using an alpha level at .01, revealed that it is more difficult to discriminate RFPs of three radial frequencies compared to five ($p < .01$) and ten ($p < .01$) radial frequencies, and it is more difficult to discriminate RFPs of five radial frequencies compared to ten radial frequencies ($p < .01$). These main effects will not be discussed further, since a significant Group X RFP interaction was evidenced.

A second analysis [Groups (between) X RFP (within)] was conducted to evaluate differences between age groups for texture-defined RFPs of varying number of curvatures (three, five, ten RFs). From this analysis, no significant Group X RFPs interaction was noticed, $F(3.96, 83{,}15) = 1.03$, $p = .40$, $\eta^2_{partial} = 0.05$. However, a significant main effect of group was evidenced, $F(2, 42) = 13.27$, $p < .001$, $\eta^2_{partial} = 0.39$. Tukey post hoc tests revealed that children performed worse compared to adolescents ($p < .001$) and adults ($p < .001$). No significant difference between adolescents and adults was evidenced. This result signifies that for texture-defined RFPs children performed worse for both global and local visual processing. There was also a significant main effect of RFP, $F(1.98, 83.15) = 16.87$, $p < .001$, $\eta^2_{partial} = 0.29$. Tukey post hoc tests, calculated by hand using an alpha level at .01, revealed that it is more difficult to discriminate RFPs of three radial frequencies compared to five ($p < .01$) and ten ($p < .01$) radial frequencies, but similar discrimination thresholds were identified for RFPs of five and ten radial frequencies. These results are evidenced on *Figure* 3, which

[INSERT FIGURE 3 HERE]

demonstrates that children's performance thresholds is poorer as compared to adolescents and adults, suggesting that global and local visual processing is more difficult when stimuli are defined by texture-defined information.

In general, school-aged children are less sensitivity than adolescents and adults when RFPs are texture-defined, regardless of radial frequency conditions (local or global). However, for luminance-defined RFPs, the performance of school-age children is similar to that of adults only when RFPs are discriminable using a local processing style (the ten RF condition) but is inferior when RFPs require more global processing (three and five RF conditions).

3.5 Discussion

The principle objective of the present study was to evaluate the developmental interplay between intermediate and low-level vision by assessing the ability to discriminate circular shapes whose contour was characterized by differing stimulus attributes (luminance -

texture) and number of deformations (local and global processing). Overall, our results demonstrated that the type of local information, whether the number of curvatures or the type of stimulus attributes, defining the contour of the shape, differentially influences visual processing in school-aged children.

For luminance-defined RFPs, children performed worse compared to adolescents and adults on shapes with fewer curvatures (three and five radial frequencies) but similarly on the RFP condition with the most radial frequencies (ten). For school-aged children, the ability to discriminate luminance-defined shapes is *adult-like* only when visual processing is biased towards local processing, which suggests that for such stimulus characteristic children's performance is reduced only when a global visual processing style is required. Past research has proposed that processing of RFPs is separate depending on the number of curvatures surrounding the contour of the shape (Jeffrey et al., 2002; Loffler et al., 2003; Bell, Badcock, Wilson, & Wilkinson, 2007). For RFPs with fewer numbers of curvatures, global pooling is solicited, whereas for RFPs with greater numbers of radial frequencies, probability summation is required (Wilkinson et al., 1998; Jeffrey et al., 2002; Loffler et al., 2003; Bell, Badcock, Wilson, & Wilkinson, 2007). Based on such evidence, it is likely that mechanisms underlying global pooling take longer to mature since our school-aged group was not adult-like for the processing of RFPs with fewer numbers of curvatures (i.e. three and five). However, school-aged children were adult-like for RFPs with greater numbers of curvatures, suggesting that mechanisms underlying probability summation mature faster, especially when stimuli are luminance-defined.

A different pattern of results was observed for texture-defined RFPs. When texture information is added to the contour of the shape, targeting multiple visual mechanisms and is therefore more complex to visually process (Ashida, Lingnau, Wall, & Smith, 2007; Larsson, Landy, & Heeger, 2006), school-aged children's performance is worse as compared to adolescent and adult groups on all RFP conditions (three, five, and ten radial frequencies). These results suggest that school-aged children's performance is affected for both global (RFP of three and five) and local (RFP of ten) shape processing when texture information defines the shape. Therefore, longer periods of development are not only identified for processes underlying global pooling but also for those underlying probability summation. The delayed maturation for both local and global processing of texture-defined RFPs might be a consequence of the fact that texture information is more complex to visually process since it requires an extra processing stage (Lin & Wilson, 1996; Habak, Wilson, & Wilkinson, 2009). Visual mechanisms underlying the processing of texture information may therefore take longer to develop which may in turn generally affect the processing of RFPs in our school-aged group.

Altogether, the present results indicate that the timing of adult-like sensitivity depends on the type of local information (number of curvatures) and the physical attributes (luminance versus texture) defining the shape. Precisely, when luminance information defines the shape, adult-like sensitivity occurs earlier when visual processing is locally biased (before 12 years of age) than when it is globally oriented (after 12 years of age). On the other hand, adult-like sensitivity occurs later for both local and global visual processing (after 12 years of age) when texture information defines the shape. Therefore, timing of adult-like sensitivity is similar for both luminance- and texture-defined shapes when a global processing style is targeted. The difference in development occurs when a local processing strategy is advantaged, with adult-like sensitivity occurring earlier when patterns are luminance-defined than when texture-defined. Overall, this suggests that development of luminance-defined shapes is faster than for texture-defined shapes. Sensitivity to texture-defined RFPs does not only take longer to develop but also appears to deteriorate at a faster rate, with sensitivity being significantly reduced for older adults (i.e. 60-76 years old) than for younger adults (i.e. 20 to 30 years old) (Habak, Wilkinson, Wilson, 2009).

Differential sensitivity to luminance- and texture-defined shapes throughout development was also identified by Bertone and colleagues (2010), who found that sensitivity to global Landolt-C patterns defined by texture (a second-order characteristic) reaches maturity later in development compared to those that are luminance-defined. They proposed that the later development for forms defined by texture might be a consequence of the extensive recruitment of extra-striate visual areas, which are still immature in school-aged children (Bertone et al., 2010). Immature cortical networks might explain therefore why our school-aged children exhibit reduced sensitivity to texture-defined RFPs. It is worth noting however, that some controversy exists in the present literature. Sensitivity to texture-defined, bandpass gratings seems to reach adult-type levels before (5 years old) that of luminance-defined gratings (10 years old; Bertone et al., 2008; Armstrong et al., 2009). According to these authors, less specialization might be required for early mechanisms responsible for the processing of second-order attributes and therefore would require a shorter developmental time course to reach adult levels compared to that of first-order attributes. Overall, sensitivity reflecting the relative maturation of texture-defined perception seems to depend on the stimuli and behavioral paradigm used, with findings of longer maturation associated with more complex types of visual information (i.e. forms, shapes) compared to more simple stimuli (i.e. gratings).

Past research and a recent review article have also described differential development for local and global visual processing: local visual processing matures earlier than global visual analysis (see van den Boomen, van der Smagt, & Kemner, 2012 for review). Such delayed maturation for global visual processing is thought to be a consequence of restricted interactions between spatial cues at an earlier age (Kovács et al., 1999) as well as under-developed long-range connections (Gervan, Berencsi, & Kovács, 2011). Likewise, feedback and horizontal connections, which are useful for integrating contours, demonstrate delayed maturation (Lee, Birtles, Wattam-Bell, Atkinson, & Braddick, 2012). Along with delayed maturation, feedback pathways are also less synchronized at an early age, which might result from diminished myelination, maturation, and learning through repeated exposure (Werkle-Bergner, Shing, Müller, Li, & Lindenberger, 2009). Based on such accounts, children's overall inferior performance for RFPs that are processed globally in adults might be a consequence of inefficient visual integration, possibly mediated by immature feedback and horizontal connections underlying global form detection (Lamme, Supèr, & Spekreijse, 1998). However, the tuning of orientation-selective mechanisms operating locally in primary visual areas seem to be adult-like in our school-aged children since performances demonstrated to be equivalent across groups for luminance-defined RFPs with greater numbers of curvatures (ten radial frequencies), necessitating a local processing style (Jeffrey, Wang & Birch, 2002; Loffler, Wilson, & Wilkinson, 2003).

The finding that school-aged children demonstrate inferior sensitivity to global RFP conditions for both luminance *and* texture conditions is similar to past studies that have investigated the development of mechanisms mediating the perception of faces, an ability that requires visual processing similar to that of RFPs (Loffler, 2008; Wilkinson et al., 2000).

Behaviorally, it appears that at a young age, a local or featural (focusing on facial features) processing style is predominant. With age, the processing strategies used to represent faces becomes more configural or holistic (global). Being able to process faces globally is advantageous, as it allows for better identification and discrimination (Carey, Diamond, & Woods, 1980; Mondloch, Le Grand, & Maurer, 2002). Imaging studies have also identified delayed maturity for the facial processing areas. For example, physiological studies demonstrate that adult-like latencies when processing faces configurally are attained more progressively (Taylor, McCathy, Saliha, & DeGiovanni, 1999; Taylor, Edmonds, McCathy, & Allisson, 2001).

3.6 Conclusions

Overall, we have demonstrated that local information defining circular shapes interacts with the visual analysis of intermediate level (global) information, such as that preceding object and face perception, across different periods of development. This was evidenced by the finding that for luminance-defined RFPs, children performed worse than adolescents and adults when a global processing strategy was required, but for texture-defined RFPs, children performed worse compared to adolescents and adults across both local and global processing styles. The poorer performance in children compared to other age groups might be a consequence of poor visual integration between low and intermediate visual mechanisms and could be attributed to immature feedback and horizontal connections as well as under-developed visual cortical areas.

3.7 Acknowledgements

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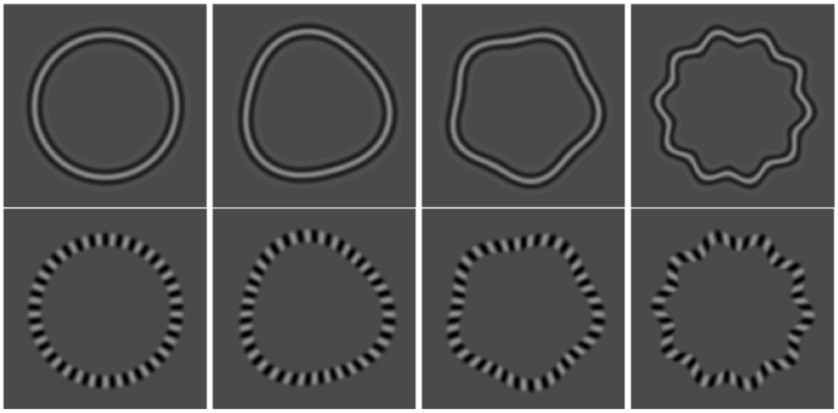

Figure 1. The stimuli located at the top row of the image are luminance-defined RFPs of zero, three, five, and 10 radial frequencies. Located at the bottom row of the image are texture-defined RFPs of zero, three, five, and 10 radial frequencies.

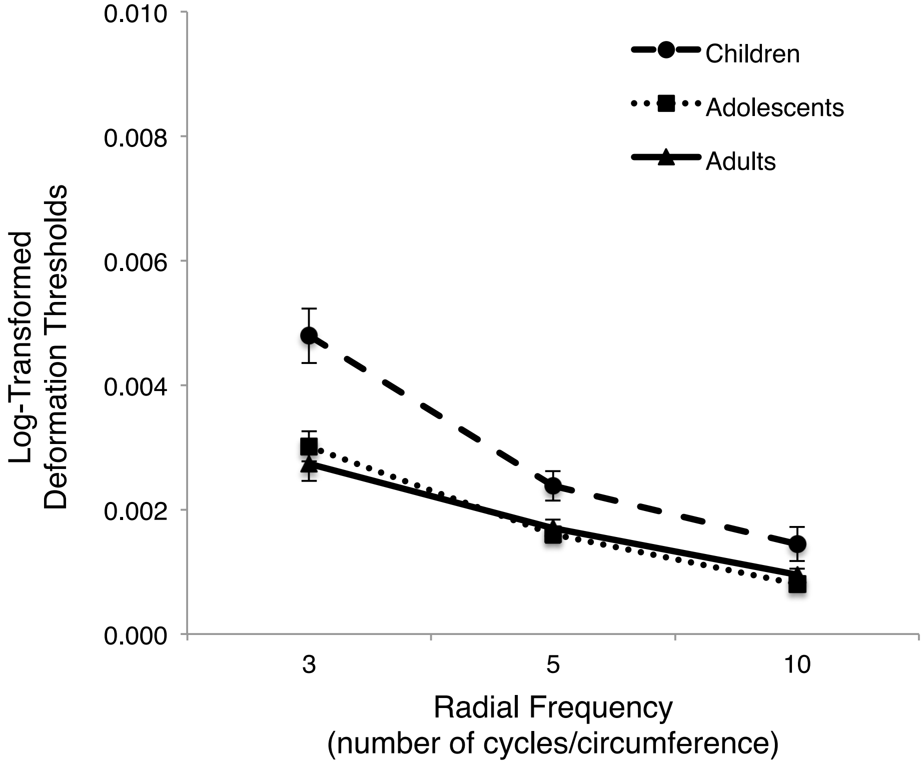

Figure 2. Mean deformation thresholds (+SE) for children (circles), adolescents (square), and adults (triangle) as a function of luminance-defined RFPs.

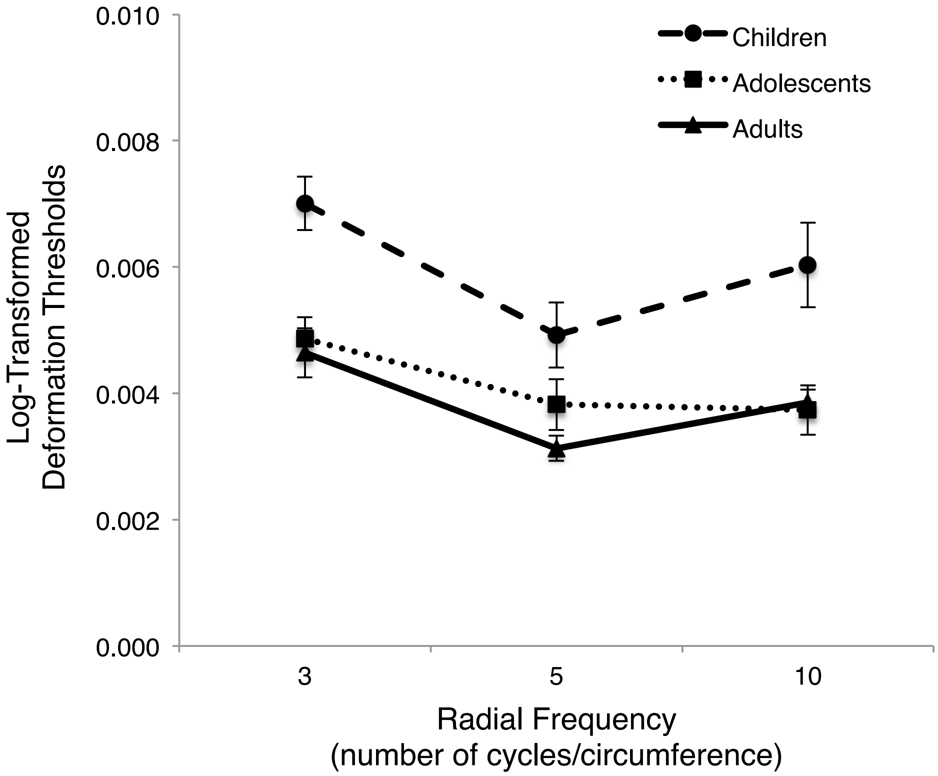

Figure 3. Mean deformation thresholds (+SE) for children (circles), adolescents (square), and adults (triangle) as function of texture-defined RFPs.

Chapter 4: Visual Perception in Autism Spectrum Disorder

4.1 Autism Spectrum Disorder: Definition and Diagnosis

In the early 1940s, Leo Kanner, an American child psychiatrist, described in his manuscript entitled, “Autistic disturbances of affective contact,” a subgroup of children whom he noticed demonstrated behavioural characteristics that he believed formed a “specific syndrome” (Kanner, 1943, p. 242). Children with this specific syndrome presented abnormal development of communication skills. Complete lack of language skills was evidenced in some children, whereas for others, language was possible, but pronoun reversals and echolalia were frequently observed. In his report, Kanner (1943) also described that these children had very little interest in relating with others, demonstrated little affectionate contact with their parents, and often preferred being alone. In fact, these children demonstrated greater interest towards objects in comparison to others. Finally, rigidity and repetitious behaviours, as well as a need for sameness were observed. For example, disturbances in the child’s routine often led to great tamper tantrums. In turn, Kanner described this “specific syndrome” as autism (Kanner, 1943).

