Université de Montreal

A Psychophysical Assessment of Visual Motion Processing among High-Functioning Persons with Autism

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Cette thèse intitulée :

A Psychophysical Assessment of Visual Motion Processing among High-Functioning Persons with Autism

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RÉSUMÉ

Mots-clés : autisme, perception du mouvement, traitement de l'information visuelle, premier-ordre, deuxième-ordre, complexité du stimulus, mécanismes neuro-intégratifs, déficit de cohérence centrale, voie visuelle dorsale, voie visuelle ventrale

L'autisme est un trouble envahissant du développement d'origine neurobiologique dont le diagnostic est basé sur une symptomatologie de comportements anormaux. Bien qu'un tel comportement est habituellement caractérisé qualitativement en termes d'une triade de signes concernant l'interaction sociale, la communication et l'imagination, des troubles non-sociaux sont également considérés comme étant universellement présents dans l'autisme et sont employés en tant que caractéristiques diagnostiques. Une proportion importante de ces signes implique le domaine visuo-perceptif, caractérisé par une approche « locale » dans l'analyse de l'information visuelle. Tel que suggéré par la théorie du *défcit de la cohésion centrale*, les personnes autistes semblent intégrer l'information visuelle moins efficacement que les personnes non-autistes. Le but principal de cette thèse était d'adresser cette proposition en évaluant l'intégrité des mécanismes neuronaux responsables du traitement intégratif de l'information visuo-perceptuelle chez les autistes en mesurant leur sensibilité à des stimuli de mouvement exigeant un traitement neuronal de divers degrés de complexité (le mouvement de premier- et de deuxième-ordre). Les résultats démontrent que les personnes autistes sont sélectivement moins sensibles aux stimuli de mouvement complexes de deuxième-ordre, suggérant un fonctionnement moins efficace des mécanismes neuro-intégrateurs opérant à un niveau visuo-perceptif. En outre, nous suggèrons que ce résultat n'est pas dû a un dysfonctionnement de la voie visuelle dorsale parce que les stimulus de premier-ordre utilisés dans l'étude sont également traités par les mécanismes de mouvement spécialisés qui opèrent dans la voie dorsale. Basé sur ces résultats, nous concluons que les personnes autistes n'intègrent pas l'information visuo-perceptuelle de façon efficace, résultant possiblement en des représentations internes incongrues de leur monde externe, ce qui pourrait constituer une origine possible de leur comportements autistiques. Nous discutons de ces résultats en termes de mécanismes neurobiologiques pouvant possiblement être à l'origine de la perception holistique compromise dans l'autisme ainsi que d'autres conditions neurobiologiques partageant une symptomatologie perceptive et cognitive semblable, tel la schizophrénie et le vieillissement non-pathologique. En conclusion, nous présentons un paradigme psychophysique qui a pour but de dissocier l'explication voie-spécifique (déficit de la voie dorsale) de l'explication complexité-spécifique (déficit neuro-intégrateur) du fonctionnement visuo-perceptuel dans l'autisme ainsi que dans d'autres conditions. Des études utilisant ce paradigme pour évaluer le traitement visuo-perceptif dans les populations autistes et du syndrome du X fragile sont également présentés.

ABSTRACT

Keywords : autism, motion perception, visual information processing, first-order, second-order, stimulus complexity, neuro-integrative mechanisms, weak central coherence, dorsal visual stream, ventral visual stream

Autism is a pervasive developmental disorder of neurobiological origin whose diagnosis is based abnormal behavioural symptomology. Although such behaviour it is most often characterized qualitatively in terms of a triad of impairments regarding social interaction, communication and imagination, non-social impairments are also thought to be universally prevalent in autism and used as diagnostic features. An important proportion of such impairments implicates the visuo-perceptual domain, characterized by an atypical bias towards local information processing. As suggested by the *weak central coherence* theory, persons with autism seem to integrate visual information less efficiently than non-autistic persons. The main purpose of this thesis was to evaluate this proposition by assessing the integrity of neural mechanisms mediating integrative processing at a visuo-perceptual level in autism by measuring their sensitivity to motion stimuli requiring neural processing of varying complexity (first- and second-order motion). Results showed that persons with autism are less sensitive to the complex second-order motion stimuli only, suggesting less efficient functioning of neuro-integrative mechanisms operating at a perpetual level in autism. Furthermore, we argue that this finding is not the result of deficient dorsal visual stream functioning since the first-order stimuli used in the study are also processed by specialized motion mechanisms operating within the dorsal stream. Based on these findings, we conclude that persons with autism do not integrate visuo-perceptual information efficiently, possibly resulting in incongruous internal representations of their external world that may result in characteristic autistic behaviour. We discuss these findings in terms of neurobiological mechanisms that may possibly underlie impaired wholistic perception in autism and other neurobiological conditions sharing similar perceptual and cognitive symptomology, such as non-pathological aging and schizophrenia. Finally, we present an experimental psychophysical paradigm that can be used to dissociate a *pathway specific* (dorsal pathway deficit) from a *complexity specific* (neuro-integrative deficit) account of visuo-perceptual functioning in autism and other conditions. Studies using this paradigm to assess visuo-perceptual processing in both autistic and Fragile-X populations are also presented.

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LIST OF ABBREVIATIONS

2AFC	: two alternative forced choice
ADI	: Autism Diagnostic Interview
ADOS-G	: Autistic Diagnostic Observation Schedule General
ANOVA	: analysis of variance
CMS	: Classic Motion System
cd/m^2	: candela per meter squared
cm	: centimeter
cpd	: cycles per degree
DSM-IV	: Diagnostic and Statistical Manual of Mental Disorders, Fourth Edition
EFT	: Embedded Figures Test
ERD	: Elaborated Reichardt Detector
FXS	: Fragile-X syndrome
Hz	: Hertz or cycles per second
MT	: medial temporal area
msec.	: millisecond
MST	: medial superior temporal area
MSTd	: dorsal region of the medial superior temporal area
LGN	: lateral geniculate nucleus
LTP	: long-term potentiation
NMDA	: N-methyl-D-aspartate
RF	: receptive field
RMS	: Relative Motion System
SAND	: Simultaneous Access Network Deficit hypothesis
STS	: superior temporal sulcus
ToM	: Theory of Mind
V1	: primary visual cortex
V2	: visual area two
V3	: visual area three
V4	: visual area four
WCC	: weak central coherence

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" Maestro, I tuoi ragionamenti mi son si' certi e prendon si' la mia fede, che li altri mi sarien corboni spenti. " - Dante Alighieri, Divina Commedia - Canto XX

I would like to thank my parents, Ida and Antonio, and my sister Lisa for making my life a special one. Since my earliest memories to the present, you have encouraged and supported me blindly, regardless of my life or academic situation. Thank you Linda, my friend, my wife. Because of you, I have been able to accomplish certain things previously unattainable. More importantly, because of you, I am content, for I feel that my life is complete. Ti ameró per sempre, amore mio.

Thank you to my friends for scolding me when necessary and for being there in times of need. Sometimes we must cry, but other times we can choose whether to laugh or to cry. When all is said and done, there's nothing like a good laugh ... Thanks to my lab mates and friends with whom I spent an important part of the last few years. Special thanks to Clo, Dave, Odile, Vasile, Rémi " Trois Steak " Allard, Michel O., Michel P. as well as Hugo and Dan " Régis " Mimeault.

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I dedicate this doctoral thesis to my grandfather, Domenicantonio Colace (1922-2002). After arriving home from years of military service, this dedicated husband and father decided to return to public school (*Scuola Popolare*) to complete his elementary school education. At thirty-two years of age and despite being ridiculed, he persevered and achieved a goal that circumstance disallowed him as a child. My diploma will hang proudly next to his, for he is a true scholar.

Chapter 1

Thesis overview

From the first phenomenological demonstrations of specialized motion mechanisms (e.g., Waterfall Illusion) to the most recent investigations using increasingly powerful medical imaging techniques, interest in understanding the neural mechanisms underlying motion perception has been constant within the realm of experimental psychology. Consequently, there has probably been thousands of manuscripts and studies using a variety of experimental approaches published on the topic of visual motion perception. This overwhelmingly large body of research has allowed for vision scientists to propose relatively well-defined brain mechanisms underlying visual motion analysis. Such mechanisms have been shown to be exemplary of the specialized and hierarchical information processing, defined by computational and neural network models based on existing physiological properties of mechanisms analyzing increasingly complex types of visual motion information. Computational and neural network models derived from motion perception research have contributed to the better understanding of perceptual processing and to theories linking psychological, phenomenological and neurobehavioural findings in applied research domains. Because we know much about motion perception and its underlying mechanisms, it has been the model of choice to investigate visual information processing and its effect on behaviour in many clinical populations, including autism. In essence, this is the general purpose of the present thesis.

This thesis is presented as a series of chapters. Chapter 2 describes first- and second-order motion perception (Cavanagh & Mather, 1989) and how the mechanisms underlying their analysis are modeled. It also demonstrates how research, used to dichotomize the first- and second-order motion classes, has been for the most part based on unidirectional motion stimuli. Consequently, relatively little is known about complex second-order motion processing and how it is analyzed by the visual system. The article entitled " How is second-order motion processed ? ", presented in Chapter 3, is a basic psychophysical investigation that attempts to elucidate how complex configurations (e.g., radial and rotational) of second-order motion are processed. It represents a first attempt at explaining how second-order motion is analyzed by mechanisms operating in extrastriate motion areas (the medial temporal (MT) & medial superior temporal (MST) areas). Recapitulated in a proposed model, results demonstrate that complex second-order motion is processed by the same specialized " hard-wired " mechanisms responsible for complex first-order motion perception, but not before the pre-processing of local second-order motion signals occurs. As is described in Chapter 4, the motion model has become the model of choice to investigate the integrity of visuo-perceptual processing in autism. Specifically, current neuro-cognitive theories suggest that the integrative functioning of neural mechanisms mediating visuo-pereptual processing in autism is inefficient, termed weak central coherence (Happé, 1999). The purpose of the second study, entitled " Motion perception in autism : a ' complex ' issue." (Chapter 5), was to evaluate the ability of autistic individuals to integrate visuo-pereptual information by measuring their sensitivity to the simple and complex types of first-order and second-order motion patterns used in the first study. Results demonstrate that persons with autism are selectively less sensitive to all types of second-order motion. However, no differences were found for first-order motion sensitivity, suggesting persons with autism do not have a 'motion perception' impairment *per se*, as previously suggested (Gepner et al., 1995). However, they do seem to integrate complex perceptual information (second-order motion stimuli) less efficiently than non-autistic participants. These results are consistent with other demonstrations of decreased motion sensitivity to complex motion in autism (e.g., Spencer et al., 2000; Milne et al., 2002; Blake et al., 2003). Similar difficulties regarding neuro-integrative functioning using the motion model have been described in other conditions, including schizophrenia (Chen et al., 2003). Referred to as deficient cognitive coordination, Philips and Silverstein (2003) suggest that NMDA-receptor dysfunction may be the fundamental neurobiological mechanism underlying and associating impaired holistic perception and cognitive coordination in schizophrenia. In Chapter 6, we present two invited commentaries to a Philips and Silverstein (2003) target article on schizophrenia discussing how their hypothesis shares certain aspects of the weak central coherence account of autism in that persons with either condition do not integrate visuo-perceptual information efficiently, possibly resulting in incongruous internal representations of their external world that may result in abnormal behaviour in either condition.