Since Kanner’s observations, greater knowledge on autism has resulted in an evolving diagnostic criteria for this condition. The Diagnostic Manual for Mental Disorders - 4th ed. Text rev. (*DSM-IV-TR*: APA, 2000) described Autism Spectrum Disorder (ASD) as a neurodevelopmental condition that is defined behaviourally by impairments in communication, social interaction, and patterns of restricted interests and repetitive behaviours. Moreover, a significant proportion of such autistic behaviours are related to visual perception, including lack of interpersonal eye contact, preoccupation with flickering or spinning objects as well as with parts of objects, idiosyncratic responses to visual stimulation and islets of visual abilities (APA, 2000). Our understanding of autism has changed throughout the years as a result of much research being conducted in the field. Such enhancement in knowledge has led to changes in the diagnostic criteria for autism as depicted in the recently published Fifth edition of the *Diagnostic and Statistical Manual of Mental Disorders* - 5th ed. (*DSM-V*: APA, 2013). Briefly, the standards for ASD now include two main criteria, which encompass (1) deficits in social communication and interaction as well as (2) presence of restricted interests and repetitive behaviours or activities. Furthermore, specifiers were added to the diagnostic criteria, where the presence or not of different particularities (e.g. ASD with or without intellectual disability, language delay, etc.) must be specified (see APA, 2013 for further details). These revised criteria for autism will not be discussed further, since all participants recruited for all research projects were diagnosed using the *DSM-IV-TR* (APA, 2000). It is, however, important to note that the diagnostic changes in the *DSM-V* place a relatively larger diagnostic importance on the presence of non-social behaviours in autism, such as restrictive interests and repetitive behaviours, which are a defining feature of ASD especially since perceptual anomalies appear to be related to such atypical behaviours (APA, 2013).

4.2 Prevalence and Possible Origins

Epidemiology studies have revealed that approximately 20 per 10 000 children are on the Autism Spectrum (AS) (Fombonne, 2009). The cause of ASD is still unknown. This being said, genetics appears to play a major role, given that there is 70-80% heritability to the development of ASD (Geschwind, 2011). Environmental factors also seem to play a part, interacting with one's genetic predisposition to contribute to the development of ASD (Geschwind, 2011). Studies also demonstrate that interactions residing between genetic variants and epigenetic factors also play an important role in increasing the risks for ASD (Fakhoury, 2015; Lai, Lombardo, & Baron-Cohen, 2014; Tordjman et al., 2014). Moreover, different behavioural traits commonly identified in ASD appear to be a consequence of specific genetic factors that underlie the development of a variety of brain circuits (Geschwind, 2008, 2011). In addition with the notion that ASD is a complex genetic condition, there also appears to be an important gender difference in ASD, where there are many more males than females diagnosed with the condition with a ratio of approximately four to one, respectively (Fombonne, 2009).

Although the cause of this gender difference is unknown, studies propose that genetic and hormonal factors may contribute to the increased prevalence in boys. These factors have been summarized in a recent review article (Werling & Geschwind, 2013), whereby four genetics factors are described as contributing factors to the gender difference in ASD. Firstly, the multiple-threshold multifactorial liability model has been used to explain increased prevalence of ASD in boys. Using this model, it was proposed that girls are less susceptible than boys as a consequence of having higher threshold for reaching diagnosis. Therefore, for a girl to be diagnosed with ASD, many more genetic and environmental factors are required. As a consequence, girls with ASD are thought to have greater heritability factors as compared to boys. Moreover, genetic variants may also be used to explain differences in gender ratios in ASD, given that girls appear to have different genetic variants as compared to boys. Another factor that may explain gender differences in ASD is the fact that girls may be more genetically resilient to developing ASD. This is supported by findings that have demonstrated that unaffected girls have many more genetic mutations (Sanders et al., 2011). Therefore, girls appear to be able to endure many more genetic mutations before developing ASD as compared to boys (Werling & Geschwind, 2013). Lastly, sex chromosomal genes appear to play a protective role in the development of ASD. Although more research is needed, Werling and Geschwind (2013) propose that the Y chromosome may be a risk factor for ASD, whereas the presence of a second X chromosome is thought to be a protective factor for the development of ASD. In terms of hormonal factors, sex hormones can be a risk factor for ASD.

As described in Werling and Geschling's (2013) review article, increased foetal testosterone levels may be a risk factor for the development of ASD. This is based on the Extreme Male Brain Theory, which stipulates that ASD is a consequence of hypermasculinization of the brain leading to cognitive particularities such as less empathizing but greater systematizing (Baron-Cohen, 2002). Based on this theory, research has demonstrated that elevated levels of foetal testosterone may lead to cognitive hypermasculinization and act as a predisposing factor for the presence of a particular cognitive phenotype commonly found in ASD (Werling & Geschwind, 2013).

Along with different hypotheses put forward to explain the potential causes to ASD, Mottron, Belleville, Rouleau, and Collignon (2014) have recently proposed the Trigger-Threshold-Target (TTT) Model to explain how the autism phenotype surfaces. According to this model, genetic mutations *trigger* specific reactions *targeting* different cortical areas to be modified according to neuro-plastic events. This is believed to occur in individuals who have genetically-determined low *thresholds*. The biological changes arising from these plastic reactions will then lead to differential functioning of specific brain regions and networks (i.e. associative perceptual cortex or language regions depending on whether individuals have a language delay or not) thereby contributing to the presence of particular strengths and weaknesses in autism. Mottron et al. (2014) suggest that genetic mutations engender plastic reactions beginning at the synapse and ending during the organization of cortical regions. They also propose that environmental factors, such as an individual's experiences, will further influence neuro-plastic events. Finally, changes in the organization, connectivity, and functioning of the cortex is believed to result in the presence of different particularities commonly identified in autism (e.g. enhanced perceptual functioning, poor social skills, speech difficulties, or poor motor coordination).

4.3 Visual Perception in Autism Spectrum Disorder

There is a significant proportion of social and non-social atypical behaviours in autism that is related to the processing of visual information, which is exemplified by atypically absent (i.e., lack of interpersonal eye contact) or present (i.e., preoccupation with flickering or spinning objects) behaviours. Given their importance, these traits are now thought to be related to the autism phenotype and are in fact now taken into account in the newly revised diagnostic criteria of ASD (APA, 2013). However, the origin of these behaviours, which extend across both social and non-social domains in autism, remains unknown. One plausible hypothesis is that atypical development of perceptual functions ultimately results in a perceptual signature or profile that distinguishes autism from both typical development and other neurodevelopmental conditions (e.g., Bertone & Faubert, 2006; Bertone, Hanck, Kogan, Chaudhuri, & Cornish, 2010a). This signature takes into account findings demonstrating that autistics process visual information at multiple different levels of analysis in an atypical manner (Bertone et al., 2010; Mottron, Dawson, Soulières, Hubert, & Burack, 2006; Simmons et al., 2009).

In terms of early or elementary processes, individuals with ASD seem to have atypical contrast sensitivity when information is defined by luminance and texture information (Bertone, Mottron, Jelenic, & Faubert, 2003, 2005; Franklin et al., 2010; Vandenbroucke et al., 2008). For example, Bertone and colleagues (2005) demonstrated that individuals with ASD have increased sensitivity to static visual information when it is luminance-defined whereas sensitivity to texture-defined information is decreased. When presented with dynamic visual information, individuals with ASD are also identified as being worse than neuro-typical individuals for texture-defined information, but similar performances between individuals with ASD and controls are noticed for the processing of luminance-defined dynamic visual information (Bertone et al., 2003). From such findings, it appears that individuals with ASD are impaired for early (or non-social) visual information that requires the recruitment of multiple cortical areas, as is the case for texture information, compared to more neurally-simple, luminance information that is processed by standard mechanisms within the primary visual cortex (V1). Using both behavioural and electrophysiological approaches, Vandenbrouke and colleagues (2008) also demonstrated that individuals with ASD present greater difficulty on a texture-segregation task compared to neuro-typical individuals. These authors suggest that such reduced sensitivity may be due to atypical lateral and feedback/forward connectivity between primary visual areas in autism (Vandenbroucke et al., 2008). Kéïta and colleagues (2011) also reported the presence of atypical lateral connectivity within early visual areas in autism through the use of a lateral masking paradigm. Their results demonstrated that individuals with ASD were facilitated to a greater extent by the contextual information surrounding the target stimulus when compared to typically developing individuals (Kéïta et al., 2011).

Differential visual perception has also been identified at mid- or intermediate level of visual analysis. For example, individuals with ASD have reduced ability for perceiving color information, which is believed to target different cortical mechanisms (V1, V2, V4, V8) located along the ventral and dorsal pathways (Franklin, Sowden, Burley, Notman, & Alder, 2008; Franklin et al., 2010). Spatial-form coherence with noise or spaced elements is also more difficult in ASD (Evers et al., 2014; Spencer & O'Brien, 2006), although noise may have a greater influence on visual integration than the spacing between individual segments (Del Viva, Igliozzi, Tancredi, & Brizzolara, 2006). Grinter and colleagues (2010) have also investigated mid-level perception in ASD through the usage of complex circular shapes. Their results demonstrated intact local processing in the ventral stream but less efficient global processing of spatial information for ASD children (Grinter et al., 2010). Overall, it is unknown whether such difficulty with mid-level visual processing in ASD is due to less efficient visual integration or simply a consequence of better ability to segregate visual information, which is observed by an enhanced capacity to perceive detail (Baldassi et al., 2009). Although it has been demonstrated that there is less efficient perception of global forms, performance in ASD appears to be superior when visual stimuli contain structure such as symmetry. When presented with such visual information, individuals with ASD have an enhanced ability to detect symmetry embedded in an array of dots. Such results suggest that individuals with ASD may be better able to extract both local and global visual information at once (Perreault, Gurnsey, Dawson, Mottron, & Bertone, 2011; see Appendix A for full article).

In addition to the aforementioned early to mid-level, or non-social perceptual abnormalities regarding processing within primary to intermediate visual areas, individuals with ASD also demonstrate atypical higher-level visual processing, such as for the processing of biological motion, faces, and complex emotions (Simmons et al., 2009). In relation to biological motion, children with ASD are not only less capable at discriminating such stimuli but also demonstrate less preference towards point-light displays depicting biological motion compared to typically developing children (Annaz, Campbell, Coleman, Milne, & Swettenham, 2012; Annaz et al., 2010). Similarly to these findings, greater preference for moving geometric figures than dynamic social images was also identified in young children at risk of developing autism (Pierce, Conant, Hazin, Stoner, & Desmond, 2011). Abnormal face discrimination and recognition is also present in autism (see Weigelt, Koldewyn, & Kanwisher, 2012 for review). Specifically, individuals with ASD seem to process faces locally, whereby the processing of facial attributes is predominately identified in autism (Behrmann, Thomas, & Humphreys, 2006; Jemel, Mottron, & Dawson, 2006; Mottron et al., 2006). Individuals with ASD also demonstrate more difficulties in comparison to matched controls at identifying perceptual similarities in faces (Scherf, Behrmann, Minshew, & Luna, 2008) and use information surrounding the eye region of the face to a lesser extent (Riby, Doherty-Sneddon, & Bruce, 2009; Rutherford, Clements, & Sekuler, 2007; Wolf et al., 2008). In addition to atypical visual processing of faces, individuals with ASD also demonstrate impairments when processing complex emotions (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Boraston, Corden, Miles, Skuse, & Blakemore, 2008).

High-level visual processing deficits in ASD are also evidenced during cognitive tasks. For example, performance in ASD on tasks is often superior when a local visual processing style is advantageous. For example, research has demonstrated that individuals with ASD are better at completing the block design task, whereby they are faster and more accurate at putting a set of blocks together to reproduce the presented figure (Caron, Mottron, Berthiaume, & Dawson, 2006; Dennis et al., 1999; Ehlers et al., 1997; Happé, 1994; Ruhl, Werner, & Poustka, 1995; Shah & Frith, 1993; Siegel, Minshew, & Goldstein, 1996; Spek, Scholte, & van Berckelaer-Onnes, 2008). Better performance in autism is also commonly identified for the embedded figures task. In such a task, individuals with ASD are better at identifying a geometric figure within a more complex image (de Jonge, Kemner, & van Engeland, 2006; Jarrold, Gilchrist, & Bender, 2005; Pellicano, Gibson, Maybery, Durkin, & Badcock, 2005). Finally, individuals with ASD are more accurate and faster at completing visual search tasks (Caron et al., 2006; Jarrold et al., 2005; O'Riordan, 2004; Plaisted, O'Riordan, & Baron-Cohen, 1998). Overall, based on previous findings, the type of perceptual information being analyzed may determine whether individuals with ASD perform better or worse than neuro-typical individuals.

4.4 Neurocognitive Theories Explaining Atypical Visual Processing in Autism

4.4.1 Weak Central Coherence Model

The Weak Central Coherence (WCC) (Happé, 1999; Happé & Booth, 2008; Happé & Frith, 2006) model posits that superior performance on visuospatial tasks in ASD is the result of an apparent local processing bias when locally-oriented analysis is considered to be advantageous. According to the WCC model, the presence of such a local processing bias also predicts an impaired construction of global visual representations, a perceptual trade-off analogous to not being able to see the forest for the trees. This type of visual processing strategy is the result of a cognitive style and not of a cognitive deficit (Happé, 1999; Happé & Booth, 2008; Happé & Frith, 2006), since autistics are capable of perceiving visual information coherently when asked to do so. The local processing advantage in autism seems to occur only when a spontaneous approach is permitted, such as in natural settings or when perceptual tasks favour a local processing strategy, such as for the embedded figures task (Happé, 1999).

4.4.2 The Enhanced Perceptual Functioning Model

The Enhanced Perceptual Functioning (EPF) model (Mottron et al., 2006), also describes perception in ASD as being more locally oriented compared to neuro-typical individuals. However, according to this model, individuals with ASD are able to construct global representations but do so atypically, such that the efficient analysis of global percept in autism is done without losing access to local information, which is the case within typical processing hierarchies (Mottron et al., 2006). The EPF model further proposes that performance in ASD is dependent on the type of stimuli used, with worse performance being demonstrated for tasks that solicit increasing neural complexity (see Bertone et al., 2003; Bertone et al., 2005 for further information). Mottron and colleagues (2006) further stipulate that atypical performances during perceptual tasks are a result of abnormal activation of primary perceptual and associative cortical areas. For example, increased activation is evidenced for primary perceptual areas in autism whereas decreased activation is observed for higher-order cortical mechanisms, such as for regions related to the analysis of social information (fusiform face area) as well as for frontal areas (Mottron et al., 2006). According to the EPF model, top-down processing, which is automatic in typically developing individuals, is also believed to be optional in autism, as depicted by lack of global precedence, gestalt laws, and effects of categorization (Mottron et al., 2006). Finally, the EPF model predicts that atypical perceptual performances in autism are the result of superior functioning and greater autonomy of primary perceptual cortical areas during cognitive task completion in autism as compared to control subjects (Samson, Mottron, Soulieres, & Zeffiro, 2012). Overall, the EPF model posits that superior performance in ASD for a variety of cognitive tasks is a result of an increased role and autonomy of perception, with a disproportionately increased functional involvement of early and associative perceptual cortices (Mottron et al., 2006; Samson et al., 2012).

4.4.3 Bayesian Framework to Autistic Perception

Pellicano and Burr (2012) propose that sensation and perception in ASD can only be understood by obtaining a better understanding of how uncertainty is processed through sensory systems. Therefore, these researchers used the Bayesian framework to explain atypical perception in ASD, which attempts to elucidate how one can optimally perceive information in the presence of uncertainty. According to this theory, past experiences and multiple other forms of knowledge are used to assist processing of ambiguous information. Such knowledge and past experiences are referred to as ‘priors’. Based on the Bayesian theory, Pellicano and

Burr (2012) suggest that atypical perception in ASD may be a consequence of altered usage of priors, where individuals with ASD may have difficulty integrating sensory information or constructing priors. In fact, they propose that priors may be attenuated in ASD, what they refer to as ‘hypo-priors’. This suggests that priors would influence perception to a lesser extent in ASD as compared to neuro-typical individuals. According to their suppositions, the presence of hypo-priors could explain why ASD perception is at times more accurate and at other times worse. For example, better perceptual skills could arise when hypo-priors result in a perception that is less distorted from prior knowledge and experiences. Alternatively, in the presence of ambiguity, hypo-priors would lead to worse performance in ASD, given that past experiences and knowledge become useful to solve ambiguities in perceptions. According to Pellicano and Burr (2012), hypo-priors in ASD could account for some of the identified phenotypes. For example, these authors provide an explanation for the presence of hypersensitivity to sensory information in ASD. Specifically, the presence of hypo-priors leads to sensory information that is much more variable and reduces the ability to generalize previously learnt information, which is typically used to assist in the interpretation of sensory input. Together, these factors result in sensory input that is unpredictable which in turn leads to hypersensitivities. Finally, using the Bayesian framework, Pellicano and Burr (2012) also posit that non-social atypical behaviours in ASD might be a consequence of hypo-priors, in that decreased influence of priors would place a greater emphasis on bottom-up connections, resulting in increased sensitivity to sensory input.

4.4.4 Models oriented towards poor prediction abilities in ASD

Van de Cruys and colleagues (2014) have recently put forward a new model to explain cognitive deficits in ASD. They propose that the core deficit in ASD resides in high, inflexible precision of prediction errors in autism (HIPPEA) (Van de Cruys et al., 2014). Their theory is based on ideas stemming from perception-as-inference (von Helmholtz, 1962) or perception-as-hypothesis (Gregory, 1980) models. According to such beliefs, people use previously learnt associations and the current perceptual input to infer what will be experienced next, thereby making predictions of what is to come. Such predictions involve top-down processes. When comparisons are made between current predictions and actual sensory input, errors often result especially when the prediction is far from the actual sensory input. This is known as a prediction error, stemming from bottom-up processes. When such instances occur, the system must decide to either update general predictions or to ignore the error itself because it may be irrelevant. According to Van de Cruys and colleagues (2014), there might be an imbalance between adapting current predictions and ignoring prediction errors in ASD. In fact, these authors believe that too much importance is placed on prediction errors in ASD. Based on this theory, a greater emphasis placed on prediction errors results in increased precision that is often out of context. These authors believe that increased precisions could in turn lead to poor meta-learning, poor abstract representation of input, redundant learning, and non autonomous and inflexible attentional resources (Van de Cruys et al., 2014).

Although the HIPPEA has been used to explain multiple spheres of atypical cognitive functioning in ASD, only aspects regarding visual perception will be discussed here. According to Van de Cruys and colleagues (2014), greater emphasis on prediction errors prevents visual input from being integrated at a higher-level of visual analysis, given that more importance is placed on lower levels of processing. Therefore, instead of forming high-level predictions, lower level predictions are predominately formed, signifying that there is more attention to details even in instances where such details are unimportant. Due to such focus on details, global (i.e., more gestalt) representations are less easily formed. According to the HIPPEA, individuals with ASD are able to perceive global representation but can only do so consciously. When global processing needs to be done unconsciously, individuals with ASD are less likely to perceive information globally, considering that more emphasis is placed on details, driven by bottom-up processing. From such a processing style, low-levels of perceptual analysis are therefore favoured (Van de Cruys et al., 2014).

Similarly to Van de Cruys et al. (2014), Sinha et al. (2014) have also proposed that difficulties identified in autism are a consequence of poor prediction abilities. Despite this similarity, the basis of Sinha et al. (2014)'s predictive impairment in autism hypothesis is different from the HIPPEA, given that it stems from a Markov system (i.e., an individual forms probabilities as a way to estimate the occurrence of a future event). According to Sinha et al. (2014), individuals with ASD may have difficulties estimating the relationship between two instances. These authors further believe that such difficulties in predicting the probability of a future event can account for some aspects of the autism phenotype. For example, sensory hypersensitivities in autism are thought to be a consequence of lack of habituation to different types of stimuli (Sinha et al., 2014). This in turn makes individuals with ASD less able to form predictions of what types of sensory input are to be expected and therefore contributes to the presence of hypersensitivities. Overall, models proposed by Van de Cruys et al. (2014) and Sinha et al. (2014) suggest that atypical behaviours and cognitive abilities in ASD stem from poor prediction abilities, resulting from a greater reliance on bottom-up over top-down mechanisms.

4.4.5 The Complexity-Specific Hypothesis

The complexity-specific hypothesis was proposed to explain atypical visual processing at low-levels of perceptual analysis in ASD (Bertone et al., 2005). This hypothesis resulted from studies demonstrating enhanced ability of ASD to process simple luminance-defined information while having a reduced ability to process information that is texture-defined (Bertone et al., 2003, 2005). Bertone and colleagues (2005) suggested that a superior ability to process simple luminance-defined information might be a consequence of excessive lateral inhibition in ASD. As discussed by Bertone and colleagues (2005), the role of lateral inhibition is to increase the selectivity of orientation neurons. Therefore, in ASD, excessive lateral inhibition would result in greater tuning of cells resulting in greater sensitivity to luminance-defined information, and this is especially evident given that luminance-defined information can be processed through the activation of a single orientation-selective neuron located in V1 (Bertone et al., 2005). Such atypical neural functioning could in turn have negative effects on the processing of other types of low-level information, such as texture-defined information. According to these authors, increased lateral inhibition would not facilitate processing of texture information given that extra processing stages are needed and many more neurons within V1 as well as V2/V3 need to be targeted (Bertone et al., 2005). The complexity-specific hypothesis predicts that both lateral and feedback connections are altered in ASD, and Bertone and colleagues (2005) propose that higher-level visual abnormalities and possibly atypical behaviours in ASD may result from such alterations.

4.5 Rational for Study 2. Assessing a functional link between low- and mid-level visual perception in the Autism Spectrum

As was described in this chapter, atypical perception of both early and higher-level visual information is believed to be involved in autism's cognitive and behavioural phenotype. Although much research has been undertaken to better understand each level of processing, it is not known how these two levels of perception functionally interact (Dakin & Frith, 2005). Therefore, the second article of this thesis assesses whether perceptual alterations at an early level of perception affect the subsequent perception of more complex visual information in autism, such as that mediating shape perception, an intermediate level of visual analysis that precedes the perception of important objects, such as faces.

To assess how low and intermediate levels of visual analysis interact in ASD, a study was conducted to follow-up on findings reported by Grinter and colleagues (2010). Using RFP (see Chapter 1 for description of these stimuli), these authors demonstrated reduced ability in children with ASD to discriminate such shapes (needed the curvatures to have larger amplitudes) when the circles have fewer deformations (i.e., three) compared to neuro-typical individuals. Conversely, the ASD group performed similarly to the control group when the RFPs had many deformations (i.e., 24). These results were interpreted as evidence for abnormal cortical integration within the ventral visual pathway in autism (Grinter et al., 2010). However, it remains unknown whether shape discrimination in autism is differentially affected by manipulating the low-level, physical attributes defining the contour of the global RFP shape.

Therefore, the objective of the second study of this thesis was to assess whether the ability to discriminate between a circular and non-circular RFP in autism is differentially affected by the manipulation of primary stimulus elements (luminance vs texture). In order to assess this objective, shape discrimination thresholds were measured for RFP of two, three, five, and 10 RF whose contour was defined by luminance or texture information. Thirty individuals with ASD and thirty neuro-typical individuals between 14 and 27 years old participated in the study. Similarly to the first study, six different levels of amplitude modulations, representing the depth of the deformations and dips as a proportion change in radius (Wilkinson et al., 1998), were used, and shapes had a radius of 1.5 degrees. A method of constant stimuli with a two-interval forced choice paradigm was used again to measure threshold for all participants. Threshold was estimated at 75% correct responses. Once again, participants had to detect which of two stimuli presentations was the RFP. The other stimulus was a perfect circle, with no deformations in the radial contour. Based on previous findings demonstrating differential sensitivity to luminance and texture information in autism (Bertone et al., 2003, 2005; Vandenbroucke et al., 2008), it was hypothesized that individuals with ASD would generally perform equivalently or superiorly compared to controls for luminance RFP conditions, whereas a worse performance in autism was hypothesized for texture-defined RFP conditions. Furthermore, it was hypothesized that for luminance-defined shapes a worse performance in autism would be identified for RFP targeting a global processing style (i.e., two, three and five RF), whereas no difference between groups would be observed for RFP targeting a local processing style (i.e. 10 RF). For texture-defined shapes, it was hypothesized that individuals with ASD would perform worse as compared to neuro-typical individuals for both global and local conditions.

Overall, if the hypotheses for the second study of this thesis are supported – i.e., the ability to discriminate global shapes in the ASD group is differentially affected by the manipulation of physical elements defining its contour (luminance vs texture) - it can be argued that atypical visuo-perceptual analysis for higher-level information may have an early, low-level origin in autism.

Chapter 5: Article

This is an exact reproduction of the following published article:

Behavioral evidence for a functional link between low- and mid-level visual perception in the Autism Spectrum

Audrey Perreault (1,2), Claudine Habak (3), Franco Lepore (2), Laurent Mottron (4) & Armando Bertone (1,4,5)

(1) Perceptual Neuroscience Lab for Autism and Development (PNLab), Rivière-des-Prairies Hospital, Montreal, Canada
(2) Centre de Recherche en Neuropsychologie et Cognition (CERNEC), Department of Psychology, Université de Montréal, Montreal, Canada
(3) Centre de Recherche, Institut Universitaire de Gériatrie and Visual Perception and Psychophysics Lab, Université de Montréal, Montreal, Canada
(4) Centre d'excellence en Troubles envahissants du développement de l'Université de Montréal (CETEDUM), Hôpital Rivière-des-Prairies, Montréal, Canada
(5) School /Applied Child Psychology, Department of Education and Counselling Psychology, McGill University, Montreal, Canada

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5.1 Abstract

Background: Most investigations of visuo-perceptual abilities in the Autism Spectrum (AS) are level-specific, using tasks that selectively solicit either lower- (i.e., spatial frequency sensitivity), mid- (i.e., pattern discrimination) or higher-level processes (i.e., face identification) along the visual hierarchy. Less is known about how alterations at one level of processing (i.e., low-level) interact with that of another (i.e., mid-level). The aim of this study was to assess whether manipulating the physical properties (luminance vs. texture) of local contour elements of a mid-level, visual pattern interferes with the discrimination of that pattern in a differential manner for individuals with AS.

Methods: Twenty-nine AS individuals and thirty control participants (range 14-27 years) were asked to discriminate between perfect circles and Radial Frequency Patterns (RFP) of two, three, five, and 10 radial frequencies (RF), or deformations along the pattern's contour. When RFP have few deformations (< five RF), a global, pattern analysis is needed for shape discrimination. Conversely, when RFP contain many deformations (≥ 10 RF), discrimination is dependent on the analysis of local deformations along the RFP contour. The effect of manipulating RF on RFP discrimination was assessed for RFP whose local contour elements were defined by either luminance or texture information, the latter previously found less efficiently processed in AS individuals.

Results: Two separate mixed factorial ANOVAs [2 (Group) x 4 (RF)] were conducted on mean deformation thresholds for luminance- and texture-defined conditions. A significant

Group x RF interaction was found for the luminance-defined condition where thresholds were higher in the AS group for the two and three RF conditions; no between-group differences were found for the five and 10 RF conditions. A significant main effect of group was identified for the texture-defined condition, where mean thresholds were higher for the AS group across all RF conditions assessed (two, three, five and 10); a Group x RF interaction effect was not found. Performance for each RFP condition was not affected across group by either chronological age or intelligence, as measured by either Weschler scales or Raven Progressive Matrices.

Conclusions: The ability of AS individuals to discriminate a circular pattern is differentially affected by the availability (number of deformations along the RFP contour) and type (luminance versus texture) of local, low-level elements defining its contour. Performance is unaffected in AS when RFP discrimination is dependent on the analysis of local deformations of luminance-defined contour elements, but decreased across all RF conditions when local contour elements are texture-defined. These results suggest that efficient pattern perception in AS is functionally related to the efficacy with which its local elements are processed, indicative of an early origin for altered mid-level, pattern perception in AS.

Keywords: Autism Spectrum, visuo-spatial perception, low-level vision, intermediate level vision

5.2 Introduction

Autism Spectrum (AS) is a neurodevelopmental condition defined by qualitative and quantitative alterations in social communication and interaction, and by restricted interests and repetitive behaviors (American Psychiatric Association, 2013). Over the last few decades, interest in perceptual atypicalities in AS has increased, reflected by recent reviews (Simmons, Robertson, McKay, Toal, McAleer, & Pollick, 2009; Berhmann, Thomas, & Humphrey, 2005; Dakin & Frith, 2006; Marco, Hinkley, Hill, & Nagarajan, 2011) and theoretical articles (Pellicano & Burr, 2012; Markram & Markram, 2010; Van de Cruys et al., 2014; Mottron, Belleville, Rouleau, & Collignon, 2014). Clinically, greater importance has been recently placed on the presence of non-social, visually-related diagnostic criteria of AS in the DSM 5; i.e., hyper- or hyporeactivity to sensory input, or unusual interests in sensory aspects of the environment, such as intense preoccupation to light or spinning objects (American Psychiatric Association, 2013).

Atypicalities are present at different levels of processing along the visual hierarchy. Differential sensitivity and brain responses to certain types of *elementary* or low-level visual information (Boeschoten, Kenemans, van Engeland, & Kemner, 2007; Bertone, Hanck, Kogan, Chaudhuri, & Cornish, 2010; Franklin et al., 2010; Kéïta, Guy, Berthiaume, Mottron, & Bertone, 2014; Pei, Baldassi, & Norcia, 2014; Behrmann, Thomas, & Humphrey, 2006), reflecting the earliest levels of visual feature extraction, differ in AS. Performance on spatial visuo-cognitive tasks, targeting intermediate (or mid-level) levels of visual analysis that mediate more global, yet non-social visual information are also atypical in AS (Brosnan, Scott, Fox, & Pye, 2004; Farran & Brosnan, 2011; Muth, Hönekopp, & Falter, 2014). Finally, the processing of higher-level, socially-relevant information conveyed by faces, gestures, and voices present autism-specific particularities under certain conditions (see Weigelt, Koldewyn, & Kanwisher, 2012 for review; Pelphrey, Yang, & McPartland, 2014).

The majority of perception studies in AS have evaluated perceptual processes in isolation, using tasks and stimuli that solicit a single level of analysis, such as spatial frequency, pattern or face perception. Other studies have attempted to evaluate whether atypical performance on socially-contingent perceptual tasks stem from perceptual or social abnormalities. They have done so by assessing cross-level associations between elementary, low-level information such as spatial frequency and high-level constructs, such as face perception and recognition (for examples, see Deruelle, Rondan, Salle-Collemiche, Bastard-Rosset, & Da Fonséca, 2008; Leonard, Karmiloff-Smith, & Johnson, 2010b; Vlamings, Jonkman, van Daalen, van der Gaag, & Kemner, 2010). However, limited information is gained from these studies, because their methods cannot measure the way in which local information is integrated over space into a global percept. A more advantageous way to investigate the relationship between elementary, low levels and higher levels of processing, is to evaluate intermediate levels of processing, where local, non-social information is integrated over space, preceding the perception of objects and faces (Chen, Yan, Gong, Gilbert, Liang, & Li, 2014; Loffler, 2008).

The few studies that have assessed mid-level perception in AS have reported less efficient spatial-form coherence with spaced elements and noise (Spencer & O'Brien, 2006; Evers, Panis, Torfs, Steyaert, Noens, & Wagemans, 2014), with noise possibly having a greater influence on visual integration in AS than the spacing between individual segments (Del Viva, Igliozzi, Tancredi, & Brizzolara, 2006). Whether cause or result of less efficient visual integration, individuals with AS might better segregate visual information, which possibly expresses itself in the enhanced ability of AS individuals to perceive detail (Baldassi et al., 2009). This enhanced ability to segregate visual information may explain why individuals with AS are less affected by crowding (Baldassi et al., 2009; Kéïta, Mottron, & Bertone, 2010). Moreover, differential pattern perception might result from alterations in the cortical network responsible for the integration of local attributes into global percepts (Baldassi et al., 2009; Kéïta, Mottron, & Bertone, 2010). Such conclusions are supported by electrophysiological studies indicating that neural correlates of contour integration in low functioning children with AS are atypical and possibly nonexistent (Pei et al., 2009). However, when visual stimuli contain structure such as symmetry, AS individuals are better at perceiving both local and global visual information (Perreault, Gurnsey, Dawson, Mottron, & Bertone, 2011). Therefore, while performance on "global" tasks is sometimes demonstrated to be unaffected in AS, it is not the default visual processing style, as is the case in neurotypical individuals (Behrmann et al., 2006b).

Radial Frequency Patterns (RFP) are complex circular patterns that are obtained by creating curvatures (bumps) or radial frequencies (RF) along the contour (Wilkinson, Wilson, & Habak, 1998). In order to adequately perceive RFP, an object-centered visual approach is used, where the surround contour information of the stimulus is integrated with reference to the center (Wilkinson et al., 1998). Local element information around the contour is first identified via the activation of oriented spatial filters or neurons that are located within V1 and V2. At a second-stage of analysis, the local deformations (or curvatures) are spatially integrated and detected by cortical mechanisms operating within extra-striate visual areas that are responsible for the detection of forms or shapes (Poirier & Wilson, 2006; Loffler, 2008).

Evidence suggests that intermediate level mechanisms, such as V4, underlie the processing of such shapes (Pasupathy & Connor, 1999, 2001, 2002; Loffler, 2008). Therefore, varying the amplitude or size of the curvatures (bumps or RF amplitude) as well as their number about the contour (RF), targets intermediate level perception, such as that mediated by visual cortical area V4 (Wilkinson et al., 1998; Wilkinson, James, Wilson, Gati, Menon, & Goodale, 2000; Habak, Wilkinson, Zakher, & Wilson, 2004). Furthermore, visual processing can shift from local to global depending on the number of curvatures surrounding the contour of the RFP (Loffler, Wilson, & Wilkinson, 2003; Poirier & Wilson, 2006). When RFP have fewer curvatures (i.e. less than five - eight RF), integration is global over the entire RFP and an object-centered approach is used, where contour information of the shape is integrated with reference to the center (Loffler et al., 2003; Loffler, 2008; Wilkinson et al., 1998). Alternatively, with a greater number of curvatures (i.e. RF of 10 and greater), information is integrated locally by sequentially adding information along the contour of the shape, a processing style known as local, possibly reflecting probability summation (Loffler et al., 2003; Loffler, 2008; Schmidtmann, Kennedy, Orbach, & Loffler, 2012; Wilkinson et al., 1998).