Given the fact that complex motion perception is 1- the result of integrative visuo-perceptual processes and 2- that it is mediated by motion sensitive extra-striate mechanisms operating within the dorsal visual pathway, decreased sensitivity to complex motion (e.g., second-order motion, global motion or biological motion) can be interpreted as the result of either a *complexity specific* or a *pathway specific* account of visuo-perceptual processing in autism. Previous authors who have demonstrated reduced sensitivity to complex motion in autism have interpreted their results as evidence for a dorsal stream deficiency, or a *pathway specific* account of autistic visuo-perceptual processing (e.g., Spencer et al., 2000; Milne et al., 2002; Blake et al., 2003). In the general discussion (Chapter 7), we challenge this interpretation based on both methodological and interpretive grounds and present an alternative experimental paradigm that we believe is better able to dissociate a *complexity specific* form a *pathway specific* account of perceptual abilities in autism. What differentiates this experimental paradigm from the others is that is assesses dorsal and ventral functioning processing along both pathways at comparable levels of complexity. Using this paradigm, we present data from both autistic (Chapter 9) and Fragile-X populations (Chapter 10) to demonstrate how this method is sensitive to both inefficient neuro-integrative analysis as well as pathway specific dysfunction.

Chapter 2

First- and second-order motion perception

2.1. Computational models of motion detection

The earliest algorithmic model (Marr, 1982) concerning motion detection was proposed by Reichardt (1961), who initially introduced the concept of " motion detector " as the basic motion-detecting unit to explain the optomotor behaviour of insects. This influential model, known as the Reichardt detector model, has been adopted as a working hypothesis for motion detection in the human visual system (e.g., Mather, 1990). In its simplest form, a Reichardt detector computes a direction-selective motion response by comparing temporally offset neural signals from two adjacent receptive field (RF) locations on the retina. Inputs from the two RFs converge at an interaction site, where the signals are multiplied and integrated. Directional selectivity is possible because of a spatial asymmetry, attributing different temporal characteristics to each input, introduced by delaying one of the signals before comparing them at the site of multiplication. As seen in Figure 1a, the signal coming from the left RF is delayed (Δt) relative to that coming from the center RF. Therefore, for rightward motion, the two signals will arrive at the site of multiplication at the same time (the earlier signal from the left is compensated with the delay) that results in a positive multiplication that in this case, signals rightward motion.

Based on Reichardt's motion detector, van Santen and Sperling (1984; 1985) proposed the Elaborated Reichardt Detector (ERD), which they argue is a more appropriate model for human vision, emphasizing the importance of both spatial and temporal filtering performed for each of the inputs, or receptors, before multiplication. The spatiotemporal filtering is important because it eliminates spatial aliasing that would otherwise result in incorrect direction prediction. These authors describe a drifting

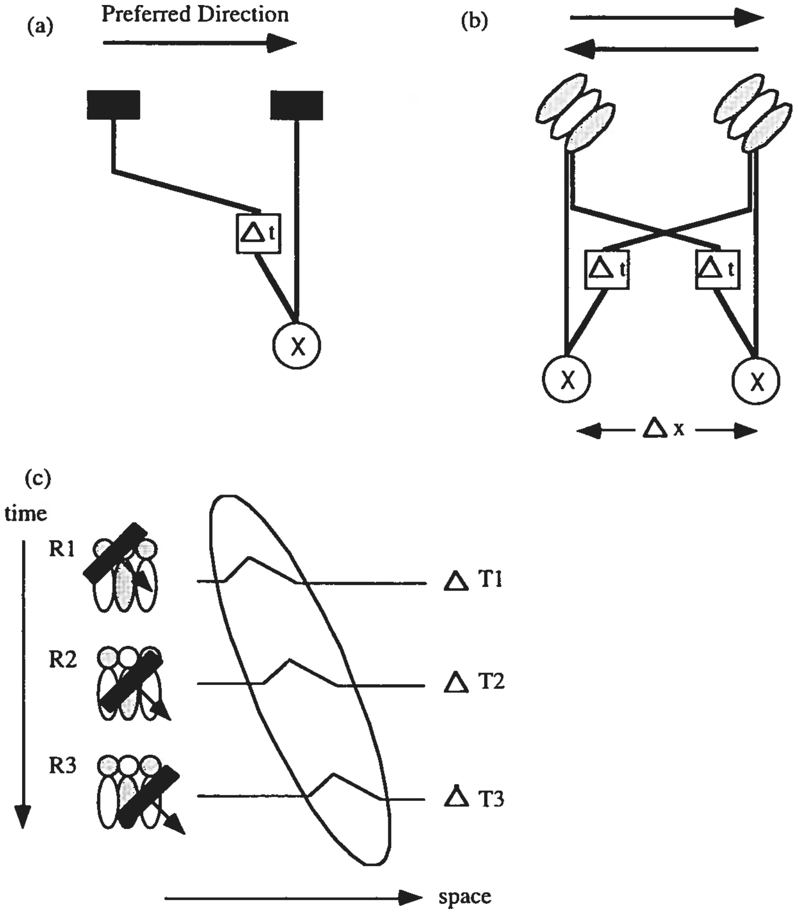

Figure 1. Schematic representations of (a) the basic Reichardt motion detector, (b) the Elaborated Reichardt motion detector (ERD) and (c) the directionally selective responses of the Motion-energy model viewed in terms of a tilted receptive-field profile.

sinusoidal grating as being a temporal luminance pattern (e.g., sine-wave) varying as a function of spatial location. Motion detection is carried out by comparing the delayed temporal luminance pattern of one output to that of the other non-delayed luminance pattern at the other spatial location. If the two signal outputs or intensities correlate well at the site of multiplication, the direction of the grating is detected. Essentially, the basic ERD model compares and integrates the responses of two spatial-frequency selective mechanisms displaced in time and space (see Figure 1b).

Motion-Energy models (Adelson & Bergen, 1985) are another important class of motion detection models. These models differ from the ERD model in that detection of motion direction is determined as orientation in space-time. The spatial asymmetry of motion-energy models is distributed across different locations in one receptive field instead of across two RFs. Consider, for example, a luminance defined contour moving across a receptive field of a motion-energy detector (see Figure 1c). If the contour is moving in the preferred direction, the region of the RF initially reached by the edge (R1) will respond first (Δt1), followed by the response elicited by the next region (R2) (e.g., Δt1 > Δt2 > Δt3, etc.). Therefore, different spatial locations within the receptive field will elicit different time courses of responding. A space-time plot of the time course of responses of different positions of the RF reveals motion energy (the output of motion energy filters) at a certain spatiotemporal orientation that can be detected as motion by motion selective cortical cells. The Elaborated Reichardt Detector and Motion-Energy models are just two of several computational models (e.g., Watson & Ahumuda, 1985) that provide systems theoretically capable of detecting motion directions. Most models share one important aspect; a low-level filtering stage where the analysis of **luminance-defined** components of the motion signals, defined by local variations in retinal image intensity, occurs.

2.2. What are first- and second-order motion?

Usually, the contour of an object is defined by a difference in luminance with respect to its background (e.g., luminance step). When the object moves, so does its contour, which is cast across the retina of the observer. According the Cavanagh and Mather (1989), this is an example of a first-order motion defined by the coherent spatiotemporal displacements of the luminance difference on the retinal image. Second-order motion, however, is defined by displacements of stimulus characteristics other than luminance (e.g., disparity contrast, texture, etc). For example, if an object and its background have the same mean luminance but differ in the distribution of luminance over their area, movement of the stimulus will not result in a coherent displacement of luminance over time. Chubb and Sperling (1988) defined such stimuli as being " drift-balanced " because the motion energy of second-order stimuli is equal in opposite directions. They also refer to this class of stimuli as " non-Fourier " because the Fourier components of these stimuli cannot be used to predict the perceived direction of motion using low-level, energy-based motion detectors.

The study of second-order motion processing is of theoretical importance because energy-based motion-detection models, such as the ERD or Motion-energy models, are based on detection mechanisms that respond to net directional motion energy. Theoretically, these detectors are not able to extract the directional information of second-order or " drift-balanced " stimuli. Regardless, second-order motion is readily perceived.

2.3. Models of second-order motion processing

As mentioned earlier, most current models of motion detection include a low-level spatiotemporal filtering stage where the analysis of Fourier or luminance components of the motion signal takes place. These models, however, are theoretically incapable of processing second-order motion because stimuli defining second-order motion do not contain net directional motion energy, e.g., " non-Fourier motion " (Chubb & Sperling, 1988). For this reason, standard motion analysis, which determines the direction of motion by performing a spatiotemporal correlation of intensity in the visual field, is unable to process second-order motion. Where and how then, is second-order motion detected?

As outlined by Smith (1994), the two possible strategies our visual mechanisms might adopt to detect second-order motion are defined by correspondence- and energy-based models. Correspondence-based models are based on the matching of identified features of an image over time (Ullman, 1979; Georgeson & Shackleton, 1989). Although there is no general agreement as to what specifies a feature, it is probable that second-order stimuli contain identifiable, low-level features (e.g., regions of high contrast) that can be matched (Anstis, 1980; Braddick, 1980) or attentively tracked (Cavanagh, 1992). In its simplest form, feature tracking may simply represent the awareness of a positional change in attentional focus. Feature-tracking may also be detect motion direction of most first-order motion patterns. Ullman's (1979) *minimal mapping theory* provides algorithms for computing probable correspondences between the " matched " or " tracked " features that are detected at different times. These strategies are considered to be mediated by higher-level mechanisms that do not use low-level, energy-based operations to detect motion.

Correspondence-based models provide theoretically capable mechanisms of second-order motion detection. However, the substantial psychophysical evidence involving low-level mechanisms in motion detection of both types favours models that use, at least at some point, motion energy information contained in the image (see Chubb et al., 2001, for review). Energy-based models explain second-order motion detection in terms of low-level, passive mechanisms. These models fall into two broad classes. The first class of models suggests that first- and second-order motion are detected by a common low-level mechanism, initially introduced by the spatiotemporal gradient model of Johnston et al. (1992) and that of Grzywacz (1992). The spatial luminance variations in a moving pattern results in temporal variations at different points in space when it is in motion. If the assumption is made that all temporal variations in a space-time image is caused by movement, it becomes possible to use the relation between spatial and temporal variations at any position in time to deduce the direction of the motion. Elaborated gradient models have been shown to be able to detect many different types of second-order motion stimuli by spatiotemporal filtering followed by rectification of motion signals and motion energy detection (Benton et al., 2001).

The second class of models suggests that first- and second-order motion processing is carried out at least initially, by separate low-level mechanisms but which operate in parallel using qualitatively similar principles of motion detection. Chubb and Sperling (1988) were the first to demonstrate that theoretically, non-linear processing (e.g., such as rectification or response squaring) of the luminance profile of a second-order stimulus results in the production of luminance components in the image that can be processed by standard motion analysis. Essentially, the visual input is subjected to some gross nonlinearity that basically translates texture motion into luminance motion so that it becomes accessible to standard motion analysis. This type of analysis characterizes filter-rectify-filter models that describe neural mechanisms that detect second-order motion (see Baker, 1999).

Using this second conceptualization, Wilson et al. (1992) proposed a model of two-dimensional motion processing consisting of two parallel, low-level motion detection pathways, the outputs of which are integrated at a higher level. In one pathway, first-order or " Fourier " motion energy is detected by a spatiotemporal filtering stage (presumably RFs of V1 neurons) that is then followed by conventional, linear motion energy computation (or standard motion analysis). The second is a " non-Fourier " pathway that includes a non-linear transformation (e.g., rectification) of the luminance profile of " non-Fourier" information. The rectified signals can then be detected conventionally by a second stage of filtering at a different orientation and lower spatial frequency. Wilson et al. (1992) suggest that the second filtering stage could be located at V2, which contains cells responsive to non-luminance defined motion (e.g., illusory contours (von der Heydt & Peterhans, 1984)). The " Fourier " and " non-Fourier " signals are then integrated at a final processing stage, presumably at the medial temporal (MT) area (see Figure 2).

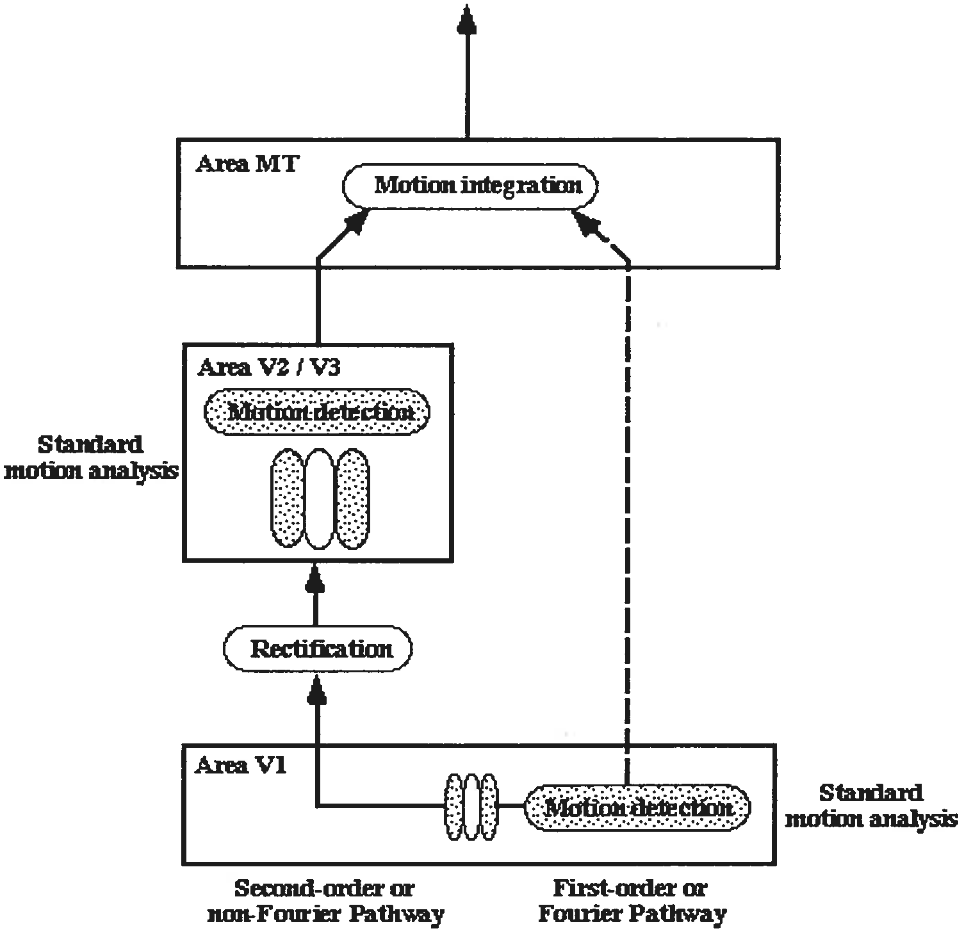

Figure 2. Schematic representation of Wilson et al. (1992) hypothetical model.

Wilson et al.'s (1992) model for two-dimensional motion perception is arguably the most influential second-order motion processing model to date, due in part to its incorporation of both psychophysical and physiological considerations regarding the processing of both motion classes. In essence, this model posits that first- and second-order motion is initially and passively processed by independent, low-level mechanisms before ultimately being integrated at a higher level. As described by Chubb et al. (2001) in their short review, the results from most investigations of first- and second-order motion detection have demonstrated the existence of two early and passive motion-sensing pathways: a first-order system for analyzing luminance-defined motion and a second-order motion system that applied a rectifying transformation to the visual input before extracting motion from it. Using a selective adaptation technique, Nishida et al.,

(1997) demonstrated that initial filtering within both first- and second-order pathways is characterized by multiple-scale channels regarding both direction- and spatial-frequency selectivity. Their results support the suggestion that first- and second-order motion are initially processed by separate pathways and provide sustain that such processing is multi-scale in nature. Congruent evidence for such analysis has been provided by psychophysical (e.g., Harris & Smith, 1992; Ledgeway & Smith, 1994; Nishida et al., 1994; Nishida & Sato, 1995; see Chubb et al. (2001) and Clifford & Vaina (1999) for reviews), neurological (e.g., Vaina LM & Cowey, 1996; Vaina et al., 1998; Vaina & Soloviev, 2004), electrophysiological (e.g., Baker, 1999; Mareschal & Baker, 1999; Baker & Mareschal, 2001) and imaging studies (e.g., Smith et al., 1998; Wenderoth et al., 1999; Dumoulin et al., 2003; see Seiffert et al., 2003 for alternative view). Other more complete models based on that of Wilson et al. (1992) have since been proposed (Nishida et al., 1997; Baker, 1999; Clifford & Vaina, 1999; Mareschal & Baker, 1999; Lu & Sperling, 2001) and shared the notion that first- and second-order motion are initially processing separately.

Inherent in models describing second-order motion perception as including additional processing (i.e. rectification and additional filtering) is the assumption second-order motion processing requires more time to be analyzed. For example, Wilson & Yo (1992) suggest that the perceived direction of type II plaid patterns changes with duration because second-order motion analysis takes longer than that of first-order. Therefore, when their stimulus is presented briefly, only first-order mechanisms are able to provide direction information but as exposure duration increases, motion signals from the ‘ slower ’ second-order mechanisms progressively become available and weight on the computation of motion direction. Derrington et al. (1993) demonstrated that second-order mechanisms that process the motion of beat patterns are slower than those responsible for first-order analysis (luminance-defined sinusoidal gratings). Furthermore, they demonstrated that for exposure duration less than 100 msec., only first-order motion analysis was possible. Consistent with filter-rectify-filter models, they suggest that their results of ‘ slower ’ second-order processing may be due to the characteristic low-pass filtering defining second-stage second-order motion analysis, needed to allow second-order mechanisms to correlate over long delays without aliasing.

An alternative explanation to the low-pass temporal filtering (i.e., Derrington et al., 1993) and the processing-delay (i.e, Wilson et al., 1992) hypotheses regarding is forwarded by Ledgeway & Hess (2002). Their hypothesis, the direction-selectivity hypothesis, is generally based on the suggestion that second-order motion detectors are less selective for motion direction than first-order motion detectors. They demonstrated that although drift-direction was preferentially affected for second-order motion with decreasing exposure duration, second-order orientation discrimination was not. They suggest that second-order motion detectors are more negatively affected by decreased stimulus duration in that directional ambiguity caused by brief exposure has a greater impact on second-order, compared to first-order, motion analysis. Ledgeway & Hess (2002) suggest that their findings cannot be explained by either low-pass temporal filtering or the processing-delay hypotheses.

Latency-dependent results have also been demonstrated using complex second-order motion patterns. For example, Allen & Derrington (2000) demonstrated that observers' ability to discriminate between centered (i.e., coherently expanding or contracting) and distorted (i.e., directionally incoherent local patterns) patterns was affected by the attribute defining their motion. Specifically, the detection of the complex second-order optic flow patterns took a greater amount of time (i.e., 2 sec compared to 100 msec) when compared to first-order patterns. Based on these results, Allen and Derrington (2000) suggested that complex second-order motion analysis is not mediated by specialized optic flow, but rather, by the sequential analysis of local second-order motion signals. Ledgeway & Hess (2002) propose that this result may be at least in part the result of the differential direction-selective properties of first and second-order local motion detectors. The study by Bertone & Faubert (2003), presented in Chapter 3 of this thesis, will attempt to elucidate if differences exist between complex first- and second-order analysis at higher-levels of processing responsible for complex motion perception.

2.4. The first- and second-order motion dichotomy: a " unidirectional " one

The development of the first- and second-order motion dichotomy has been based for the most part on studies using simple linear or translational motion stimuli. Such motion is computed locally early on in the visual motion hierarchy and is related to the direction of object motion. However, our adaptive behaviour is contingent for the most part on our ability to perceive *complex* types of motion. One of the most fundamental sources of visual motion is that created from one's own motion, also referred to as ego-motion. The locomotion of an observer through the environment results in a global streaming of the visual field on the retina known as optic flow. For example, when an observer moves through the environment, the retinal image consists of whole visual field movements of expanding and/or rotating directions. The analysis of these wide-field movements on the retina must therefore be undertaken by mechanisms which integrate and converge local motion information in order to process more complex patterns of motion. For example, if one moves forward in a straight line, the visual flow will spread out from the center of heading represented by the black dot (see Figure 3a), a type of optic flow that is called *expansion*. Self-motion in the opposite direction will result in the contraction of the optic flow. Tilting one's head sideways will result in the *rotation* of the visual flow field (Figure 3b). Although expansion and rotation are globally coherent types of motion patterns, the direction of the local motion signals that constitute these types of complex motion are different and sometimes in opposition with each other.

Although not much is known about how the visual system combines local motion information, several authors have postulated that these more complex motion types activate higher-level motion mechanisms found in extra-striate cortical areas by receiving local input from unidirectional receptive fields belonging to standard motion analysis mechanisms (e.g., Snowden & Milne, 1996; Bex, Metha & Makous, 1998; Burr et al., 1998). Electrophysiological investigations have shown neurons with characteristic large receptive fields in the dorsal region of the medial superior temporal area (MSTd) of the monkey that are selectively activated by radial and rotational motion patterns (e.g., Tanaka, Fukada & Saito, 1989; Graziano et al., 1994).

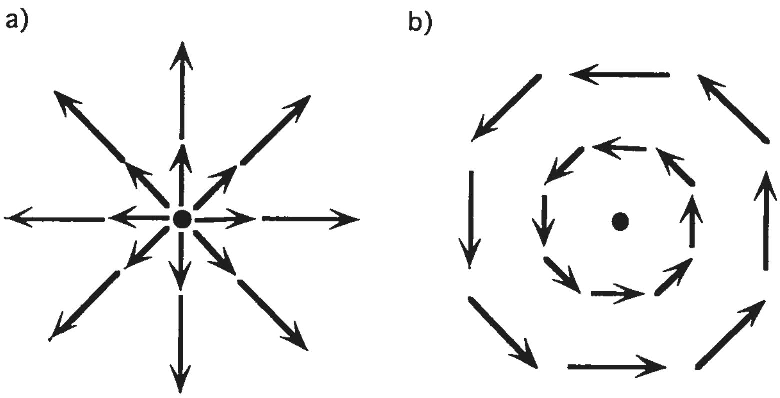

Figure 3. Examples of different types of complex optic flow patterns. The arrows represent the direction and speed of local motion at each point in space for a) expansion and b) rotation.