The purpose of the present study was to evaluate the relationship between low- and intermediate-levels of visuo-spatial processing in AS by measuring sensitivity to RFP while manipulating the availability (number of deformations along the RFP contour) and type (luminance versus texture) of local, low-level contour elements defining its contour. Using luminance-defined RFP, Grinter, Mayberry, Pellicano, Badcock, and Badcock (2010) previously demonstrated that AS children were inferior at RFP discrimination when the RFP had fewer numbers of deformations along its contour (i.e. three RF), with no group differences found for the "local" (i.e. 24 RF) condition. The results were interpreted as evidence for intact local processing in the ventral visual stream, and less efficient global processing of spatial information for AS children. In the present study, a similar approach was used, but with performance measured across a larger number of local contour deformations (two RF, three RF, five RF, and 10 RF) for adolescents and adults with AS. In addition, we were also interested in whether manipulating the physical properties (luminance vs. texture) (Bell & Badcock, 2008; Loffler et al., 2003) of local contour elements of the aforementioned RFP conditions differentially interfered with AS performance. We chose this approach based on characteristic perceptual profiles in AS defined by equivalent or superior sensitivity to local, luminance-defined information in AS (Bertone, Mottron, Jelenic, & Faubert, 2003; Bertone, Mottron, Jelenic, & Faubert, 2005; Meilleur, Berthiaume, Bertone, & Mottron, 2014), with concurrent decreased sensitivity for local, texture-defined information (Bertone et al., 2003; Bertone et al., 2005). This complexity-specific hypothesis (Bertone et al., 2005) suggests that AS individuals process local, texture-defined information less efficiently than neurotypical observers (Bertone et al., 2003; 2005). This perceptual profile has been supported by electrophysiological findings for both AS adults and children (Vandenbrouke, Scholte, van England, Lamme, & Kemner, 2008; Rivest, Jemel, Bertone, McKerral, & Mottron, 2013).

Based on previous findings (Grinter et al., 2010), it is expected that the ability of AS individuals to discriminate luminance-defined RFP will increase as the number of local deformations or curvatures (RF) along its contour increases. However, a decreased ability to discriminate texture-defined RFP is expected in AS across all RF, given previous demonstrations of less efficient local, texture-defined information processing in AS (Bertone et al., 2005). Such a differential performance would suggest that mid-level, pattern perception in AS is functionally related to the efficacy with which its local elements are processed.

5.3 Methods

5.3.1 Participants

Thirty AS individuals and thirty neuro-typical individuals participated in this study. All participants were recruited from the Clinique d'Évaluation des Troubles Envahissants du Développement (CETED), at Rivière-des-Prairies Hospital, which contains information for typically developing individuals as well as for individuals who have an AS diagnosis. Autism Spectrum was diagnosed using the Autism Interview Revised - General (ADI-R; Lord, Rutter, & Le Couteur, 1994), the Autism Diagnostic Observational Schedule - General (ADOS-G; Lord, Cook, Leventhal, & Amaral, 2000), or both, which were conducted by a trained and expert clinician (LM) who obtained research reliability on these measurements. Only participants with a diagnosis of Autistic Disorder based on the Diagnostic and Statistical Manual of Mental Disorders IV-TR (APA, 2000) were recruited. The comparison group was composed of neuro-typical adolescents and adults, screened using a semi-structured interview to exclude participants with a history of psychiatric treatment or learning disabilities, a familial history (1st degree) of mood disorders, autism or schizophrenia, defective vision or audition, and who are taking medication. All participants recruited had a Wechsler IQ (i.e. WISC-III, WISC-IV, WAIS-III, WAIS-IV, or WASI) of 70 or higher (see Table 1).

Participants were matched on chronological age, performance IQ, and Raven Progressive Matrices percentile scores. Full-scale Wechsler IQ was not used as a matching criterion because it is known to underestimate intelligence in autism (see Barbeau, Soulières, Dawson, Zeffiro, & Mottron, 2013). All participants had normal or corrected-to-normal far and near vision, which was assessed using both near and far acuity charts (i.e. near point directional C cards and LogMAR charts).

5.3.2 Apparatus and Stimuli

The apparatus and stimuli are the same as those described in Perreault, Habak, Lepore, and Bertone (2013). Customized Matlab software was used for stimulus construction, presentation, and data recordings, which incorporated routines from the Psychophysics and Video Toolbox (Brainard, 1997; Pelli, 1997). A gamma-corrected, 19-inch Viewsonic CRT G90fb monitor, driven by a MACBOOK PRO laptop, was used for stimulus presentation. Luminance/color reading and monitor gamma-correction was carried out with a CS-100 Minolta Chromameter. The monitor's mean luminance was 30.00 cd/m^2 (u' = 0.1912, v' = 0.4456 in CIE color space) with minimum and maximum luminance levels of 0.5 and 59.5 cd/m^2, respectively.

Stimuli were radial frequency patterns (RFP), which are circular shapes with curvatures (bumps) in their contour. As described in Perreault et al. (2013), these stimuli are defined by a sinusoidal modulation to a circle's radius according to the following equation: $r(\theta) = r_o(1+A \sin(\omega\theta + \varnothing))$. r and θ are the polar coordinates of the contour and r_o is the mean or average radius (that of the base circle). The remaining parameters define the shape's geometry: ω is the radial frequency, representing the integer number of sinusoidal modulation cycles around the circumference (number of curvatures or bumps and dips, yielding the overall shape), ϕ is the angular phase, which controls the overall orientation of the shape, and A is the amplitude of the radius (Wilkinson et al., 1998). Along with the curvature manipulation, stimuli were defined either by luminance or texture information. Similarly to Perreault et al. (2013), luminance-defined RFP (Figure 1, top) were constructed using a fourth derivative of a Gaussian (D4) with a peak spatial frequency of 4 cpd (bandwidth = 1.24 cycles) and a luminance contrast of 90% (see Wilkinson et al., 1998).

Texture-defined RFP (Figure 1, bottom) were created by multiplying a radially modulated Gaussian Window with a radial carrier grating of 4 cpd (spatial frequency) and a luminance contrast of 90% (see Habak, Wilkinson, & Wilson, 2009). The texture-defined patterns had a sinusoidal carrier so that spatial frequency could match to that of luminance-defined RFP. The selection of a noise carrier (or other) would contain higher spatial frequencies and would confound any differential effects of group on stimulus characteristics with spatial frequency sensitivity. The position of the patterns was slightly jittered, overall orientation (phase) was randomized, and presentation time was set at 200 ms to encourage participants to perceive the patterns globally. Radial frequencies of two, three, five, and 10 cycles per circumference were used (number of deformation cycles - see Figure 1). Separate runs were used for each RFP condition. Six different levels (0.001, 0.002, 0.004, 0.008, 0.016, and 0.032) of amplitude modulation (proportion change of the radius) were chosen for each RFP condition based on pilot testing. Non-target stimuli were perfect circular shapes with radial frequency and amplitude of zero.

[INSERT FIGURE 1 HERE]

5.3.3 Procedure

The procedure is also similar to Perreault et al. (2013). The method of constant stimuli was used in a two-interval forced choice paradigm (2-IFC). Participants had to detect which of two presentations contained the deformed circle or RFP (amplitude > 0). The alternative presentation was a perfect circle (amplitude = 0). Target and non-target stimuli were presented for 200 ms with a 400 ms inter-stimulus interval, during which the mean-gray background was maintained. Thresholds, defined as the minimal deformation (or amplitude) needed to detect the RFP stimuli, were measured for RFP of varying radial frequency (two, three, five, & 10 RF) with contours defined by either luminance or texture, for a total of eight experimental conditions. In each block, a single combination of radial frequency and contour-definition was shown. Within each block, six levels of deformation (amplitudes of .001, .002, .004, .008, .016, and .032) were presented 20 times in pseudo-random order, for a total of 120 trials per condition.

All participants completed a brief practice session, with the same 2-IFC procedure as the experimental conditions, before commencing data collection. However, to facilitate comprehension of the task during practice, radial frequency patterns were presented from easiest to hardest (amplitude of .062, .032, .016, .008, .004, .002, and .001). Throughout the entire testing session, participants were reminded to fixate the center of a uniform screen and short breaks were provided after each condition in order to avoid participant fatigue. The experimenter entered the participants' responses (first or second interval) by pressing a key on the computer's keyboard. Conditions were counterbalanced across all subjects. The entire testing session took approximately 1½ to 2 hours. This study was carried out in accordance with the Declaration of Helsinki as well as was approved by the ethics committee at Rivière-des-Prairies Hospital. All participants provided informed consent and were given financial compensation for their time.

5.3.4 Data Analysis

Data from each block were fit with a Weibull function (Weibull, 1951) using maximum likelihood estimation, and thresholds were estimated at 75% correct responses. After analyzing the data for basic assumptions, one participant was identified as having extreme scores (i.e. two standard deviations above the mean) on almost all conditions tested. He was removed from all analyses. The final sample size was 59, with 29 participants included in the AS group and 30 included in the control group. All other basic assumptions were met except for that of sphericity. To control for lack of sphericity, Greenhouse-Geisser estimated *F*-value was used. Finally, minimal deformation thresholds were log-transformed; all analyses were performed on log-transformed thresholds.

Before conducting main statistical analyses, multiple *t*-tests were done to evaluate whether there are significant differences between groups for full-scale IQ, verbal IQ, performance IQ, and Raven Progressive Matrices percentile scores (see Table 1). Significant differences were noticed between groups for full-scale IQ and verbal IQ scores. The difference for full scale IQ is likely due to lower verbal IQ scores in the AS group, which is expected considering reduced verbal abilities in AS.

[INSERT TABLE 1 HERE]

Pearson bivariate correlations were also conducted between chronological age, IQ scores, Raven Progressive Matrices scores, ADI-R and ADOS scores for each RFP condition. Overall, no significant correlation was identified for either group. Considering that there were no differences between groups in terms of performance IQ and Raven matrices percentile scores as well as no significant correlations, IQ was not controlled for in the main analyses. Two separate mixed ANOVAs were conducted, one for luminance-defined RFP and the other for texture-defined RFP.

5.4 Results

The first mixed factorial design [2 (Group) x 4 (RF)] was conducted to evaluate group differences for luminance-defined RFP of two, three, five, and 10 RF. A significant Group x RF interaction was identified [$F(1.45, 82.02) = 4.27$, $p < .05$, $\eta^2_{partial} = .07$]. Simple main effects tests, conducted to evaluate group differences on the different types of luminance-defined RFP revealed that AS individuals had higher discrimination thresholds (worse performance) for *global* RF conditions of two [$F(1, 57) = 7.81$, $p < .01$, $\eta^2_{partial} = .12$] and three [$F(1, 57) = 7.54$, $p < .01$, $\eta^2_{partial} = .12$] RF. No significant difference between groups was identified for *local* RF conditions of five [$F(1, 57) = 3.40$, $p = ns$, $\eta^2_{partial} = .06$] and 10 [$F(1, 57) = 0.90$, $p = ns$, $\eta^2_{partial} = 0.02$] RF (Figure 2). Furthermore, a significant main effect of group was noticed [$F(1, 57) = 13.18$, $p < .05$, $\eta^2_{partial} = .19$], suggesting that overall, AS individuals perform worse than controls. As expected, a significant main effect of RFP was also identified [$F(1.44, 82.02) = 305.24$, $p < .05$, $\eta^2_{partial} = .84$], with thresholds decreasing systematically (better performance) for both groups as the number of RF increases. Tukey post hoc tests revealed that all RFP conditions were significantly different from one another (i.e. all significant at $p < .01$), with RFP of fewer curvatures requiring more change to discriminate than RFP of more curvatures.

[INSERT FIGURE 2 HERE]

A second mixed factorial analysis [2 (Group) x 4 (RF)] was conducted to evaluate differences between groups for texture-defined RFP. No significant Group X RF interaction was found [$F(1.85, 105.32) = 0.87$, $p = ns$, $\eta^2_{partial} = .02$]. However, a significant main effect of group was identified [$F(1, 57) = 16.38$, $p < .05$, $\eta^2_{partial} = .22$], revealing that the ability of AS individuals to discriminate RFP was below that of controls. These results signify that for texture-defined RFP, AS individuals perform worse for *both* global (i.e., two and three RF) *and* local RF (i.e., 10 RF) conditions. There was also a significant main effect of RFP [$F(1.85, 105.32) = 182.32$, $p < .05$, $\eta^2_{partial} = .76$]. Tukey post hoc test, conducted to evaluate differences for this main effect, indicated that it is more difficult to discriminate two RF compared to three RF ($p < .01$), five RF ($p < .01$), and 10 RF ($p < .01$). Furthermore, it is more difficult to discriminate three RF compared to five RF ($p < .01$) and 10 RF ($p < .01$). Finally, discrimination abilities were identified to be similar between five RF and 10 RF ($p = ns$). As shown in Figure 3, these results demonstrate that when RFP are texture-defined, discrimination thresholds for individuals with AS are increased across all RF conditions.

[INSERT FIGURE 3 HERE]

5.5 Discussion

We assessed the ability of AS adolescents and adults to discriminate circular, RFP as a function of (i) the availability of local curvature making up its contour (RF of two, three, five, and 10), and (ii) the physical attributes (luminance vs texture) defining the RFP. Therefore, performance across four RF levels was assessed, allowing for the evaluation of RFP perception as a function of accessibility to local, luminance- and texture-defined curvature during task completion. For luminance-defined RFP conditions, mean deformation thresholds were higher in the AS group for the two and three RF conditions (global conditions), but unaffected for the five and 10 RF (local) conditions. Our findings for luminance-defined RFP are consistent with those of Grinter and colleagues (2010) who suggest that this RF-dependent performance in AS reflects intact early, or local ventral-stream processes but less efficient visuo-spatial integration at later stages of information processing.

For texture-defined RFP, mean discrimination thresholds in the AS group were higher across *all* RF conditions assessed. Unlike luminance-defined performance, the ability of AS individuals to discriminate texture-defined RFP was not affected by increasing the availability of local curvature elements defining the contour; AS performance was decreased even for the five and 10 RF conditions when local contour elements were texture-defined. These findings are explained within the context of Bertone et al.'s (2005, 2010) complexity-specific hypothesis, which posits that local, texture-defined information is processed less efficiently in AS. This hypothesis is relevant, because RFP discrimination is initially dependent on the analysis of curvature information around its contour before being spatially integrated and detected in extra-striate visual areas (Poirier & Wilson, 2006; Loffler, 2008). Therefore, when the curvature information available (i.e., five and 10 RF conditions) is texture-defined, the resulting RFP is less efficiently perceived. The differential pattern of performance suggests that mid-level, pattern perception in AS is functionally related to the efficacy with which its local elements (luminance vs texture) are processed. In fact, our findings suggest that impaired global pattern perception is not an absolute characteristic of perception in AS, but rather, is dependent on the availability of local, luminance-defined information. Abnormal lateral or feedforward / feedback connectivity within primary visual areas in AS, which may arise from excitatory / inhibitory signaling imbalance, have been suggested as a possible origin of the differential efficacy with which luminance and texture information is processed in AS (Bertone et al., 2005; Vandenbrouke et al., 2008; Vandenbrouke, Scholte, van England, Lamme, Kemner, 2009; Kéïta, Mottron, Dawson, & Bertone, 2011; Kéïta et al., 2014). Accordingly, it is suggested that local neural alterations in AS could be a contributing cause of mid- and higher-level neural dysfunction in AS (see Bertone et al., 2003; Bertone et al., 2005; Rubenstein & Merzenich, 2003; Belmonte et al., 2004; Herbert, 2005; Tommerdahl, Tannan, Holden, & Baranek, 2008), where different alterations of low-level, local connectivity affect the function of the larger neural networks they feed into (Bertone et al., 2010) in a specific manner.

Imaging research, using fMRI, also supports the conclusion that alterations at low-levels of visual processing are possibly at the origin of atypical mid- and high-level visual analysis in AS. A recent meta-analysis demonstrated enhanced activation of cortical regions responsible for visual perception (Samson, Mottron, Soulière, & Zeffiro, 2012). Along these same lines, Kana and colleagues (2013) showed differential cerebral activation in autism compared to controls, while participants performed an adapted block design task. AS individuals showed greater activation in occipital and parietal regions but less activation in frontal regions. Combined with these findings, theories of enhanced perceptual functioning (EPF) and local overconnectivity in AS propose that atypical visual perception arises from greater autonomy of posterior regions from top-down processing because of reduced connectivity between frontal and posterior regions (Mottron, et al., 2006, 2014; Just, Keller, Malave, Kana, & Varma, 2012). This interpretation is corroborated by a recent imaging study which demonstrated a relatively decreased activation in superior frontal and medial frontal brain regions, and reduced functional connectivity between medial frontal and posterior regions during a tasks targeting local visual processing in AS. However, a different pattern of results was noted when participants completed a task targeting global visual processing, where no differences in cerebral activation were identified between AS participants and control participants (Liu, Cherkassy, Minshew, & Just, 2011). Similarly, electrophysiological studies, demonstrating differential responses during the visual processing of illusory contours, also suggest that the autonomy of early visual areas in AS individuals might be a consequence of greater connectivity in V1 between lateral connections along with underconnectivity of long-range connections, resulting in an imbalance of visual processing areas residing between lower- and higher-order regions (Stroganova et al., 2012).