Psychophysical evidence for such a hierarchy of motion detecting mechanisms is considerable. For example, Freeman & Harris (1992) suggest that complex motion patterns are processed by at least two stages of motion analysis. The first stage consists of conventional motion analysis which is carried out by a process they term the Classic Motion System (CMS). This process, which is similar to standard motion analysis, is responsible for processing the speed and direction of local motion elements in the pattern. The second system, termed the Relative Motion System (RMS), combines the CMS outputs to produce a mechanism which is selectively sensitive to the relative relationship of local motion elements. Demonstrating that the direction-identification threshold for simple translation motion was higher than that of either radial or rotational motion, Freeman & Harris (1992) conclude that the detection of the complex motion patterns cannot be carried out by the CMS mechanisms only. They conclude that specific types of complex motion, such as expansion and rotational motion, necessarily evoke specialized higher-level mechanisms to be perceived. Theoretically similar hypotheses of functional hierarchy of motion processing have been proposed by other researchers based on findings using different psychophysical methodologies (e.g., Regan & Beverly, 1978; Morrone, Burr & Vaina, 1995). Electrohysiological evidence of a motion pathway defined by direct connections between local, low-level mechanisms in the primary visual cortex (V1) and the medial temporal cortex (MT) (Ungerleiger & Mishkin, 1979), which in turn projects to MST (Maunsell & van Essen, 1983) also supports the functional hierarchy hypothesis. However, both psychophysical and electrophysiological studies providing evidence supporting distinct functional mechanisms responsible for processing complex patterns have used patterns whose motion was defined by the displacement of luminance-defined spatial structures, or first-order motion.

As mentioned earlier, our ability to behave adaptively to our dynamic surroundings is contingent on efficiently processing *complex* dynamic information. For the most part, such information, whether dynamic or static, is luminance-defined or first-order. Consequently, specialized neural mechanisms have evolved that efficiently analyze particular configurations of complex luminance-defined motion patterns (e.g., such as the ones operating in extrastriate motion-sensitive areas dMST and MT). However, how ecologically important is second-order motion perception on visually-related behaviours such as heading and self-navigation? Do specialized mechanisms exist for the processing of complex second-order information and do they differ from those mediating first-order complex motion perception? Questions such as these have for the most part been ignored; only few studies have recently investigated second-order motion processing using complex or multi-directional stimuli (e.g., Gurnsey et al., 1998; Dumoulin et al., 2001; Hanada & Ejima, 2000; Badcock & Khuu, 2001). This is reflected by the fact that most investigations on second-order motion perception have focused on processing before the first- and second-order signals are integrated at area MT (refer to Wilson et al., (1992) model). Consequently, no model exists explaining how complex configurations of second-order motion information are processed. In order to assess whether or not second-order motion is important or even used during visually-related behaviour, a systematic assessment of complex second-order motion is necessary. In order to do so, one must demonstrate how the second-order motion hierarchy differs, if at all, from that mediating first-order motion. The question that remains is the following: how is complex second-order motion processed?

Chapter 3
Article 1

This chapter is an exact reproduction of the following published article:

Bertone A & Faubert J (2003).
How is complex second-order motion processed?
***Vision Research*, *43*, 2591-2601.**

Visual Psycholphysics and Perception Laboratory
Ecole d'optométrie, Université de Montréal
Montréal, Québec, Canada

3.1. Chapter overview

The purpose of the present experiment was to investigate whether a second-order motion hierarchy exists and whether it is functionally similar to that mediating complex first-order motion. The present study represents a systematically investigation of complex second-order motion perception by comparing direction-identification thresholds for simple (translation) and complex (radial and rotational) motion patterns form both first- and second-order motion classes. All patterns were presented at different exposure durations in order to further dissociate differences in functional hierarchies between the two motion classes. The findings were used to develop a novel motion model of first- and second-order motion processing that dissociates the two motion classes beyond area MT.

3.2. Abstract

Converging psychophysical and electrophysiological evidence suggests that first-order (luminance-defined) complex motion types i.e., radial and rotational motion, are processed by specialized extrastriate motion mechanisms. We ask whether radial and rotational second-order (texture-defined) motion patterns are processed in a similar manner. The motion sensitivity to translating, radiating and rotating motion patterns of both first-order (luminance-modulated noise) and second-order (contrast-modulated noise) were measured for patterns presented at four different exposure durations (106, 240, 500 and 750 milliseconds). No significant difference in motion sensitivity was found across motion type for the first-order motion class across exposure duration (i.e., from 240 to 750 milliseconds) whereas direction-identification thresholds for radiating and rotating second-order motion were significantly greater than that of the second-order translational stimuli. Furthermore, thresholds to all second-order motion stimuli increased at a significantly faster rate with decreasing exposure duration compared to those of first-order motion. Interestingly, simple and complex second-order thresholds increased at similar rates. Taken together, the results suggest that complex second-order motion is not analyzed in a sequential manner. Rather, it seems that the same 'hard-wired' mechanisms responsible for complex first-order motion processing also mediate complex second-order motion, but not before the pre-processing (i.e., rectification) of local second-order motion signals.

3.3. Introduction

Psychophysical investigations of human motion perception have attempted to define and distinguish between motion systems differing in functional architecture and complexity. The simplest of these systems, the 'first-order' system, extracts motion signals through standard motion analysis (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985) by operating on local luminance variations in the retinal image. The 'second-order' motion system (Chubb & Sperling, 1988; Cavanagh &

Mather, 1989) is believed to extract motion signals from non-luminance defined visual information (i.e., texture, contrast, disparity, etc). In the latter case, additional nonlinear processing, such as rectification or response squaring, is required before standard motion analysis results in a motion percept. One class of second-order motion models suggest that first- and second-order motion are initially processed in parallel by separate passive mechanisms using similar motion detection principles (i.e., Chubb and Sperling, 1988; Wilson et al., 1992; Nishida et al., 1997). Experimental support for such second-order motion detection has been provided for the most part by psychophysical studies which have demonstrated differences between first- and second-order motion detection over a large range of stimulus parameters and experimental paradigms (see Clifford & Vaina (1999); Chubb et al. (2001), for review).

The dichotomy between the two motion classes has been based for the most part on findings comparing 'simple' (i.e., translational or unidirectional), first- and second-order motion. Although potential mechanisms underlying the processing of simple second-order motion have been developed and elucidated, relatively little is known about how 'complex' second-order motion, such as radial and rotational motion types, is processed by the visual system. To better understand the ecological function and importance of second-order motion information on behaviours such as heading and navigation, we measured the sensitivity to such complex types of motion configurations since they approximate to a greater extent the visual array produced by self-motion.

3.3.1. Specialized detection for complex first-order motion

Several authors have postulated that complex first-order motion is processed by specialized motion mechanisms operating in extrastriate brain areas (i.e., Freeman & Harris, 1992; Burr, Morrone & Vaina, 1998). These mechanisms are believed to integrate local motion signals from directionally selective neurons belonging to the standard motion analysis mechanism, operating locally at the primary visual cortex (V1). Specialized motion mechanisms differ functionally from those underlying standard motion analysis because they specifically and efficiently detect complex motion types, such as radial and rotational motion. Psychophysical evidence for such a specialized or ‘multi-staged’ motion detection mechanism is considerable (Regan & Beverly, 1978; Regan & Beverley, 1985; Freeman & Harris, 1992; Morrone, Burr & Vaina, 1995; Gurney and Wright, 1996; Snowden & Milne, 1996; Burr, Morrone & Vaina, 1998; Bex et al., 1998). Physiological evidence has shown that motion information is analyzed at various cortical levels within a hierarchical motion pathway which includes the primary visual cortex (V1), and extrastriate motion areas MT (medial temporal) and MST (medial superior temporal). Dorsal MST (dMST) neurons, which have characteristically large receptive fields and receive input significant from MT, are selectively activated by radial and rotational motion patterns (i.e., Tanaka & Saito, 1989; Duffy & Wurtz, 1991; Graziano, Andersen & Snowden, 1994). These neurons have been shown to be involved in the processing of wide-field movements caused by ecologically important behaviors of heading and locomotion.

3.3.2. Complex second-order motion perception and heading

A relatively small but growing body of research has addressed the general question regarding 'complex' second-order motion detection and its relation to heading judgements. Although a dynamic visual array produced by self-motion may contain both first- and second-order motion information, the extent to which second-order information contributes to the computation of heading behaviors remains unclear. Gurnsey et al. (1998) demonstrated that second-order motion signals alone are sufficient to produce the illusion of self-motion, albeit to a significantly lesser extent than first-order information. Since this illusory percept is believed to be dependent on the analysis of optic flow information, the authors suggest that mechanisms mediating optic flow perception (i.e., dorsal MST) may use both first- and second-order motion signals to resolve heading direction after being integrated in area MT. Additional support for second-order involvement in optic flow processing was put forth by for Dumoulin et al. (2001) who found a centrifugal bias for second-order motion detection (i.e., selective bias to expanding Gabor micropatterns) in the peripheral visual field. Finally, Hanada and Ejima (2000) demonstrated that heading judgements, as measured by the preciseness of the perceived heading with simulated pursuit, differed significantly for first- and second-order defined optic flow arrays. A possible interpretation put forth by these authors was the less accurate speed estimates (i.e., velocity and directional tuning) for second-order information needed for correct heading recovery. More recently, Badcock and Khuu (2001) used a radial global motion task consisting of first- and second-order signals (Edwards & Badcock, 1993) to show that first- and second-order motion are processed independently after MT (i.e., MST), where the specialized motion mechanisms are believed to operate. Based on these findings, the authors suggested that radial optic flow patterns defined by first- and second-order characteristics are detected by separate mechanisms after MT.

3.3.3. Main goal of the present study

The results derived from the studies mentioned in the previous section provide important information regarding the involvement of first- and second-order motion signals towards optic flow perception and heading behavior. However, the functional nature of the mechanisms mediating the analysis of complex second-order information has of yet not been elaborated. The purpose of the present study is to further explore the characteristics of mechanisms mediating radial and rotational second-order motion perception to better understand *how* such second-order configurations are analyzed by motion mechanisms operating after MT. For example, can specialized or 'multi-staged' motion analysis that underlie complex first-order motion be applied to moving patterns defined purely by second-order characteristics? If not, how is complex second-order motion analyzed? We approached this question by comparing the direction-identification thresholds of simple (i.e., translational) and complex (i.e., radial and rotational) motion types in both first- and second-order motion classes. In order to elaborate possible differences underlying complex motion processing between the two motion classes, we manipulated stimulus exposure duration. This was done since it has been demonstrated that reducing the exposure duration decreases the sensitivity to simple second-order stimuli to a greater extent when compared to first-order stimuli, possibly reflecting additional neural operations required for simple second-order motion perception (Derrington et al., 1993; Smith & Ledgeway, 1998; see Schofield & Georgeson (2000) for alternative view). Using complex optic flow patterns constructed using local first- and second-order motion apertures, Allen and Derrington (2000) demonstrated that observers' ability to discriminate between centered (i.e., coherently expanding or contracting) and distorted (i.e., directionally incoherent local patterns) patterns was affected by their being defined by first- or second-order characteristics. They found that the detection of the complex second-order optic flow patterns took a much greater amount of time (i.e., 2 sec compared to 100 msec) when compared to first-order patterns. Based on these results, Allen and Derrington (2000) suggested that complex second-order motion analysis is not mediated by specialized mechanisms (i.e., 'second-order driven' optic flow detectors) but rather, by the sequential analysis of local second-order motion signals.