5.6 Conclusions

Our results demonstrate that the ability of AS individuals to process mid-level, RFP is dependent on the analysis of local deformations of luminance-defined contour elements but decreased across all RF conditions when local contour elements are texture-defined. These findings represent behavioral evidence for a functional link between early and intermediate-levels of visual processing in AS, and suggests that atypical low-level (local) perception in AS might influence the processing of intermediate and higher-level visual information, consistent with an earlier, rather than later perceptual origin for atypical higher-level perception in AS (Belmonte et al., 2004; Bertone et al., 2010; Müller R.A., 2008).

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Table 1. Descriptive Statistics for Participants

	AS Group (n=29)	**Control Group (n=30)**	***t*-tests**
Gender			
Men	27	25	*p*=.42*
Women	2	5	
Age			
Mean	*18.59*	*19*	*p*=.64
SD	*3.80*	*3.44*	
Range	14-27	14-26	
Global IQ			
Mean	*96.45*	*107.07*	*p*=.001
SD	*11.81*	*10.66*	
Range	77-117	74-122	
Verbal IQ			
Mean	*93.76*	*107.48*	*p*<.001
SD	*15.91*	*10.19*	
Range	63-124	85-127	
Performance IQ			
Mean	*103.83*	*105.78*	*p*=.56
SD	*12.96*	*11.63*	
Range	71-134	70-122	
Raven's matrices percentiles			
Mean	*73.00*	*69.58*	*p*=.57
SD	*20.85*	*23.84*	
Range	13-98	13-96	

* Note. Fisher test was conducted to evaluate whether there was a difference between groups for gender ratios.

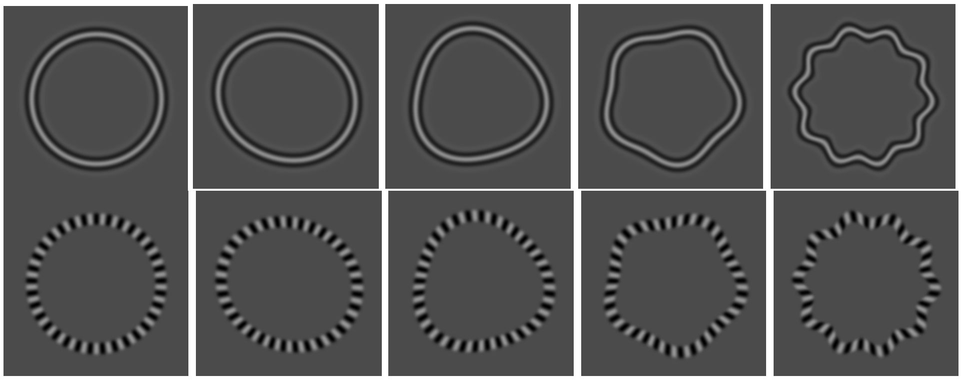

Figure 1. The top row depicts luminance-defined RFP of zero, two, three, five, and 10 radial frequencies (number of radial frequencies, or bump/dip cycles yielding the overall shape), whereas the bottom row depicts texture-defined RFP of zero, two, three, five, and 10 radial frequencies. The overall shapes are identical, but the information defining the contour differs.

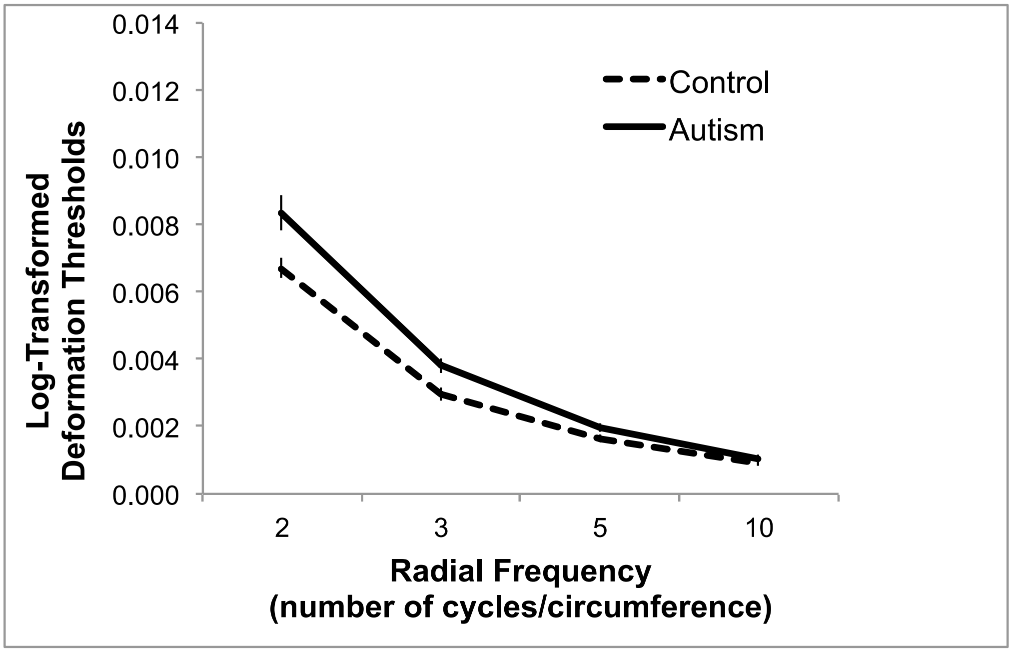

Figure 2. Mean deformation thresholds (+*SE*) for autistic and non-autistic participants as a function of luminance-defined RFPs.

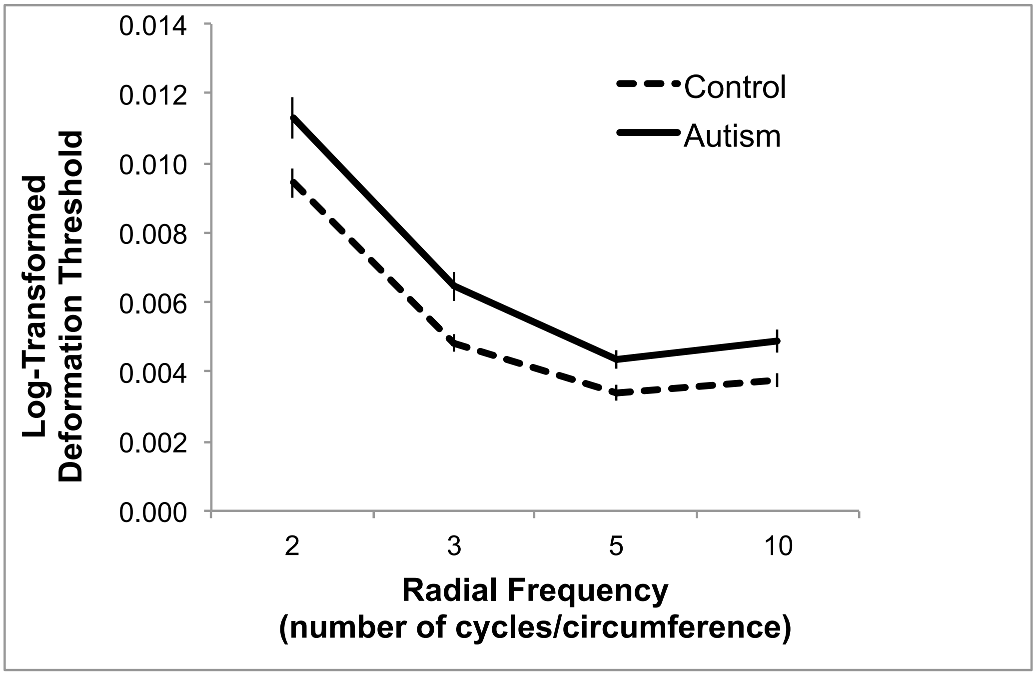

Figure 3. Mean deformation thresholds (+*SE*) for participant sin AS and control groups as a function of texture-defined RFPs.

Chapter 6: General Discussion

6.1 Summary of research objectives and hypotheses

The present thesis had two principle objectives. The first objective was to assess whether the differential development of early visual areas affects the visual processing of intermediate levels of visual analysis (Study 1). It was hypothesized that sensitivity to RFP containing fewer curvatures around their contour, which targets a global visual processing style, would take longer to reach adult-like sensitivity as compared to when RFP have greater numbers of curvatures surrounding their contour, a manipulation that targets a local processing style. Secondly, it was hypothesized that visual development for texture-defined shapes would take longer to reach adult-like sensitivity as compared to luminance-defined shapes.

The second objective was to assess whether atypical perceptual abilities in ASD originate from alterations at lower levels of visual processing (Study 2). Specifically, the aim was to assess whether manipulating the physical properties (luminance versus texture) of local contour elements of RFP differentially impacts intermediate visual analysis in ASD. It was hypothesized that participants with ASD would perform equivalently or superiorly compared to neuro-typical individuals for shapes defined by luminance information. Alternatively, it was hypothesized that individuals with ASD would perform worse for shapes defined by texture information. It was further hypothesized that a worse performance would be identified for luminance-defined shapes in participants with ASD for conditions targeting a global visual analysis, whereas a superior or equivalent performance was expected for shapes targeting a local processing style. Finally, for texture-defined shapes, it was hypothesized that participants with ASD would perform worse as compared to neuro-typical individuals for shapes targeting either global or local visual processing styles.

6.2 Discussion of Results of Study 1

The aim of Study 1 was to assess the typical development of the relationship between low- and intermediate levels of visual processing. To assess this objective, complex circular shapes (i.e. RFP) were used. The shape's contour was manipulated, so that both global (three and five RF) and local (10 RF) visual analysis could be targeted. In addition, the local physical elements of the shape's contour were also manipulated by defining it with either luminance- or texture-defined information. Results for luminance-defined RFPs revealed that children performed worse as compared to adolescents and adults for the detection of RFP containing fewer numbers of curvatures surrounding the contour of the shape (three and five RF). No group differences were identified for shapes containing greater numbers of curvatures surrounding the contour (10 RF). Thus, children's performance was relatively decreased only for conditions necessitating a global visual analysis. Given the study's results, it appears that mechanisms underlying global pooling take longer to reach adult-like sensitivity as compared to mechanisms underlying probability summation, and this is especially evident when patterns are luminance-defined.

On the contrary, findings for texture-defined shapes revealed that children performed generally worse as compared to the other age groups for conditions targeting both global and local visual processing. Therefore, longer periods of development are not only identified for mechanisms underlying global pooling but also for mechanisms responsible for probability summation. The delayed maturation for both global and local processing when shapes are texture-defined may be associated to the increased complexity of texture-defined information, given that an extra processing stage is required (Habak et al., 2009; Lin & Wilson, 1996).

Therefore, visual mechanisms responsible for the processing of local texture-defined information may take longer to develop, leading to a reduced ability to process RFPs in school-aged children.

Such results demonstrate that the timing of adult-like sensitivity depends on the type of local information, whether the number of curvatures or the type of local physical elements (luminance versus texture) defining the contour of a shape. When processing targets global pooling mechanisms, maturation appears to be similar for both luminance- and texture-defined shapes. Alternatively, timing of adult-like sensitivity for processes targeting probability summation appears to be influenced by local physical elements defining the contour of the RFP, with delayed maturation being evidenced for stimuli that are texture-defined. Overall, these results suggest that adult-like maturation of luminance-defined shapes is achieved before that of texture-defined shapes. Results also demonstrate that adult-like maturation of global visual processing is achieved later during development as compared to local visual analysis (Perreault, Habak, Lepore, & Bertone, 2013).

The study's results are consistent with other studies that have also identified delayed maturation of texture-defined stimuli, which target intermediate levels of visual analysis (see Bertone et al., 2010 for further details). However, given that other studies have identified quicker development for texture-defined information as compared to luminance-defined information when stimuli target earlier levels of visual processing (see Armstrong, Mauer, & Lewis, 2009; Bertone et al., 2008 for further details), it is possible to suggest that maturation of texture-defined perception may depend on the type of visual stimuli used (i.e., gratings vs shapes). Furthermore, the study's results are also in accordance to other studies that have identified delayed maturation of mechanisms responsible for global visual processing as compared to those responsible for local visual analysis (see van den Boomen et al., 2012 for review). As was described in the first article, delayed maturation of global visual processing may be attributed to underdeveloped long-range cortical connectivity as well as feedback and horizontal connections (Gervan, Berencsi, & Kovacs, 2011; Lee, Birtles, Wattam-Bell, Atkinson, & Braddick, 2012). On the other hand, orientation selective mechanisms that operate locally in primary visual areas appear to reach adult-like sensitivity faster, reflected by the finding that the school-aged group performed equivalently to the other age groups for luminance-defined shapes containing greater numbers of curvatures.

Overall, the results from Study 1 suggest that local information defining circular shapes interacts with the visual analysis of intermediate level (global) information, such as that preceding object and face perception, across different periods of development. The relatively decreased performance in children for global, luminance defined conditions as well as for both local and global texture-defined conditions may result from poor visual integration between low and intermediate visual mechanisms, and could be attributed to immature feedback and horizontal connections as well as under-developed visual cortical areas.

6.3 Discussion of Results of Study 2

Over the years, many studies have been interested in investigating visual perception in ASD at low- and high-levels of processing, given that differential visual analysis has been identified at each level (see Behrmann et al., 2006; Dakin & Frith, 2005; Marco, Hinkley, Hill, & Nagarajan, 2011; Simmons et al., 2009 for review). However, the majority of such studies have assessed each level of processing in isolation. It therefore remains unknown whether alterations at lower-levels of processing affect subsequent intermediate level visual analysis. The objective of the second study of this thesis was therefore to evaluate the relationship between low- and intermediate levels of visual processing in individuals with ASD by measuring sensitivity to RFP while manipulating the number of curvatures and the local physical elements defining the contour of the shape. It was hypothesized that better performance in ASD for luminance-defined shapes would be evidence as the number of deformations around the contour increase. For texture-defined shapes, it was hypothesized that performance would be worse in ASD for all RF assessed, given that previous studies have identified worse performance for texture-defined information in ASD, as proposed by the complexity-specific hypotheses (Bertone et al., 2005).

The methodology of the second study was similar to that of the first study presented in this thesis. Results revealed that for luminance-defined conditions, individuals with ASD performed worse when presented with RFP of two and three RF but performed equivalently when presented with RFP of five and 10 RF. Therefore, the ability to discriminate RFP in individuals with ASD decreased as information available along the contour of the shape moved from a local to a global visual processing style. These results are consistent with findings of Grinter et al. (2010), who also found worse performance in individuals with ASD for shapes having three deformations in the contour. As was concluded by these authors, it is possible that worse performance for conditions that solicit global visual processing reflects preserved early, local ventral-stream processing but less efficient visuo-spatial integration at higher levels of information processing in ASD. Furthermore, given that visual analysis of RFP with fewer curvatures targets mechanisms involved in global pooling, it could be argued that such mechanisms in ASD are altered.

A different pattern of results was observed for texture-defined RFP. Specifically, results revealed that individuals with ASD performed worse as compared to neuro-typical individuals across all RF conditions assessed. Therefore, when the RFP's contour was defined by texture information, both local and global visual processing was affected in ASD. Inferior sensitivity to texture-defined RFP is consistent with the complexity-specific hypothesis, which proposes that local, texture-defined information is processed less efficiently in ASD (Bertone et al., 2005). This less efficient processing of second-order information is thought to be a consequence of alteration in lateral or feed-forward and feedback connections within primary visual areas in ASD. Therefore, less efficient analysis of texture-defined information in individuals with ASD may have negatively impacted visual perception of RFP for both local and global visual analysis, thereby affecting not only mechanisms involved in global pooling but also those involved in probability summation.

Overall, these results represent behavioural evidence for a functional link between early and intermediate-levels of visual processing in ASD. Based on such findings, it is suggested that atypical low-level (local) perception in ASD might influence the processing of intermediate and higher-level visual information. The present results add to the existing literature and are consistent with an earlier, rather than later perceptual origin for atypical higher-level perception in ASD (Bertone, Hanck, Kogan, Chaudhuri, & Cornish, 2010; Luckhardt, Jarczok, & Bender, 2014; Robertson et al., 2014). Such a proposal is also supported by imaging research, which has demonstrated that there is enhanced activation of visual cortical regions when processing different types of visual information (Kana et al., 2013; Samson et al., 2012).