In the present experiment, direction-identification thresholds for simple and complex motion patterns were measured in both first- and second-order motion classes. The spatial and temporal characteristics of first- and second-order patterns were identical except for the characteristic defining their movement; luminance-modulation for the first-order stimuli and contrast-modulation for the second-order stimuli. If complex second-order motion analysis is mediated by sequential processing, it is expected that the direction-identification thresholds for complex types of second-order motion (i.e., radial and rotational) will increase at a faster rate compared to simple (i.e., translational) second-order motion as stimulus duration is decreased. However, if some type of specialized analysis is involved, no differential effect of exposure duration would be expected between simple and complex second-order direction-identification thresholds. Since it is well accepted that complex first-order motion is efficiently mediated by 'hard-wired' specialized mechanisms, it is expected that reducing stimulus duration should have no differential effect, or at least less of a differential effect, on simple and complex first-order thresholds.

Our results demonstrated that direction-identification thresholds to complex second-order motion stimuli were significantly increased at all exposure durations compared to that of simple second-order motion. This was not the case for the first-order motion class where the thresholds for all motion types (i.e., simple and complex) were similar, at least for those presented longer than 240 msec. Furthermore, we found that the motion sensitivity to *all* second-order motion types decline at a faster rate relative to those of first-order motion with decreasing stimulus exposure duration, suggesting separate initial analysis of first- and second-order motion processing. However, the rate with which simple and complex second-order thresholds increased with decreasing exposure duration was similar. Finally, at very brief exposure durations (106 msec), correct direction-identification was difficult only for complex second-order motion stimuli. Interpretations of these results as well as a proposed working model for complex second-order motion analysis are presented in the discussion.

3.4. Methods

3.4.1. Observers

Seven psychophysically experienced observers ranging between 23 and 43 years of age participated in all conditions of the study. Five of the observers were naive to its purpose and all had normal or corrected-to-normal vision.

3.4.2. Apparatus and display

Stimulus presentation and data collection were controlled by a Power Macintosh G3 computer and presented on a 16-inch AppleVision 1710 monitor (frame refresh rate of 75 Hz) which was gamma-corrected using a color look-up table. The screen resolution was 832 x 624 pixels. The motion stimuli were generated and animated by the VPixx© graphics program (www.vpixx.com). Color calibration and luminance readings were taken using the Minolta Chromameter. The mean luminance of the display was 32.30 cd/m^2 (u'= .1832, v'= .4608 in CIE (Commission Internationale de l'Eclairage) u' v' color space) where L_{min} and L_{max} were 0.19 & 64.60 cd/m^2, respectively.

3.4.3. Stimuli

Motion stimuli used in this study are shown in Figure 1. They consisted of first- and second-order translating, radiating and rotating patterns, constructed by either adding or multiplying static greyscale noise to a modulating sinewave of different profiles e.g., a vertical sinusoid for translational motion, a radially symmetrical sinusoid for radial motion and an angled sinusoid for rotational motion (Bertone et al., 2003).

INSERT FIGURE 1 APPROXIMATELY HERE

The stimuli were presented within a hard-edged circular region at the center of the display subtending a visual angle of 5 deg in diameter when viewed from a distance of 114 cm. The noise consisted of dots (1 pixel x 1 pixel, measuring approximately 2.235 min arc) whose individual luminances were randomly assigned as a function of sin (x), where (x) ranged from 0 to 2π. The average contrast of the noise was set at half its maximum. For the translating and radiating patterns, the spatial and temporal frequency of the modulation were identical for points proximal to their horizontal radius. All observers were tested with motion patterns with spatial and drift frequencies were 1 cycle per degree (cpd) and 2 cycles per second (Hz), respectively. The angled modulation of the rotating pattern went through eight cycles per its 360 degrees and its angular velocity was $\pi/2$ rad per second. Direction-identification thresholds for all first-order patterns were found by varying the contrast (luminance modulation or luminance modulation depth), defined as the amplitude of the modulating sinewave, which ranged between 0.0 and 0.5:

$$\text{luminance modulation depth} = (L_{max} - L_{min}) / (L_{max} + L_{min})$$

where L_{max} and L_{min} refer to the average highest and lowest local luminances in the pattern. Second-order patterns were produced by multiplying the same modulating sinewaves with grayscale noise. Direction-identification thresholds for the second-order patterns were found by varying the contrast modulation (contrast modulation depth) of the motion patterns, defined as the amplitude of the modulating sinewave, which ranged between 0.0 and 1.0:

$$\text{contrast modulation depth} = (C_{max} - C_{min}) / (C_{max} + C_{min})$$

where C_{max} and C_{min} are the maximum and minimum local contrasts in the pattern.

3.4.4. Procedure

Participants were tested individually in a dimly lit laboratory room and viewed the display binocularly from a distance of 114 cm for all conditions. Head movements were minimized using a head and chin rest. Within a given experimental session, each participant was presented with trials consisting of first- and second-order stimuli for a particular motion type moving in either of two possible and opposing directions (i.e., left vs. right for translational motion session, inward vs. outward for radial motion session, etc.). Each stimuli were presented for either 106, 240, 500 & 750 msec. The method of constant stimuli was used to measure direction-identification thresholds for each experimental motion condition that included 6 levels of luminance modulation and 5 levels of contrast modulation for the first- and second-order motion stimuli, respectively. Stimuli were presented ten times in either direction at each level of modulation (for a total of twenty trials at each level of modulation). Participants were asked to identify the direction of motion by making a two alternative forced choice (2AFC) by pressing one of two buttons on a keypad. Weibull (1951) functions were fitted to the responses for each motion condition on order to derive direction-identification thresholds at a 75% correct level of performance. Each observer completed the three different experimental motion sessions (i.e., translational, radial and rotational).

3.5. Results

Statistical analysis was performed on averaged group data. Figure 2 shows the mean thresholds as a function of stimulus exposure duration and motion type for the first-order (filled symbols) and second-order (open symbols) motion classes.

3.5.1. First-order motion

A two way within subjects ANOVA (motion type by exposure duration) was used to analyze first-order motion sensitivity. As shown in Figure 2, the sensitivity to first-order motion patterns did not differ as a function of motion type (F (2,12) = 2.743, $p >$ .05) at all stimulus exposure durations and the difference between them did not significantly vary as stimulus exposure duration decreased (F (6,36) = 1.926, $p > .05$).

INSERT FIGURE 2 APPROXIMATELY HERE

A significant effect of stimulus exposure duration was found for all motion types (F (3,18) = 317.346, $p < .05$), due primarily to the drop in sensitivity from 250 to 106 msec. However, an analysis of simple effects showed that decreasing the exposure duration from 750 to 250 msec. significantly reduced the sensitivity to the radial motion while that of the translational and rotational stimuli remained constant.

3.5.2. Second-order motion

Since motion direction discrimination at very brief exposure duration was not possible for some observers (4 of 8 for radial motion and 2 of 8 for rotational motion), data from the 106 msec. condition was not included in statistical analysis for the second-order motion class. As represented by the filled symbols in Figure 2, the sensitivity to translational second-order motion was significantly greater compared to that of radial and rotational motion (F (2,12) = 26.869, $p < .05$) when presented for 750, 500 and 250 msec. As stimulus exposure duration decreased from 750 to 250 msec., the sensitivity of all three second-order motion types decreased significantly (F (2,12) = 25.545, $p <$ .05). The rate at which the sensitivity decreased as stimulus exposure duration decreased was equal for the three motion types and reflected by a non-significant exposure duration by motion type interaction (F (4,24) = 0.448, $p > .05$).

INSERT FIGURE 3 APPROXIMATELY HERE

All the participants showed similar patterns or responding across motion condition. As shown in Figure 3, the individual results from five of the seven participants are representative of the grouped data as direction-identification thresholds for radial and rotational second-order motion were consistently greater when compared to translational second-order motion at longer exposure durations (i.e., 750 msec). Since individual thresholds were calculated using responses form one testing session, the stability of the fitted Weibull functions are represented by 95% confidence intervals obtained using a bootstrap program developed by Foster & Bischof (1991). Qualitatively, at very brief exposure durations (i.e., 106 msec), correct direction-identification of complex second-order motion patterns was not possible for all of the observers. However, all observers were able to discriminate the motion direction of second-order translational patterns, as well as all the types of the first-order patterns.

3.5.3. Spatial and temporal characteristics

Additional testing by the author (AB) and a second psychophysically inexperienced observer (LAT) naive to the purpose of the study aimed to generalize the pattern of results across different spatial and temporal stimulus parameters. Direction-identification thresholds were measured only for the longest exposure duration since decreasing exposure did not differentially affect the relative sensitivity of translational, radial and rotational motion types for either the first- or second-order motion classes (see Figure 2). The additional spatial frequency conditions chosen were 0.5, 0.75 and 2.0 cpd with all patterns drifting a temporal frequency of 2 Hz. The angled modulation of these patterns went through 4, 6 & 16 cycles per 360 degrees, respectively. As shown in Figure 4, first-order motion thresholds were similar for each motion type at all the spatial frequencies tested for both observers. In contrast, the second-order thresholds for radial and rotational motion were consistently higher than those for the translational

INSERT FIGURE 4 APPROXIMATELY HERE

motion condition across all spatial frequency conditions. Figure 5 shows direction-identification thresholds across different temporal frequencies for each observer. The spatial frequency for each motion condition was held constant at 1 cpd (i.e., 8 cycles per their 360 degrees for the rotational condition) and thresholds were measured for patterns

INSERT FIGURE 5 APPROXIMATELY HERE

moving at 1, 4 and 8 Hz (i.e., an angular velocity of $\pi/4$, π & 2π rad per second). Again, direction-identification thresholds for complex second-order motion were higher that those of translational motion across all the drift frequencies tested.

Although complex second-order motion thresholds were found to be consistently higher than simple second-order motion at across various spatio-temporal parameters when presented for 750 msec., it cannot be concluded that this relative difference is present for other exposure durations (i.e., at 240 and 500 msec.) since they were not assessed. Therefore, the rate with which this relative difference changes with exposure duration cannot be deduced based on the present results.

3.6. General discussion

3.6.1. Simple versus complex second-order motion direction-identification

Specialized motion mechanisms differ functionally from those underlying standard motion analysis because they specifically and efficiently detect complex configurations of motion information (i.e., Regan & Beverly, 1979; Freeman & Harris, 1992; Morrone et al., 1995; Snowden & Milne, 1996). The results from the first-order motion class in our study are in accordance with such 'hard-wired' specialized mechanisms since direction of complex first-order motion patterns was identified as efficiently as simple first-order motion, reflected by the similar direction-identification thresholds for all first-order motion types across stimulus duration. Further support for specialized processing is indicated by our finding that decreasing exposure duration (i.e., from 750 msec to 240 msec) did not differentially increase the thresholds for simple or complex first-order motion; thresholds were similar for simple and complex first-order motion across stimulus duration.

The main purpose of the present study was to explore the mechanisms mediating complex second-order motion processing. Although working models describing specialized or 'multi-staged' motion detection mechanisms have been developed for luminance-defined or first-order motion perception, hypotheses regarding the functional mechanisms involved in complex second-order motion perception have yet to be advanced. The main result from the present experiments demonstrates that direction-identification thresholds to complex motion are significantly reduced compared to simple motion at different stimulus exposure durations for the second-order motion class only. This finding suggests that when compared to simple motion sensitivity, complex second-order motion configurations are not processed as efficiently as their first-order counterparts. This difference in sensitivity was consistently found under various spatial and temporal stimulus parameters at longer exposure durations (i.e., 750 msec; see Figures 4 and 5), suggesting that the summation process underlying the elevated thresholds for complex second-order direction identification is not related to the spatial nor temporal characteristics of the motion stimuli. Similarly, Burr and Santoro (2001) demonstrated that the coherence sensitivity of random dot patterns moving in radial and rotational configurations (in the absence of spurious noise) was lower than that of translating motion, decreasing linearly as exposure duration increased, suggesting the differential analysis of simple and complex motion patterns.

3.6.2. The effect of stimulus duration

As shown in Figure 2, direction-identification thresholds for all second-order stimuli increased at a significantly faster rate as compared to first-order thresholds with decreasing stimulus duration, particularly from 750 msec to 240 msec. This result may reflect reduced temporal resolution of second-order motion processing, possibly due to additional cortical pre-processing (i.e., rectification) before exact motion direction can be extracted (Derrington et al., 1993; Wilson et al., 1992; Wilson & Kim, 1994; Smith & Ledgeway, 1998). The different rate of threshold increase between the two motion classes also provides further evidence for models suggesting that first- and second-order motion are initially processed in parallel by separate passive mechanisms using similar motion detection principles (Chubb & Sperling, 1988; Wilson et al., 1992; Baker, 1999; Chubb et al., 2001).

Correct identification of direction was possible for simple, translating second-order motion for exposure durations as low as 106 msec for all observers and complex second-order motion direction-identification was possible at 240 msec for most observers (i.e., for patterns drifting at 2Hz and spatial frequency of 1 cpd). Based on these findings, the second-order motion processing mediating direction identification seems to be less affected by temporal constraints (i.e., the 'temporal hypothesis') than previously believed (Schofield & Georgeson, 2000). It therefore seems improbable that direction-identification of complex second-order motion patterns in the present study is the result of a sequential analysis of local motion signals as described by Allen and Derrington (2000). It is important to note that the motion discrimination task used by these authors differed from ours in that higher-order attentional processing, such as visual scanning, may have been implicated during their second-order motion discrimination task and may have possibly contributed to the significant threshold increases (Ashida et al., 2001).

An alternative explanation for the increased rate of second-order threshold with decreasing stimulus duration is based on the 'direction-selectivity hypothesis' (Ledgeway & Hess, 2002). It contends that the mechanisms encoding second-order stimuli are significantly less selective for motion direction than those mediating first-order motion and that the selectivity of these mechanisms may be increasingly compromised with decreased stimulus duration. Based on our results, either one of the 'temporal' or 'direction-selectivity' hypotheses may explain the overall and differential effect of stimulus duration of first- and second-order thresholds.

3.6.3. How is complex second-order motion processed ?

3.6.3.1. Sequential local analysis of complex second-order motion

Present views regarding complex second-order motion processing vary, the most elaborated of which is presented by Allen and Derrington (2000) who suggest that complex second-order motion perception is probably not used by specialized mechanisms mediating optic flow analysis. Instead, they contend that complex second-order motion analysis may implicate the integration of separate and sequential local analyses of second-order information across the visual field, a much more sequential cortical processing with respect to that of translational second-order motion. Additional cortical processing in this case could take the form of the rectification of local second-order information and higher-order integration of the rectified motion signals into radial and rotational configurations. According to the 'temporal' hypotheses, increasingly higher thresholds would be expected for complex second-order motion perception with decreased stimulus duration relative to simple motion because of sequential processing. However, our results demonstrate that stimulus duration did not differentially affect simple and complex second-order motion thresholds, suggesting that complex second-order motion analysis is not mediated by sequential processing.

3.6.3.2. Specialized processing exclusive to complex second-order motion

Alternative hypotheses suggesting that complex second-order motion perception is mediated by specialized processing can also be forwarded. The first possibility is the existence of extrastriate motion mechanisms that are *exclusively* selective to complex second-order motion information. Such mechanisms are theoretically plausible since early and late filters belonging to filter-rectify-filter models (i.e., Lu & Sperling, 1995; Wilson et al., 1992) could be arranged so that these filter sets selectively respond to radial and rotational second-order motion configurations (Baker & Mareschal, 2001). However, our results do not support the existence of such filter sets for the following reason. It has recently been demonstrated that mechanisms that encode second-order motion are less selective for direction as compared to those mediating first-order analysis (Ledgeway, 1999; Ledgeway & Hess, 2002). In addition, Ledgeway & Hess (2002) have proposed that the bandwidths of second-order motion detectors are broader than those of first-order, resulting in a less sensitivity direction selectivity, particularly when stimulus exposure duration is brief. Their direction-selectivity hypothesis therefore proposes that directional ambiguity (spurious second-order motion energy) is more pronounced for the texture-defined motion stimuli at short stimulus durations compared to that of luminance-defined motion, a result that cannot be explained by either the processing-delay hypothesis (i.e., Wilson et al., 1992) nor the low-pass temporal filtering hypothesis (i.e., Derrington et al., 1993). Based on this finding, the resulting directional ambiguity of a set of individual filters (capable of mediating complex second-order motion direction) should increase at a faster rate compared to an individual filter (capable of resolving simple second-order motion direction) as exposure duration is decreased. Behaviorally, one would predict that complex second-order thresholds should increase at a faster rate with decreasing exposure duration when compared to simple second-order motion thresholds. In contrast, our results demonstrate that simple and complex second-order motion thresholds decrease at a similar rate, suggesting that such higher-order mechanisms exclusively selective for complex second-order motion configurations, defined by such oriented filter sets, is unlikely. Additional experimental support against mechanisms exclusive to complex second-order motion processing is available from neurophysiological studies. Theses studies have failed to demonstrate the existence of mechanisms that respond exclusively to second-order motion in both lower and higher visual areas of the cat and primate (Zhou & Baker, 1993; O'Keefe & Movshon, 1998; Mareschal & Baker, 1999; Churan & Ilg, 2001).

3.6.3.3. Specialized processing common to both first- and second-order complex motion

A second possibility is that complex second-order motion analysis is mediated by the *same* specialized mechanisms that underlies complex first-order motion processing. This notion is supported in part by findings demonstrating a second-order contribution to vection, suggesting that both first- and second-order motion signals are combined (i.e, by mechanisms operating at MT) before being fed-forward to specialized mechanisms mediating optic flow analysis (Gurnsey et al., 1999). Second-order contribution to optic flow analysis is also supported by the results of Dumoulin et al. (2001), Ptito et al., (2001) and Hanada & Ejima (2000) (i.e., under specific experimental conditions). Furthermore, Smith et al. (1998) demonstrated that the human 'MT complex' (thought to be analogous to monkey MST) was activated by both first- and second-order radial patterns, similar to those used in the present experiment (see Figure 1). Taken together, these findings suggest that meaningful configurations of local second-order motion information are processed by the same specialized 'hard-wired' mechanisms that underlie complex first-order processing. This interpretation is the most congruent with the results of the present study and will be discussed in the next section.

3.6.4. A proposed model for complex second-order motion processing

The present study has demonstrated two important findings regarding complex second-order motion processing. Firstly, direction identification thresholds for complex second-order motion are significantly elevated compared to simple second-order motion at various stimulus durations (from 240 to 750 msec) and over a wide range of spatial and temporal stimulus parameters, a result not observed in the first-order motion class. Secondly, complex second-order thresholds did not increase at a significantly higher rate with decreasing stimulus duration compared to simple second-order motion, an expected result if complex second-order motion was analyzed in sequential manner. These results suggest that second-order complex motion configurations are analyzed less efficiently than complex first-order motion and involve specialized motion analysis. The question then is where and how is complex second-order motion processed ?

The difference regarding the efficiency with which such mechanisms are able to identify complex first- and second-order motion direction may depend on the properties of the motion signals originating from lower-level motion areas. A schematic representation of complex first-order motion analysis is presented in Figure 6a where MST cells are shown to respond selectively to contracting radial motion. Although the exact nature of the functional motion hierarchy including the role of MT (Gurney & Wright, 1996) is debatable, it is generally accepted that MST receives its primary input via adjacent MT which in turn receives local input from V1 and V2. Furthermore, response properties of MST neurons suggest that they integrate over specific configurations of locally oriented motion signals defined by specific spatio-temporal characteristics. Figure 6b represents a hypothetical model delineating the analysis of complex second-order motion. The main difference between the two analyses is that in the latter case, local motion information must be rectified before it can be used by higher-level mechanisms. According to 'filter-rectify-filter' models, oriented first-order filters are modeled as having higher spatial-frequency selectivity compared to second-order filters (i.e., Wilson et al., 1992). Therefore, local second-order motion signals prior to the MT level operations remain oriented but are characterized by a courser spatial frequency tuning (Sutter, Sperling & Chubb, 1995, Clifford & Vaina, 1999). Assuming that the sensitivity of the specialized mechanisms to complex motion depends on the tuning selectivity of each of the local motion inputs, it can be expected that such mechanisms would be less sensitive to configurations of local second-order motion signals since each contributing signal is less selective for orientation. Consequently, direction-identification thresholds for complex second-order patterns thresholds would be

INSERT FIGURE 6 APPROXIMATELY HERE

elevated with respect to simple motion in the same class, since less ‘pooling’ is involved in simple motion identification. As mentioned previously, the finding that simple and complex motion identification thresholds in the second-order class increased at a similar rate with decreasing stimulus duration suggests that although complex motion is less efficient with regards to simple second-order motion, it is processed by specialized mechanisms.

In conclusion, complex second-order motion analysis might not be as inefficient or qualitatively different from that mediating complex first-order motion as previously believed (Allen and Derrington, 2000; Badcock & Khuu, 2000). Instead, the same ‘hard-wired’ mechanisms may be responsible for the analysis of both first- and second-order complex motion, possibly resulting in the responding of higher-order motion areas to both first- and second-order motion in human (i.e., Smith et al., 1999) and non-human studies (i.e., O’Keefe et al., 1998; Churan et al., 2001).

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3.9. Tables, Figures and Legends

Figure 1. A schematic representation of the motion stimuli used in the present experiment. The upper panel (a) shows the luminance-defined or first-order translational, radial and rotational motion patterns. The lower panel (b) shows the same types of texture-defined or second-order patterns.

Figure 2. Mean direction-identification thresholds for translational, radial and rotational motion types as a function of stimulus exposure duration for first-order (left panel) and second-order (right panel) motion classes. Standard error bars are included. If not shown, then the standard error is smaller than the symbols used to represent it for any given motion condition.

Figure 3. Individual direction-identification thresholds for 5 of the 7 observers. For all observers tested, thresholds for simple, translational second-order motion (lower panel) were consistently lower compared to radial and rotational motion across stimulus duration.

Figure 4. Direction-identification thresholds for motion types as a function of spatial frequency for first-order (left panel) and second-order (right panel) motion classes for an author (AB) and a naive observer (LAT). All stimuli were presented for 750 msec and their temporal frequency was kept constant at 1 Hz.

Figure 5. Direction-identification thresholds for motion types as a function of drift frequency for first-order (left panel) and second-order (right panel) motion classes for an author (AB) and a naive observer (LAT). All stimuli were presented for 750 msec and their spatial frequency was kept constant at 1 cpd.