6.4 General Discussion and Relevance to ASD

As was mentioned in the previous section, results obtained in Study 2 suggest that atypical higher-level visual perception in ASD stems from alterations in early level visual mechanisms. Although not directly assessed in the presented behavioural studies, it can be argued that a potential neural origin contributes to such altered early perceptual functioning in ASD. In fact, past research has proposed that an imbalance in inhibitory and excitatory neural transmission, mediated by glutamate and GABA receptors, is present in ASD and that specific genetic mutations may contribute to such changes at the synaptic level (Bertone et al., 2010; Freitag, Staal, Klauck, Duketis, & Waltes, 2010; Luckhardt et al., 2014). Such changes at the synaptic level may then have a negative impact on the functioning and/or development of different cortical pathways in ASD. Specifically, an imbalance in inhibitory and excitatory neural transmission has been proposed as the basis of altered lateral and feedback connections mediating early vision in ASD (Bertone et al., 2010; Bertone et al., 2005; Kéïta et al., 2011; Luckhardt et al., 2014; Robertson et al., 2014). Furthermore, cortical connectivity has also been identified as being different in ASD as compared to that of neuro-typical individuals. For example, Keown et al. (2013) found local overconnectivity in primary visual areas as well as extra-striate cortical areas, and this was especially salient in individuals with ASD with greater symptom severity. Another study found reduced interhemispheric connectivity between early visual areas (Isler, Martien, Grieve, Stark, & Herbert, 2010; Luckhardt et al., 2014). Based on such findings, it can be concluded that an early imbalance in neural transmission, as well as differential connectivity along visual pathways may account for less efficient cortical integration along the visual pathways and subsequently lead to less efficient visual perception at higher-levels of analysis.

Although our results are congruent with the hypothesis that differential higher-level visual analysis stems from alterations in early level visual mechanisms, can such interpretations be generalized to other sensory modalities? O'Connor (2012) attempted to explore this question in the auditory modality in ASD by providing a summary of the literature on the subject. As described in her review article, enhanced ability to perceive low-level auditory information has been documented in ASD. For example, individuals with ASD demonstrate enhanced pitch perception and greater sensitivity to loud sounds, which appear to be especially present during childhood. At higher-levels of auditory perception, atypical processing of affective prosodic cues has been observed during the completion of complex experimental paradigms. Finally, difficulty processing auditory stimuli and speech in background noise has been noted in ASD. Therefore, research summarized in O’Connor’s (2012) review describes an enhanced ability to process simple auditory information in ASD, while more complex auditory information appears to be processed in a relatively less efficient manner. At a physiological level, O'Connor (2012) suggests that enhanced ability to process simple auditory information in ASD may be attributed to enhanced local connectivity in different auditory brain regions, whereas reduced long-range connectivity may negatively impact processing of more complex auditory information. Although not explicitly assessed in the auditory domain, it is possible to argue that alterations at early levels of auditory processing may also be associated to atypical processing of more complex auditory information in ASD.

Although fewer studies have been conducted to investigate processing of other sensory modalities, atypical somatosensory processing and olfaction has been reported in ASD. In the somatosensory domain, research has demonstrated altered tactile sensitivity in ASD when using a variety of different experimental paradigms (Puts, Wodka, Tommerdahl, Mostofsky, & Edden, 2014; Tannan, Holden, Zhang, Baranek, & Tommerdahl, 2008; Tommerdahl, Tannan, Cascio, Baranek, & Whitsel, 2007). Results demonstrating altered tactile sensitivity were interpreted as being a consequence of atypical inhibitory neural transmission in feed-forward inhibitory mechanisms (Puts et al., 2014; Tannan et al., 2008; Tommerdahl et al., 2007). Atypical short-range corticocortical connectivity in parietal regions have also been proposed to explain differential processing of tactile information in ASD (Tommerdahl et al., 2007).

In the olfactory domain, research appears to be mixed, which may be explained by differences in the methodology used (see Tonacci et al., 2015 for review). At higher-levels of processing, some studies point to reduced olfactory identification in ASD (Bennetto, Kuschner, & Hyman, 2007; Galle, Courchesne, Mottron, & Frasnelli, 2013), whereas others point to intact identification but reduced detection of olfactory stimuli in ASD (Dudova et al., 2011). At low-levels of processing, studies suggest that individuals with ASD process olfactory information similarly to neuro-typical individuals (Galle et al., 2013; Tavassoli & Baron-Cohen, 2012). However, results from a recent study (which used the Alcohol Sniff Test instead of the Sniffin' Sticks Olfactory Test to measure low-level olfactory detection thresholds) demonstrated enhanced sensitivity to olfactory stimuli in adults with ASD as compared to neuro-typical individuals (Ashwin et al., 2014). These authors believe that differences between their study's results and others might stem from the fact that their stimuli and procedures were simpler than other studies. They further suggest that the presence of enhanced sensitivity to simple olfactory stimuli in adults with ASD may once again stem from an imbalance between inhibitory and excitatory cortical signals. Given the controversy in research findings, more research is needed to investigate whether there are in fact differences in processing olfactory information in ASD as compared to neuro-typical individuals.

Overall, differences in the analysis of sensory information in ASD are present in visual, auditory, somatosensory, and olfactory domains. Although speculative, atypical perception across modalities in ASD can be explained at a cognitive level. Specifically, research demonstrates that there is a local-to-global interference in ASD, which is thought to negatively impact the way in which global perceptual information is processed. In fact, due to such local-to-global interference, global visual analysis takes longer to achieve and is more effortful in ASD (Van der Hallen, Evers, Brewaeys, Van den Noortgate, & Wagemans, 2015). Therefore, it is possible that manipulating the local, early-level physical elements of sensory information impact to a greater extent the way in which higher-level information is processed in ASD due to the presence of such local-to-global interference.

6.5 Implications of Findings to ASD

In the following section of this thesis, findings are discussed within the context of the different perception- and cognitive-based theories proposed to explain ASD phenotype. This section ends with clinical implications as related to the results of Study 2.

6.5.1 Theoretical Implications

As described in Chapter 4 of this thesis, the Weak Central Coherence (WCC: Happé, 1999; Happé & Booth; Happé & Frith, 2006) and the Enhanced Perceptual Functioning (EPF: Mottron et al., 2006) models have initially been proposed to explain differences in visual perception in ASD. Although both models stipulate that there is a local processing bias in ASD, they differ with respect to global information processing abilities in ASD. The WCC stipulates that individuals with ASD have difficulty integrating visual information, explained by less efficient connectivity between different cortical areas resulting in the presence of such abnormal visual integration (Happé & Frith, 2006). On the other hand, the EPF model stipulates that global perception is possible in ASD but that it is achieved in an atypical manner, where local visual information is not lost in the presence of global visual information. In addition, the EPF model proposes that a local processing bias in ASD is a consequence of greater autonomy of perception due to superior functioning of primary perceptual areas and associative areas. According to this model, bottom-up processing predominates visual analysis, given that top-down processing is hypothesized to be optional in ASD (Mottron et al., 2006). Overall, our results are in favour of different aspects of both models, and therefore, it is not possible at this time to select a model that best represents perception in autism.

One aspect of our results that is in accordance to the WCC and EPF models is the fact that a local processing bias in ASD was observed. This was demonstrated by findings in Study 2 where individuals with ASD performed similarly to neuro-typical individuals on conditions targeting a local processing style. This was especially evident for the luminance-defined conditions. However, when individual elements were texture-defined, the presence of a local processing bias in ASD hindered performance, as using local physical elements did not prove to be advantageous when texture-defined. In this case, individual segments must be integrated to be able to detect differences between stimuli. Considering that individuals with ASD presented difficulty for the conditions targeting a global processing style, it appears that visual integration in ASD is more difficult, a result that is more consistent with the WCC model, especially when this needs to be done preattentively. Given that sensitivity was worse in ASD for stimuli that were texture-defined, it is possible to suggest that there might not only be atypical connectivity between different cortical regions, as was proposed by the WCC model, but that there might also be abnormal functioning of primary perceptual and associative cortical areas in ASD, as suggested by the EFP model.

In addition to the WCC and the EPF models, more recent explanations have been proposed as a way to explain atypical behaviours in ASD. Pellicano and Burr (2012) propose that priors, the ability to use previously acquired knowledge and past experiences, are attenuated in individuals with ASD. According to this model, perception in ASD is influenced to a lesser extent by priors, allowing for the predominance of bottom-up connections resulting in enhanced perception of sensory stimuli. Pellicano and Burr (2012) suggest that attenuated priors would result in enhanced perception on occasions where the use of priors distorts the actual sensory input. On the other hand, inferior perceptual abilities would result on instances where the use of priors helps resolve perceptual ambiguities. According to their theory, it is not perception that is altered in ASD, but it is the interpretation of sensory input that is different. Overall, the result obtained in the second study presented in this thesis can partly be explained using the model proposed by Pellicano and Burr (2012). Specifically, it is possible that individuals with ASD have a reduced preconception of what a regular circle looks like consequently preventing them from being able to adequately discriminate between a circle and a RFP. However, given that our results demonstrate that alterations in low-level visual mechanisms have an impact on the analysis of higher-level visual information, it is unlikely that reduced prior knowledge of what a circle looks like explains all our results. It is more likely that alterations in visual processing influence the integrity of higher level perception and that atypical perception in individuals with ASD is not only a consequence of poor interpretation of sensory inputs.

Two recent models of ASD propose that atypical perception is a consequence of poor prediction abilities (Sinha et al., 2014; Van de Cruys et al., 2014). However, the basis of these models is different. On the one hand, Sinha et al. (2014) suggest that differential processing of sensory information is a consequence of diminished ability of individuals with ASD to predict the probability of a future event occurring based on past experiences. According to this theory, deficits in ASD appear to occur at a higher-level of processing. On the other hand, Van de Cruys et al. (2014) believe that poor prediction abilities in ASD arises from an imbalance between top-down and bottom-up inputs. When processing sensory signals, an individual makes predictions about sensory information perceived, targeting top-down processes. When predictions are far from the actual sensory input, prediction errors are made, stemming from bottom-up processes. Van de Cruys et al. (2014) propose that too much emphasis is placed on prediction errors in ASD. Therefore, low-level visual inputs predominate in ASD, thereby preventing visual signals from being integrated at higher levels of visual analysis.

When contrasting these prediction theories, it is clear that the results presented in this thesis do not corroborate ideas proposed by Sinha and colleagues (2014) but provide greater support for ideas proposed by Van de Cruys and colleagues (2014). Specifically, the greater reliance on low-level, bottom-up connections over higher-level, top-down connections, as suggested by Van de Cruys and colleagues (2014), prevented individuals with ASD in Study 2 from being able to integrate visual information at both low- and intermediate levels of analysis when local, early physical elements of the complex circular shapes were manipulated. If only higher-level processing was altered in ASD, as suggested by Sinha and colleagues (2014), only integration at higher-levels would have been affected, which is not what our results demonstrate.

Aside from other cognitive and perceptual models that have been previously proposed, the complexity-specific hypothesis (Bertone et al., 2005) has been suggested to explain differences at low-levels of perceptual analysis in ASD. This hypothesis was mainly proposed as a way to explain findings showing enhanced sensitivity to local, luminance-defined information and reduced sensitivity to texture-defined information (Bertone et al., 2005). As suggested by Bertone et al. (2005), altered lateral interactions in ASD may account for increased sensitivity to luminance-defined information given that such alterations would in theory result in increased orientation selectivity of such mechanisms since the response properties of early visual mechanisms responsible for the encoding of elementary visual information, such as orientation and spatial frequency, are modulated by the balance of excitatory/inhibitory activity (Edden, Muthukumaraswamy, Freeman, & Singh, 2009). Furthermore, these authors suggest that alterations in lateral and feedback connections are present in ASD, which would explain the presence of reduced sensitivity to texture-defined information. Findings obtained for texture-defined stimuli in Study 2 are consistent with the complexity-specific hypothesis (Bertone et al., 2005). Specifically, whereas performance for local RFP patterns was comparable in the luminance-defined RFPs, performance in the ASD group was decreased when the local elements of the RFP was texture-defined, whether under local or global RF conditions. Using such interpretations, it is possible that worse performance for texture-defined conditions be a consequence of abnormal lateral or feed-forward/feedback connectivity within primary visual areas, originating from an imbalance between excitatory and inhibitory signalling (Bertone et al., 2005; Kéïta, Guy, Berthiaume, Mottron, & Bertone, 2014; Kéïta et al., 2011; Vandenbroucke et al., 2008; Vandenbroucke, Scholte, van Engeland, Lamme, & Kemner, 2009). Given that lateral and feed-forward/feedback connectivity are involved in the processing of shapes (Choe & Miikkulainen, 2004; Lamme & Roelfsema, 2000), it is possible that such imbalance in connectivity in ASD contribute to reduced sensitivity even for luminance-defined shapes targeting a global processing style.

Overall, it is evident from our results that processing alterations reside in low-level visual mechanisms in ASD and that such abnormalities contribute to atypical processing of visual information at higher levels of analysis. Such findings are corroborated by electrophysiological and imaging studies. For example, a recent review article revealed that abnormal cortical activation resides at early and higher levels of visual processing (Luckhardt et al., 2014). This was evidenced by abnormal cortical activity in visual components of early visual areas (P100) and of faces (N170). From their analysis of the literature, Luckhardt et al. (2014) concluded that deficits in visual mechanisms affect the entire network responsible for face processing, and they suggest that the identified alterations at early levels have a consequence on subsequent processing stages. Studies using functional MRI have also found differences between ASD and neuro-typical individuals in terms of cortical activity and connectivity residing within or between different cortical visual areas. This has not only been noted in the ventral stream but also in the dorsal stream of visual processing. In terms of studies focusing on the dorsal stream, research has demonstrated that basic visual processing in ASD is altered, limiting the way in which local motion signals are integrated to form a global percept (Robertson et al., 2014). Local overconnectivity in primary and extrastriate visual areas has also been identified in ASD during a motion perception task, which was especially evident in individuals with ASD with greater symptom severity (Keown et al., 2013). In terms of studies investigating the integrity of the ventral visual pathway in ASD, greater reliance and activity of posterior cortical regions as well as reduced functional integration and segregation has also been observed in ASD (Kana et al., 2013; Rudie et al., 2012; Samson et al., 2012). Given that psychophysical and imaging research is now pointing towards a local or early origin for altered higher-level visual processing in ASD, it is important that models attempting to explain perception in ASD take into consideration such findings.

6.5.2 Clinical Implications

Given that the research defining the studies in this thesis were driven by fundamental questions concerning the perceptual phenotype in ASD, clinical implications of findings are somewhat limited. However, it is possible to suggest some avenues for assessment and intervention.

Firstly, it would be useful to gain greater knowledge regarding how and when trajectories of various visual functions in ASD deviate from the template of typical development. This can serve as autism-specific *perceptual phenotypes*, which could be used to optimize sub-grouping of the AS and to contrast ASD to other neurodevelopmental conditions such as dyslexia, William's syndrome and fragile x syndrome (Bertone et al., 2010). For example, increased sensitivity to luminance-defined, simple information with a concurrent decrease in sensitivity to more complex, texture-defined information has commonly been identified in ASD and is now referred to as a perceptual signature of ASD, given that it is specific to ASD (Bertone et al., 2010). Along with behavioural findings demonstrating reduced sensitivity to such visual information, physiological studies have also identified differential cortical activity when analyzing texture-defined information in ASD (Rivest, Jemel, Bertone, McKerral, & Mottron, 2013; Vandenbroucke et al., 2008, 2009). This being said, considering the results presented in this thesis, diagnostic measures should take into account visual abnormalities, not only at high-levels (such as processing of faces and emotions) but also those residing at lower levels given their impact on visual processing at higher levels in ASD. Therefore, complementary screening techniques should be used in combination to the already existent tools, such as the ADOS and the ADI-R (Lord et al., 1994; Lord et al., 2000), to evaluate the integrity of perceptual abilities. This would especially be useful in cases where ambiguity remains in whether a child should or not meet criteria for the diagnosis of ASD.

The results presented in this thesis can also be used to suggest avenues for intervention. Currently, interventions used in ASD are predominately centered on improving behavioural difficulties, such as improving a child's social and communication skills (Lai et al., 2014). However, interventions used to do not take into account atypical processing of perceptual information in ASD at different levels of analysis. This is especially important, considering that findings presented in this thesis point to an early origin for atypical higher level visual processing, such as that mediating face perception. Therefore, as was suggested by Bertone et al. (2010), interventions should not only focus on improving social and communication abilities in ASD but should also attempt to ameliorate information processing at different levels of analysis (i.e., through perceptual learning, for example). Focussing on lower levels of perceptual analysis should in turn improve higher levels of processing. At this time, it is unclear what types of intervention should be used. More research is needed to assess which strategies would work best to ameliorate information processing at different levels of analysis in ASD.

6.6 Limitations and Future Directions

Interpretations and generalizations of results presented in this thesis must be done in light of some methodological limitations. In the following section, such limitations are discussed, followed by suggestions regarding future directions.

6.6.1 Limitations

All the participants in the ASD group in Study 2 previously obtained a strict diagnosis of Autistic Disorder, according to DSM-IV criteria; the sample did not include any participants diagnosed with either Asperger Syndrome nor PDD-NOS. This allowed for the analysis of a very homogenous sample, which in turn eliminated the presence of any confounding variable related to speech onset and symptom severity. Specifically, all participants in Study 2 presented a language delay at an early age, had intellectual functioning that is considered to be in the average range (GIQ > 70), and did not present any comorbid conditions. Although the homogeneity of the sample presents an advantage, it remains that results can only be generalized to individuals presenting such stringent characteristics. Therefore, results cannot be generalized to individuals with ASD presenting behaviours consistent with those across the spectrum, such as for individuals with no language delay, having intellectual impairment, or other comorbid genetic or medical conditions. It would be interesting to assess whether alterations at early level visual processes affect the perception of higher-level information in individuals across the spectrum as to assess whether our findings are representative of individuals across the entire ASD phenotype.