Figure 6. Schematic diagram depicting a hierarchical model for (A) first- and (B) the proposed analysis of complex second-order motion. The first-order model shows that simple first-order motion signals are available after standard motion analysis at the

primary visual cortex (V1). Locally-oriented motion signals are then projected via area MT to specialized motion mechanisms operating after MT (i.e., MT complex or MST) that are able to efficiently detect to complex configurations of relatively well finely tuned spatio-temporal local motion signals, as depicted by the thin arrows. The proposed functional pathway for complex second-order is shown in the right panel (B). Unlike first-order motion analysis, simple or unidirectional second-motion signals can be analyzed by standard motion analysis only after they are pre-processed (i.e., rectification) and extracted by mechanisms operating within areas V2 or V3 at a relatively courser spatial scale. Therefore, such signals are available for further analysis by higher-order motion mechanisms at a courser spatial scale (i.e., depicted by the thick arrows), possibly resulting in less efficient 'pooling' of overall second-order motion direction at the level where specialized motion mechanisms operate.

Figure. 1. Bertone & Faubert, 2003

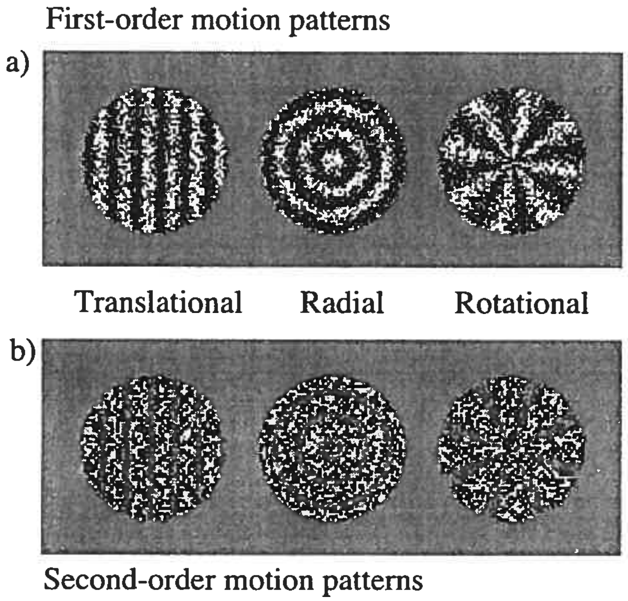


Figure. 2. Bertone & Faubert, 2003

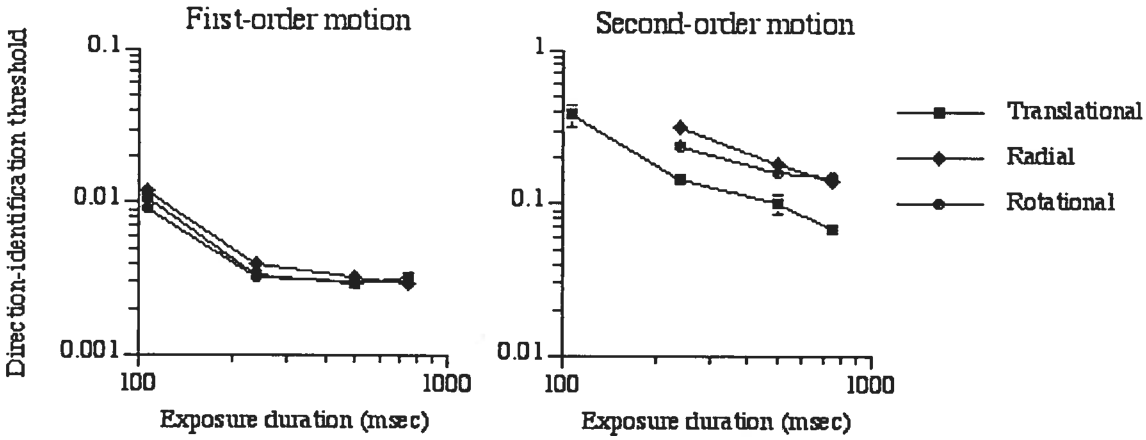


Figure. 3. Bertone & Faubert, 2003

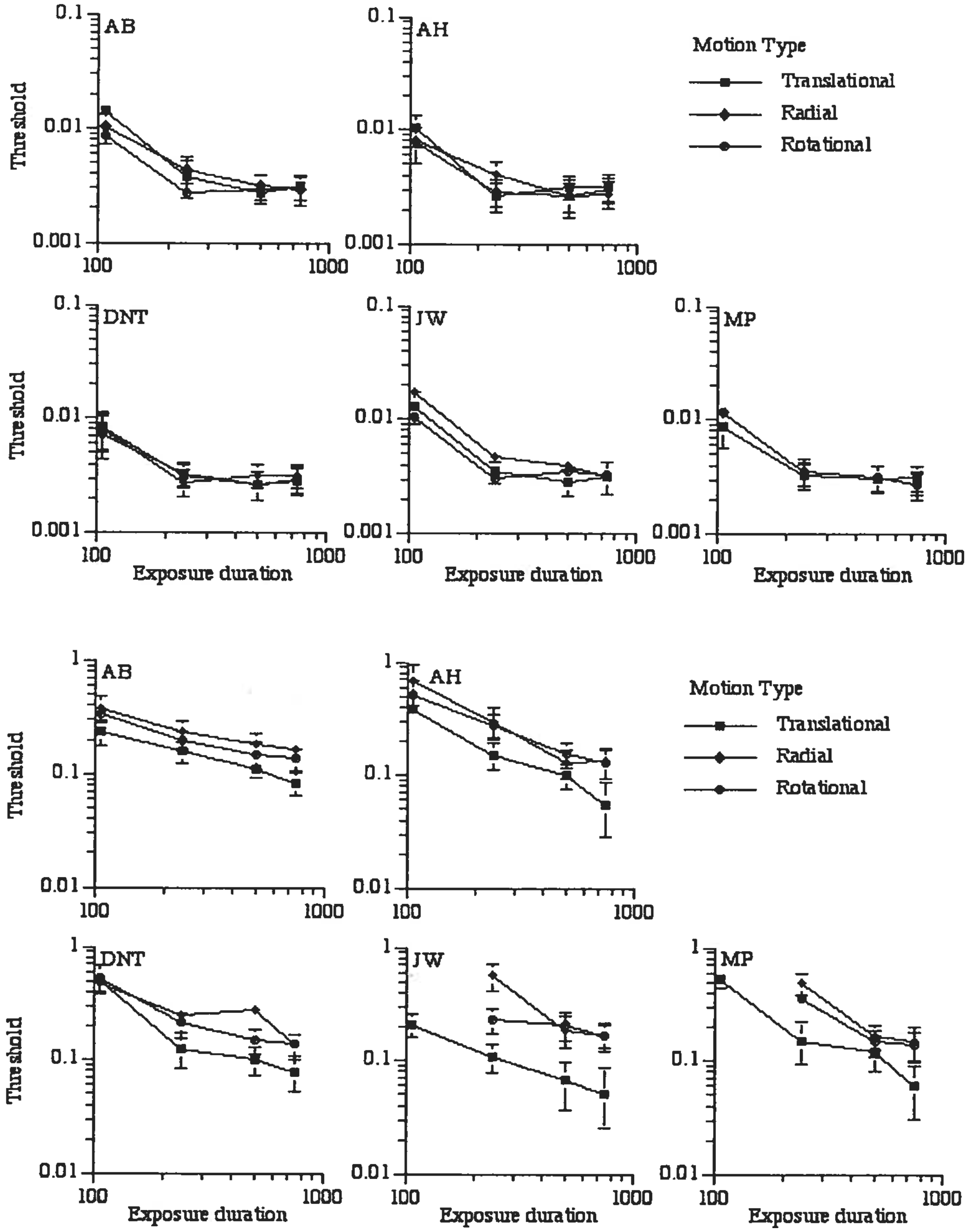


Figure. 4. Bertone & Faubert, 2003

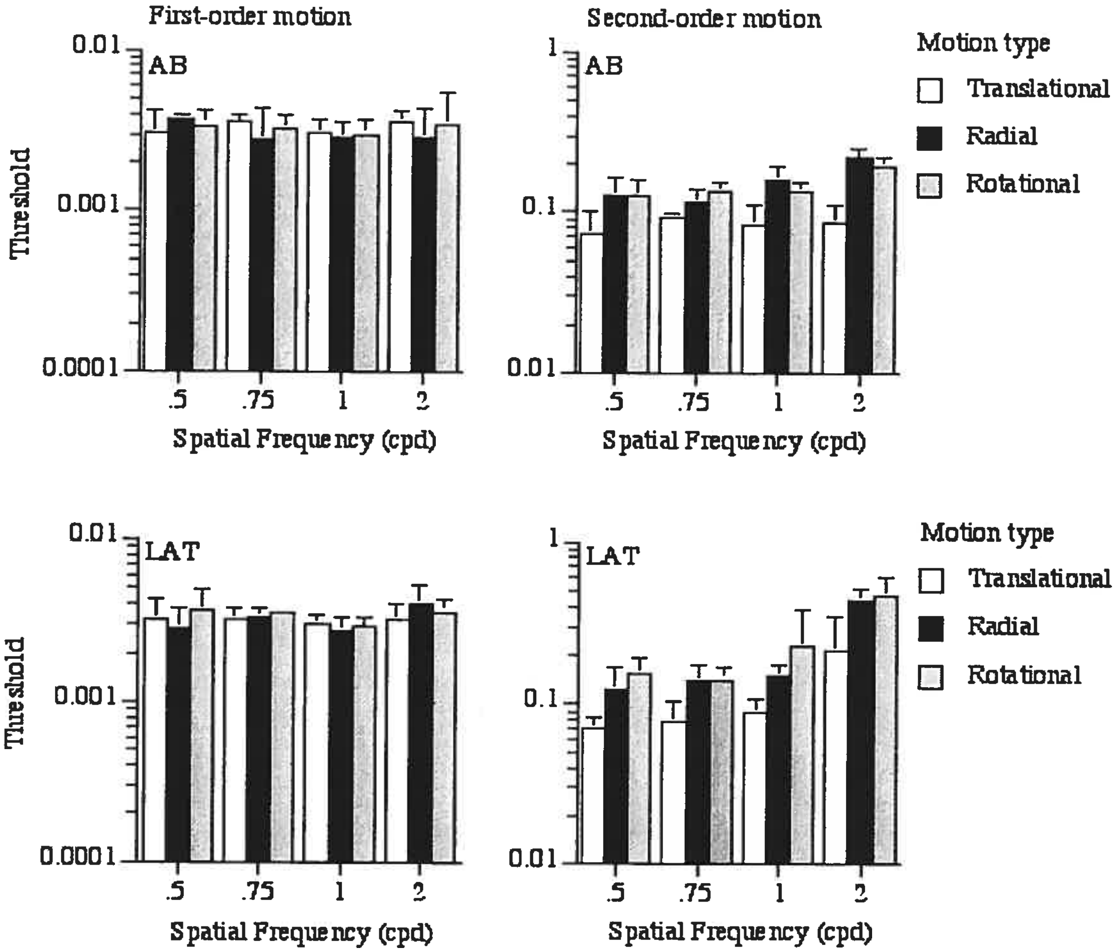


Figure. 5. Bertone & Faubert, 2003

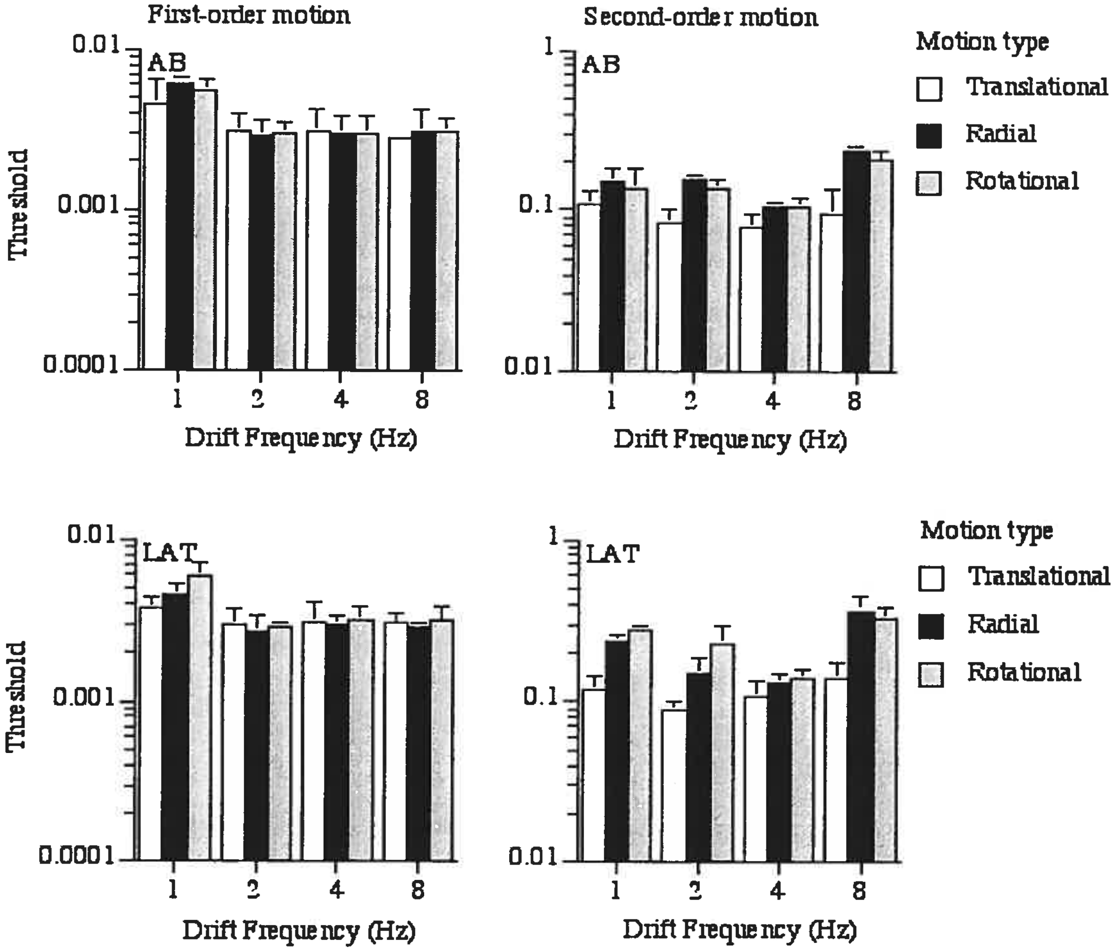
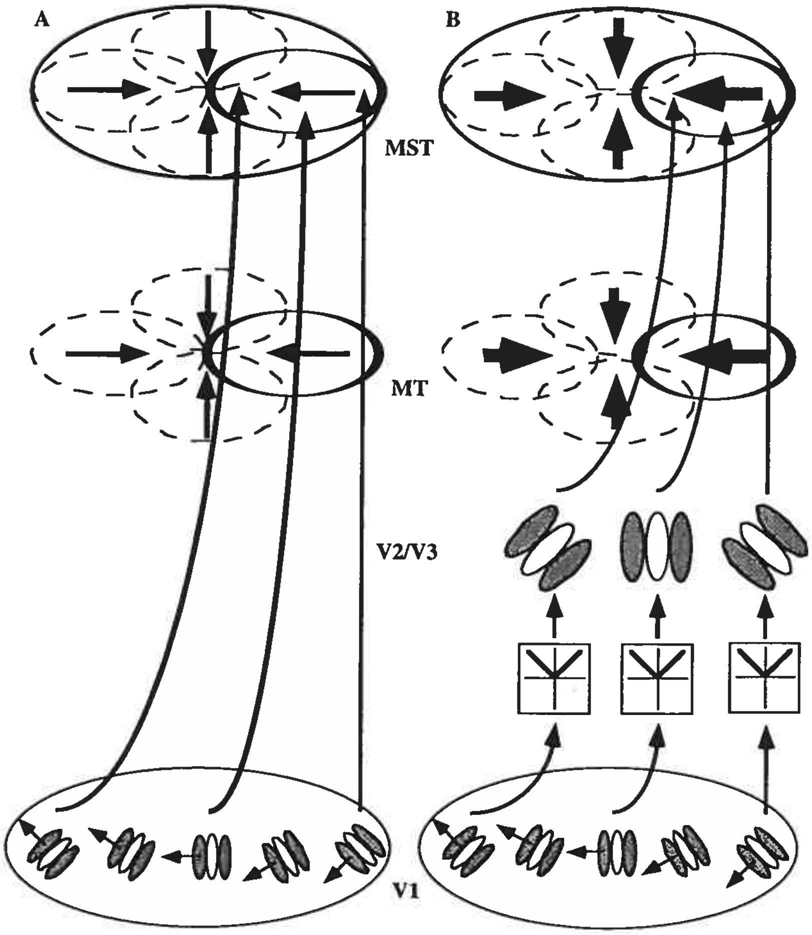


Figure. 6. Bertone & Faubert, 2003



Chapter 4
Autism

4.1. What is autism?

Autism is presently considered to be a pervasive developmental disorder of neurobiological origin that is diagnosed based on abnormal behavioural manifestations (see Bailey et al., 1996; Volkmar & Pauls, 2003; Volkmar et al., 2004, for reviews). First described independently by Kanner (1943) and Asperger (1944), this condition is most often characterized qualitatively in terms of a triad of impairments regarding social interaction, communication and imagination (Wing & Gould, 1979; World Health Organization, 1992; American Psychiatric Association, 1994). However, " nontriadic " (Frith & Happé, 1994) or non-social impairments are also thought to be universally prevalent in autism and used as features for diagnosis. Nontriadic symptomology includes preoccupation with parts of objects, restricted repertoire of interest, idiosyncratic responses to sensory stimulation, islets of abilities and savant abilities (American Psychiatric Association, 1994). A significant proportion of nontriadic symptomology implicate the visual-perceptual domain. These are negative symptoms, or absence of normal visual behaviors (e.g., absence of eye contact during interpersonal interaction), as well as positive symptoms, e.g. visual behaviors, which are specific to autism and are not found in typically developing individuals (e.g., preoccupations to certain category of visually presented stimuli). In addition, sensory hypo- or hypersensitivities to the environment are also prevalent nontriadic features of autism (APA, 1994).

4.2. Neuro-cognitive theories of autism

During the years following the initial description of autism, the cause of the condition was controversial and varied from inadequate parenting (Bettelheim, 1956) to deficits in sensory processing (Delcato, 1974). The notion that autism was of neuro-biological origin was not generally accepted until the mid-1960s (Rimland, 1964), opening the door for new hypotheses and questions regarding the origins of autism. This interest has grown exponentially ever since, reflected by an ever-increasing number of investigations related to the understanding of cognitive and neuro-biological abnormalities underlying the autistic disorder. As a developmental disorder with a biological basis and behavioural definition, neuro-behavioural theories attempting to link brain dysfunction, cognitive processes and characteristic behaviours in autism have afforded researchers a theoretical framework with which to work.