In all studies, reduced sensitivity to RFP was interpreted as being a consequence of either underdeveloped or altered connectivity between early and mid-level visual mechanisms. Such conclusions were based on studies demonstrating that feed-forward, feedback, and horizontal connections are implicated in the visual perception of complex circular shapes (Loffler, 2008). However, the studies presented in this thesis did not have an imaging component. It is therefore difficult to conclude with certainty that inferior sensitivity is actually a consequence of underdeveloped or altered connectivity or whether other factors account for differences in performance.

The developmental study presented in this thesis (Study 1) had participants placed into three different age groups (i.e. school-aged children, adolescents, and adults). By doing so, it was possible to estimate the timing with which visual processes reach adult-like sensitivity during typical development. However, using this method, it was not possible to estimate the exact age when visual mechanisms have matured. It might have been more advantageous to separate the different age groups in an age range of one to two years (e.g. 7-8, 9-10, 11-12, etc.), as other studies have done so in the past when assessing typical development (see Bertone et al., 2008; Hanck, Cornish, Perreault, Kogan, & Bertone, 2012 for examples). Furthermore, the statistical analyses performed did not allow for the analysis of developmental trajectories. It perhaps would have been helpful to use complementary statistical analyses, such as regressions, to assess developmental trajectories associated to the perception of early to intermediate level visual information.

6.6.2 Future Directions

In addition to assessing visual processing in individuals with ASD, it is also important to assess how visual mechanisms at low-, mid-, and high-levels develop in this population. This being said, future research could attempt to assess the developmental interaction between low and mid-level visual analysis. Although not included as a study in the present thesis, we have attempted to do this by assessing low- to intermediate level visual processing in ASD across different developmental periods. In this preliminary study, 46 individuals with ASD and 47 neuro-typical individuals participated and were placed into three different age groups (7-12, 13-17, and 18 to 27 years old). The stimuli and procedures used were the same as for the studies presented in this thesis. Specifically, participants had to detect which of two presentations was the RFP, which contained three, five, or 10 RF. Local physical elements were also manipulated by adding luminance- and texture-defined information.

Preliminary results (see Appendix B for Figures presenting the obtained data) show that for luminance-defined RFP conditions ASD discrimination thresholds are greater (worse performance) across all RF conditions for the adolescent age group. As shown in Figure 3 of

Appendix B, a trend towards a statistically decreased performance in the adult age groups is evidence for the RFP conditions targeting a global visual analysis (three RF condition). ASD thresholds appear to be similar to neuro-typical individuals for the school-aged groups. When taking into account findings obtained from Study 1, it is possible that mechanisms in ASD initially develop similarly to neuro-typical individuals but that visual maturity to complex circular shapes is reached later in development, closer to adulthood in ASD compared to neuro-typical individuals for local visual processing. Global visual processing does not appear to reach the same developmental level in ASD as in neuro-typical individuals. In typically developing populations, visual processing is predominately local at younger ages and becomes more configural (global) during adolescence (Greimel et al., 2014; Mondloch, Le Grand, & Maurer, 2002; Nayar, Franchak, Adolph, & Kiorpes, 2015). Visual processing is preferentially local in ASD, and it is possible that the non-difference between groups during childhood be attributed to similar local visual processing styles in neuro-typical individuals as in ASD, early on during development. While perception becomes more configural in neuro-typical individuals, it appears to remain locally-based in ASD, which may explain the differences between individuals with ASD and neuro-typical individuals for older age groups.

Preliminary results obtained for texture-defined RFP are similar to those obtained in Study 2. Specifically, ASD sensitivity to RFP appears to be inferior to neuro-typical individuals for all RFP conditions assessed across all age groups (see Appendix B for figures presenting the obtained data). This suggests that mechanisms underlying texture-defined processing do not reach the same developmental level in ASD as they do in neuro-typical individuals. Therefore, when information is more complex, as is the case for texture-defined information, ASD sensitivity to RFP is reduced across developmental periods, regardless of the type of visual processing: local and global. These preliminary results are again consistent with Bertone et al.'s (2005, 2010) complexity-specific hypothesis, which proposes that ASD individuals process local visual texture-defined information less efficiently.

Overall, these preliminary results demonstrate that the processing of mid-level RFP follow different developmental profiles in ASD as compared to neuro-typical individuals. These behavioral findings suggest that differential development of early visual processes might have a negative impact on the development of intermediate visual mechanisms in ASD. This again is consistent with accounts suggesting that there might be an early origin for atypical higher-level perception in ASD.

The second study of this thesis has centralized its efforts to relating atypical intermediate visual processing to altered low-level visual mechanisms. However, can such findings be generalized to higher-level visual abnormalities in ASD? Based on the results presented here, it is only possible to infer that because intermediate level abnormalities relate to low-level visual alterations that higher-level abnormalities will also. In order to verify such conclusions, it would be interesting to assess whether alterations residing at intermediate levels of vision relate to the integrity with which higher-level visual information, such as faces, is visually processed in ASD. Future research could therefore assess sensitivity to intermediate and high-level visual stimuli in the same participants and perform correlational analyses to evaluate whether performances on these tasks are associated to one another.

The studies in the present thesis used a behavioural approach. Such a methodology limits the extent to which conclusions can be drawn about cortical functioning in ASD. Consequently, future research could assess cortical activation as well as connectivity within and between early (V1), intermediate (V4), and high level (Fusiform Face Area - FFA) visual areas in ASD. For example, a methodology similar to the one used by Wilkinson et al., (2000) could be adapted and used to assess brain activity in ASD. In such a methodology, luminance-defined parallel, radial, and concentric patterns could be used to assess cortical activation at different levels of the ventral visual stream. Wilkinson et al., (2000) showed from their results that concentric patterns elicited greater activation than parallel and radial patterns in FFA, suggesting that the processing of concentric global structure may partly underlie face perception. Based on such findings, it would be interesting to assess whether it is possible to identify such pattern of results in ASD. Given behavioural findings presented in the second study of this thesis, it is likely that differential activation of low (V1), intermediate (V4), and high level (FFA) processes would result when perceiving such stimuli. Overall, conducting such a study would allow to validate or not the conclusions and interpretations suggested in this thesis.

Lastly, a cross-syndrome comparison could be done to assess whether a perceptual origin for higher levels visual abnormalities exists in other conditions, such as in Fragile-X or William's syndrome. This is pertinent given that abnormalities at different levels of visual processing have also been identified in these neurodevelopmental conditions (Atkinson et al., 2006; Atkinson et al., 1997; Bertone et al., 2010; Eckert et al., 2006; Kogan et al., 2004a; Kogan et al., 2004b). Therefore, it would be interesting to assess whether differential visual processing at different levels of analysis also originates from alterations in lower level visual mechanisms in these other neurodevelopmental conditions. This would permit to identify condition-specific visual abnormalities, which would in turn allow the obtainment of a better understanding of the phenotype common and specific to each condition.

Chapter 7: Conclusion

Given that most research investigating visual mechanisms has done so by assessing lower- and higher-levels of processing in isolation in both typically developing individuals and in ASD, the principle aim of this thesis was to evaluate the interaction mediating these different levels of visual analysis. Specifically, the first objective of this thesis was to assess the development of intermediate level visual processing and how it relates to the differential development of lower-level visual mechanisms (Study 1). The second objective of this thesis was to assess the relationship between early and intermediate level visual processing in ASD as to investigate whether atypical higher-level visual analysis originates from altered low-level mechanisms (Study 2).

The results obtained in this thesis demonstrate that differential development of low-level mechanisms do have an impact on the age with which intermediate level visual processes reach adult-like sensitivity. This was demonstrated by the fact that sensitivity was worse in children for global, luminance-defined conditions as well as for local and global texture defined conditions. Poor visual integration between low and intermediate visual mechanisms, immature feedback and horizontal connections, and under-developed visual cortical areas may all contribute to the developmental profile obtained.

As for the second study of this thesis, results demonstrate that alterations in low-level mechanisms do relate to the way in which intermediate visual information is processed in ASD. Specifically, when stimuli are luminance-defined, sensitivity was worse in ASD as perception moved from local to global. For texture-defined stimuli, both local and global visual processing was affected in ASD. Reduced sensitivity across all texture-defined conditions is consistent with the complexity-specific hypothesis, which posits that local, texture-defined information is processed less efficiently in ASD. It is possible that less efficient processing of such information be a consequence of alteration in lateral or feed-forward and feedback connections within primary visual areas in ASD. Overall, these results are consistent with an earlier, rather than later perceptual origin for atypical higher-level perception in ASD.

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Appendices

Appendix A: Increased Sensitivity to Mirror Symmetry in Autism

Audrey Perreault (1,2,3), Rick Gurnsey (4), Michelle Dawson (2), Laurent Mottron(2,5), Armando Bertone (1,2,5)

(1) Perceptual Neuroscience Lab for Autism and Development, Montreal, Quebec, Canada
(2) University of Montreal Centre of Excellence for Pervasive Developmental Disoders (CETEDUM), Montreal, Quebec, Canada
(3) Department of Psychology, Université de Montréal, Montreal, Quebec, Canada
(4) Department of Psychology, Concordia University, Montreal, Quebec, Canada
(5) Department of Psychiatry, Université de Montréal, Montreal, Quebec, Canada

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*Appendix A is an exact reproduction of the following published article

1. Abstract

Can autistic people see the forest for the trees? Ongoing uncertainty about the integrity and role of global processing in autism gives special importance to the question of how autistic individuals group local stimulus attributes into meaningful spatial patterns. We investigated visual grouping in autism by measuring sensitivity to mirror symmetry, a highly-salient perceptual image attribute preceding object recognition. Autistic and non-autistic individuals were asked to detect mirror symmetry oriented along vertical, oblique, and horizontal axes. Both groups performed best when the axis was vertical, but across all randomly-presented axis orientations, autistics were significantly more sensitive to symmetry than non-autistics. We suggest that under some circumstances, autistic individuals can take advantage of parallel access to local and global information. In other words, autistics may sometimes see the forest and the trees, and may therefore extract from noisy environments genuine regularities which elude non-autistic observers

2. Introduction

Autism is a neurodevelopmental variant whose current diagnostic criteria describe overt behavioral atypicalities in three domains: social interaction, communication, and restricted interests and repetitive behaviors [1]. Research addressing the interrelated social and communication domains has traditionally been dominant. In contrast, there has been relatively less impetus for understanding behaviors encompassing unusual, intense, and narrow interests or preoccupations (e.g., with specific aspects of objects or the environment), as well as repetitive routines or motor mannerisms. However, recognition that this putatively ‘‘non-social’’ domain is in fact important for identifying and understanding the autistic behavioral phenotype is increasing [2]. Several recent findings demonstrate that focused interests and repetitive behaviors related to visual perception—such as unusual visual exploration (e.g., lateral glances), longer fixations, and frequent spinning of objects—are common in and specific to autism starting early in development [3–5].

The origin of such atypical autistic visual behaviors is as yet unknown. One proposal is that atypical development of perceptual functions ultimately results in a perceptual signature or profile that distinguishes autism from both typical development and other neurodevelopmental conditions [6,7]. This signature takes into account findings of superior performance by autistics on a variety of visuospatial tasks, including visual search, block design, and embedded figures tasks [8–10]. There is also preliminary evidence that autistics have difficulty processing elementary visual attributes such as texture and color [11,12].

Together with interest in the understudied ‘‘non-social’’ domain, interest in the neural underpinnings mediating early perceptual abilities in autism has recently proliferated [13,14].

Studies have been interpreted largely within the context of two evolving neurocognitive models, whose tenets differ with regard to the origin of recurrent findings of enhanced autistic performance on several types of visual tasks. The first model, weak central coherence [15], posits that superior performance on visuospatial tasks is the result of an apparent local processing bias when locally- oriented analysis is considered to be advantageous. According to WCC, the same local processing bias also predicts a defective construction of global visual representations, a perceptual trade-off analogous to not being able to see the forest for the trees. The second model, enhanced perceptual functioning [16], posits autistics' superior performance as reflecting an increased role and autonomy of perception during the completion of cognitive tasks. One possible mechanism is an increased functional involvement of early and associative perceptual cortices [17]. In this model, autistics are able to construct global representations but do so atypically, such that access to local information is not lost in favor of the efficient analysis of a global percept, as is the case within typical processing hierarchies.

The two models of autistic perception diverge with respect to the role of global processing and thus motivate an evaluation of grouping processes in autism. Understanding of elementary, local visual perception (e.g., motion, color, texture, etc.) is growing and beginning to complement the vast literature on socially-contingent object perception (e.g., face perception). Nevertheless, the question of how local stimulus attributes are grouped into meaningful spatial patterns has not yet adequately been studied in autism [18]. The goal of this study was therefore to assess visual grouping in autism by measuring sensitivity to visual symmetry, a prototypical and ecologically-significant type of grouping that exemplifies how spatial information is organized before visual object perception occurs.

Mirror symmetry, where one half of a pattern is a mirror reflection of the other half, is a highly salient visual attribute involved in figure-ground segregation and in object perception and recognition [19,20]. The perception of mirror symmetry emerges from multiple stages of spatial processing. An encoding process, initiated by individual neurons or spatial filters, starts with the assimilation of local elements positioned at the same spatial location relative to, but on either side of, the symmetrical axis [19,21]. These local- element pairs are subsequently integrated or grouped at a comparison stage before a globally symmetric pattern is perceived [21–23]. The spatial filters compare information of similar contrasts present at two locations equidistant from a symmetry axis, and outputs of pairs of detectors relative to a given symmetry axis are summed to form the symmetry signal relative to that location.

Although symmetry perception is initiated by local processing, the extraction of global symmetric configurations has been demonstrated to selectively solicit higher-order cortical visual brain areas, including V3A, V4, V7, and LO [24]. The importance of mirror symmetry with respect to object recognition is reflected by the fact that under conditions of uncertainty, symmetry is most efficiently perceived if oriented about a vertical axis [20,23,25], an advantage argued to reflect the ecological and social significance of most vertically symmetrical objects [20].

In the present study, we assessed the ability of autistics and matched non-autistics to detect mirror symmetry oriented about vertical, oblique, and horizontal axes. A differential ability to perceive symmetry would suggest different methods of global pattern extraction in autism, an essential level of perceptual analysis preceding object perception.

3. Methods

3.1 Participants

Seventeen autistic and 15 typically developing individuals, recruited from the Rivière-des-Prairies Hospital database, participated in the study. Autism was diagnosed using the Autism Diagnostic Interview – Revised (ADI-R) combined with the Autistic Diagnostic Observation Schedule - General (ADOS-G), both of which were conducted by a trained clinician-researcher (LM) who obtained reliability on these instruments. The comparison group was composed of non-autistic adolescents and adults screened with a questionnaire for personal or familial history of neurological or psychiatric disorders. Autistic and non-autistic participants were matched on gender, global IQ as measured by Wechsler Scales, and age (see Table 1). All participants had Wechsler scores of 80 or higher, and normal or corrected-to-normal far and near vision as assessed before testing using both near and far acuity charts (i.e. near point directional –E- and –C cards, Snellen letter sequence-A-new Logmar). The ethics committee at Rivière-des-Prairies Hospital approved the study. Participants or their parents (if under 18 years) provided written informed consent. The study was carried out in accordance with the Declaration of Helsinki, and was approved by the research ethics committee at l'Hôpital Rivière-des-Prairies.

[Insert Table 1 here]

3.2 Apparatus and stimuli

Stimulus construction, presentation, and data recording were controlled by Matlab-driven routines from the Psychophysics and Video Toolbox. All stimuli were displayed on a gamma-corrected 19-inch Viewsonic monitor with a screen resolution of 11526870 pixels using a MACPRO G4 testing station. The mean luminance of the display was 20.00 cd/m2 (x = 0.2783, y = 0.3210 in CIE (Commission Internationale de l'Eclairage) u' v' color space). A Minolta CS-100 Chroma Meter colorimeter was used for the calibration and luminance readings.

Symmetrical stimuli were global patterns whose local elements, or dot-pairs, were located equidistant from either side of an axis [PL(x,y) and PR(-x,y)]. As shown in Figure 1, symmetrical dot pairs always shared the same luminance polarity, either black-black (1.0 cd/m2) or white-white (39.0 cd/m2). Symmetrical patterns (target stimuli) were composed of 500 dot-pairs (1000 total dots) presented within a circular aperture that subtended 10u in diameter when viewed at a distance of 57 centimeters; individual dots, comprising the dot-pairs, subtended < 0.1 degrees at the same distance. Signal strength was determined by the proportion of dots matched across the axis of symmetry such that 0% matching meant the pattern was perfectly random, and 100% matching meant the pattern was perfectly symmetrical (as depicted in Figure 1). Based on pilot testing, seven levels of signal strength were chosen for experimentation (30%, 36.7%, 44.8%, 54.8%, 66.9%, 81.8% and 100% symmetrical dot-pairs). Symmetrical stimuli were presented with their axes orientated either vertically (0u), obliquely (45u), or horizontally (90u). Non-symmetrical (non- target) stimuli consisted of patterns where 0% of dot-pairs were symmetrical relative to the symmetry axis.

[Insert Figure 1 here]

3.3 Procedure

On each trial participants were asked to detect which of two successively-presented stimuli contained symmetry, with one stimulus containing no symmetry (non-target) and the other containing one of the seven predetermined symmetrical signal strength levels (target). Participants responded by pressing one of two keys on a keyboard. Each stimulus was presented for 250 ms, separated by a 100 ms grey screen. Within a testing block, each of the seven signal strengths was presented at each of three orientations (vertical, horizontal, and oblique) in random order, resulting in 21 trials (3 orientations X 7 signal strengths). A complete testing session consisted of 25 blocks, resulting in 25 measures for each of the 21 experimental conditions. A 5-minute practice session containing 5 trials of highly-visible symmetry patterns for each orientation preceded testing in order to familiarize participants with fixation, stimuli presentation, and responding. All experiments were conducted in a dimly-lit room. Throughout testing, participants were reminded to fixate the center of each pattern and were encouraged to take breaks if they felt tired or distracted. The experimenter remained present throughout testing to monitor fixation and fatigue. The entire testing session took approximately 60 minutes to complete.

4. Results

Data for three of the 17 autistic participants were not used for analysis because the participants were unable to obtain threshold for any of the three symmetry conditions (i.e., vertical, oblique, or horizontal). Two of these participants were also unable to complete a separate orientation discrimination task, which suggests that their inability to reach threshold was due to difficulties in task comprehension rather than an inability to perceive symmetry.

Symmetry detection thresholds were derived for each orientation by fitting a Cumulative Gaussian Distribution function to the signal strength vs. accuracy functions. Threshold was defined as the signal strength eliciting 75% correct responses. Figure 2 shows the mean symmetry detection thresholds as a function of axis of orientation for autistic (black bars) and non-autistic (gray bars) groups. As expected, a 2 (group) x 3 (orientation) mixed factorial design, with alpha level set at 0.05, revealed a significant main effect of axes of orientation ($F(2,54) = 37.78$, $p < 0.05$; $\eta^2_{partial} = 0.58$). Tukey post-hoc analysis, with alpha level set at 0.01, revealed that mean detection threshold for vertically-oriented symmetry ($M = 58.85$, $SD = 10.66$) was lower compared to both oblique ($M = 85.48$, $SD = 14.53$) and horizontal ($M = 72.76$, $SD = 14.55$) conditions.

[Insert Figure 2 here]

A main group effect was also evident ($F(1, 27) = 4.42$, $p < 0.05$; $\eta^2_{partial} = 0.14$), with mean symmetry detection thresholds significantly lower in the autistic group compared to the non- autistic group when averaged across axis of orientation. A group x orientation interaction was not found ($F(2,54) = 0.18$, $p = ns$; $\eta^2_{partial} = 0.01$) as mean between-group differences in symmetry detection threshold did not significantly differ as a function of axis of orientation.

5. Discussion

Our aim was to assess visual grouping in autism by measuring sensitivity to mirror visual symmetry, a salient attribute inherent in many visual objects. Our findings suggest that symmetry perception is both typical and atypical in autism. It is typical in that autistics were most sensitive to vertically-oriented symmetry patterns, an expected advantage also found in the non-autistic group. However, groups differed in overall sensitivity to visual symmetry across axes of orientation conditions, with autistics displaying enhanced performance compared to their non-autistic controls.

The typical ‘‘vertical advantage’’ for detecting mirror symmetry may reflect the ecological and/or social significance of vertically symmetrical objects, such as human faces, in our every-day environment. It has been proposed that autistics are innately insensitive to the importance of socially-relevant information, particularly human faces [26]. A failure of autistics to demonstrate the vertical advantage in visual symmetry detection would support this proposal. However, we found that autistics have the same vertical advantage as nonautistics.

At the same time, we found that visual symmetry perception was atypical in autism. Autistics were more sensitive to symmetry than their non-autistic controls across all three axes of orientation. By definition, the perception of visual symmetry is a grouping task that necessarily involves spatial integration. This finding is therefore inconsistent with the WCC-based hypothesis suggesting that while autistic spatial perception can be advantageous in the processing of local elements, it is defined by inefficient integrative analysis [15]. In a comparable contour integration task, Del Viva, Igliozzi, Tancredi, and Brizzolara (2006) found an equivalent ability of young autistics and non-autistics to detect the spatial position of a circularly-configured chain of local elements (signal) embedded in background noise [27]. Our findings, however, differ from those of previous relevant studies of grouping abilities in that autistics manifested a visuo-spatial processing advantage.

We propose that this superior performance may originate from autistics' efficacy at extracting recurring complex regularities from noisy arrays of information. Symmetrical patterns are defined by multiple highly structured spatial relationships between local elements, always presented at equidistant locations relative to an axis. As suggested by Mottron, Dawson, and Soulières (2009), neural mechanisms involved in pattern detection may be particularly active in autism [28]. Further, atypically autonomous cognitive processes in autism may allow for the parallel, non- strategic integration of patterns across multiple levels and scales, resulting in autistics' ability to efficiently access and extract signal from noise at both local (i.e. symmetrical dot-pairs) and global (global symmetrical patterns) levels. In theory, such parallel access would be less likely in non-autistic individuals, whose ability to use local information from early visual areas would be diminished due to typical globally-biased processing hierarchies. A parallel processing advantage would be especially pertinent in our study given the difficulty of the task. Specifically, the global orientation of each symmetrical pattern was presented randomly within testing blocks, making it more difficult to use global spatial relationships to efficiently detect symmetry [29].

In sum, we did not find evidence for the autistic visual grouping deficit predicted by WCC. Instead our findings raise the possibility that under some circumstances autistics are atypical in seeing both the forest and the trees, leading in this case to superior detection of mirror symmetry. Autistics' enhanced ability to detect genuine regularities within noisy stimuli deserves more attention [14], particularly as these complex abilities have been found in autistic toddlers [30]. In addition, recent findings have demonstrated an autistic preference for dynamic visual regularities at a young age [31]. Our findings suggest that while autistics are sensitive to stimuli attributes that are salient to non-autistics (i.e., vertical advantage), autistics may in addition detect and respond to environmental regularities, which elude non-autistics.

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7. Author Contributions

Conceived and designed the experiments: RG. Performed the experiments: AP. Analyzed the data: AP RG AB. Contributed reagents/materials/ analysis tools: AP RG AB. Wrote the paper: AP MD LM AB. Reviewed the manuscript: AP RG MD LM AB.

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Table 1. Mean and Standard Deviations for Variables used to Match Autistics to Non-autistics.

	Autistic	Non-autistic	*t* & *p* values
Gender	17 males	15 males	
Chronological Age			*t*(30) = 1.83, *p* = 0.08
M	24.06	20.47	
SD	6.30	4.50	
Range	14-35	15-29	
Full Scale IQ			*t*(30) = -0.60, *p* = 0.56
M	102.88	105.40	
SD	12.90	10.66	
Range	81-126	88-122	
Performance IQ			*t*(25) = 1.18, *p* = 0.25
M	109.42	104.93	
SD	8.31	10.79	
Range	96-121	87-119	
Verbal IQ			*t*(25) = -0.50, *p* = 0.62
M	103.50	105.27	
SD	16.07	12.83	
Range	77-128	91-127	

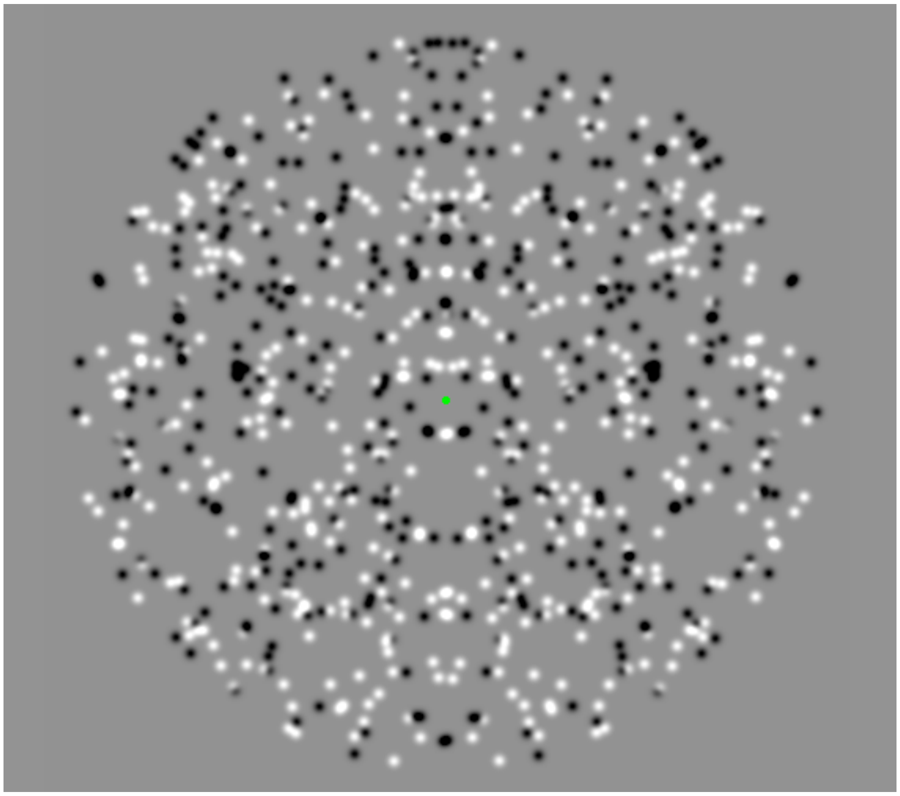

Figure 1. Example of typical symmetry pattern with a vertical axis of orientation. All stimuli were comprised of 500 dot pairs (half white and half black) presented within a circular aperture subtending 10° in diameter.

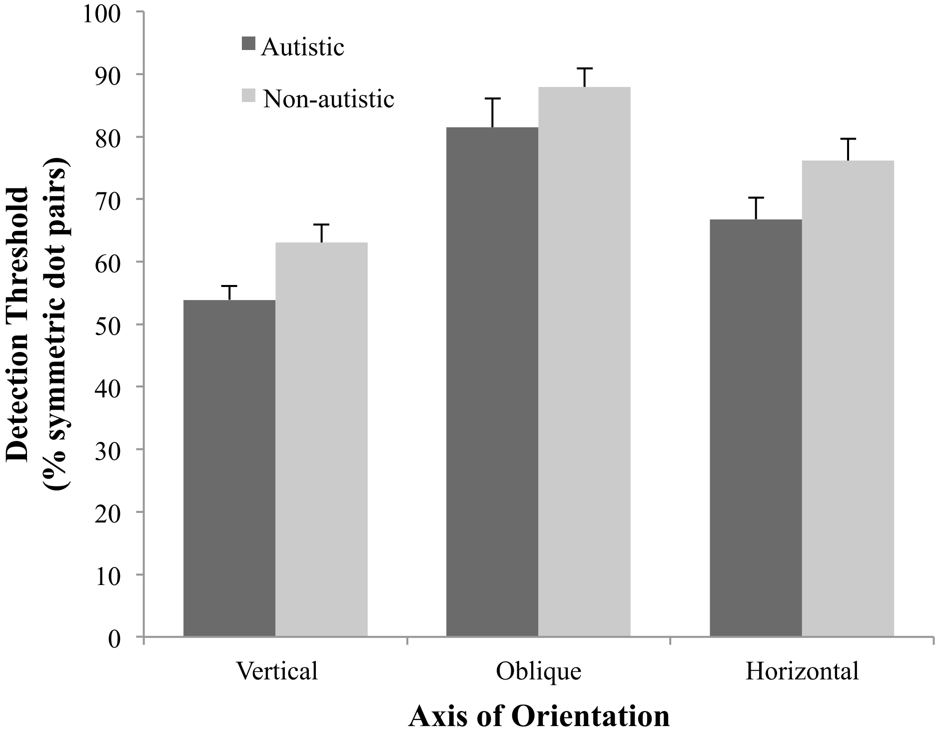

Figure 2. Mean symmetry detection threshold (+*SE*) for autistic (*n* = 14) and non-autistic (*n* = 15) groups plotted as a function of axis of orientation (vertical, horizontal, or oblique).

APPENDIX B: Graphs presenting preliminary data of the study conducted to investigate the developmental interaction between low- and mid-level visual perception in ASD

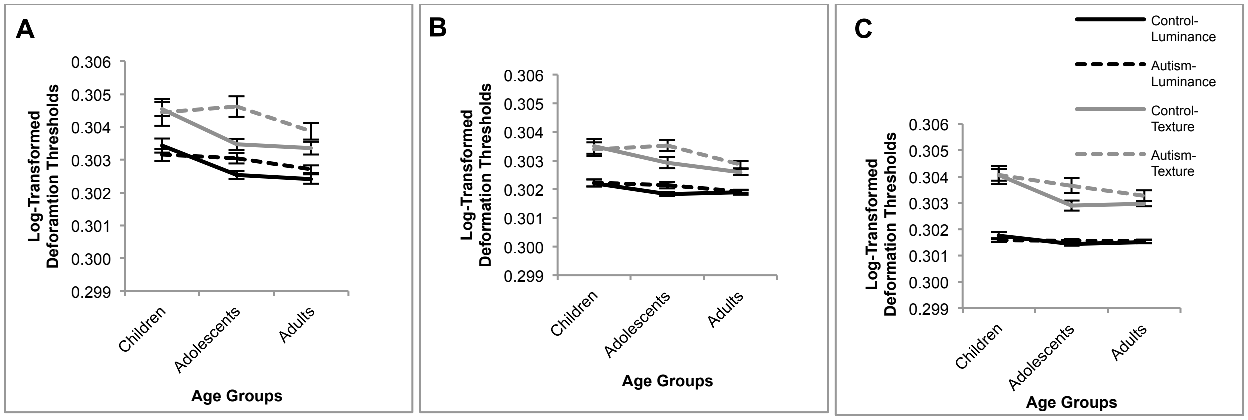

Figure 1. Graphs A (3RF), B (5RF), and C (10RF) depict luminance- and texture-defined results for AS and controls across each age group for each RFP condition.

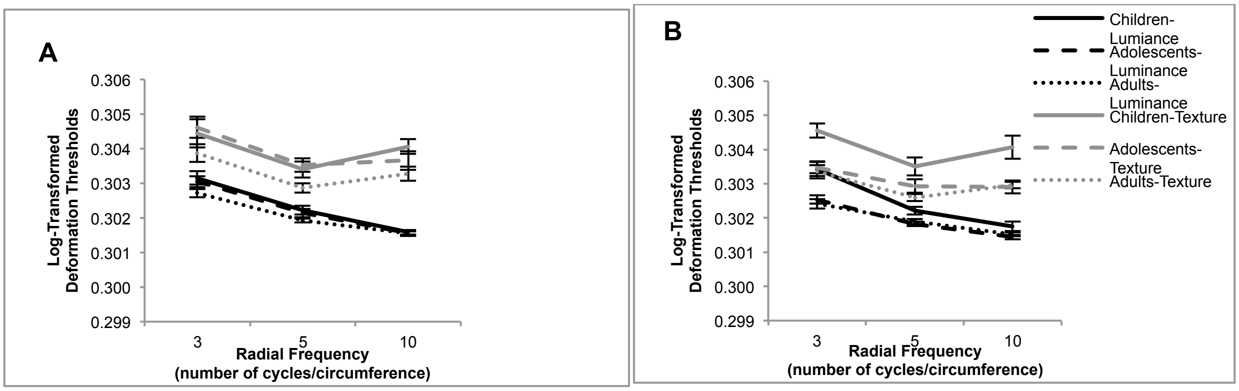

Figure 2. Graphs A (autism) and B (control) present results for luminance- and texture-defined RFP for AS and control participant thresholds across the different age groups assessed.

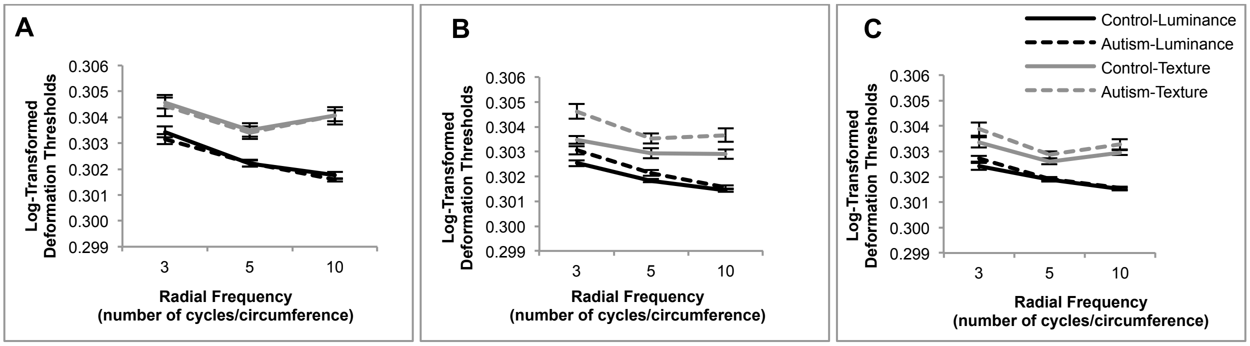

Figure 3. Graphs A (school-aged children), B (adolescents), and C (adults) depict differences between AS and controls for luminance- and texture-defined RFP for the different age groups assessed.