As mentioned, in order to associate brain dysfunction and atypical behaviour in autism, cognitive explanations of behavioural manifestations must be advanced. This brain-behaviour interface was encompassed in the theory of mind (ToM) hypothesis that posited that a specific neurologically based problem caused a deficit in understanding the " minds " of others (Baron-Cohen et al., 1985). Specifically, the ToM hypothesis suggests that the characteristic problems regarding social interaction in individuals with autism stems from the lack the intuitive understanding that others have mental states. Therefore, individuals with autism are presumed to be unable to think or understand the intentions, desires, feelings and beliefs of others and are therefore, unable to interact socially with them in an adaptive manner (Frith, 1989). This prediction was initially evaluated by Baron-Cohen et al. (1985) using the Sally-Ann task, a simple version of the false-belief task devised by Wimmer & Perner (1983). Since then, the ToM hypothesis has stimulated much research, including some studies assessing the neural correlates of " mentalizing " capacity in autism and other neurobiological disorders (see Frith, 2001; Abu-Akel, 2003 for reviews). Nevertheless, the ToM hypothesis is limited by the findings that an important correlation exists between ToM abilities and language. This is exemplified by the fact that many high-functioning individuals with autism can resolve ToM tasks while still manifesting important social difficulties (Bowler, 1992; Klin et al., 1992).

The ToM hypothesis is unable to account for all of the clinical manifestations typically manifested by individuals with autism, such as behaviours that are characterized by an obsessive desire for sameness (e.g., routines, repetitive patterns of self-chosen activities, etc.). Such behaviours are being tackled by the executive dysfunction hypothesis (Ozonoff, 1994), which posits that higher-level cognitive functioning necessary for the control of actions are deficient in autism. These functions include working memory, planification, response inhibition as well as the initiation and self-monitoring of behaviour. Impairments regarding executive functioning is presumed to reflect frontal lobe dysfunction and possibly be manifested by repetitive and restricted behaviours in autism. Although executive dysfunction has been demonstrated in autism (Pennington & Ozonoff, 1996; Russel, 1999), it is not uncommon in other neurobiological conditions and furthermore, executive dysfunction is not strongly correlated to degree of social difficulty in autism (Dawson et al., 1998).

4.3. The Central Coherence Theory

The strength of both the Theory of Mind and executive dysfunction hypothesis is that they provided researchers with a theoretical framework with which to investigate the neural underpinnings of the " triad " of social impairments in autism. Arguing that the autistic symptomology is also defined by "non-triadic' or non-social features, Frith & Happé (Frith, 1989; Frith & Happé 1994) proposed the Central Coherence Theory. Their theory differs from the Theory of Mind and executive dysfunction hypotheses in that its development was motivated by the fact that many non-triadic autistic features (e.g., restricted repertoire of interests, islets of ability, preoccupations with parts of objects, etc.) cannot be explained in terms of deficits in mentalizing capacity. Furthermore, the Theory of Mind and executive dysfunction hypotheses do not address the empirical findings of *both* deficient as well as enhanced performance on several cognitive tasks. In order to accommodate these findings into their theory, Frith & Happé proposed a theory based on one primary or fundamental cognitive deficit in autism; a specific imbalance in integration of information at different levels of processing, or weak central coherence. Frith (1989) theorized that autistic observers would be relatively advantaged for tasks requiring attention to local information processing and relatively disadvantaged for tasks requiring the integration of information into a more global percept. It is to note that *normal* information processing is mediated by holistic or gestalt processing, where the perception of the whole object is more important to our behaviour than parts of the object or scene.

The central coherence theory was initially based on findings demonstrating enhanced performance on certain visuo-spatial neuropsychological tests. For example, Shah & Frith (1983) found that autistic children performed better than control participants on the *Embedded Figures Test* (test involving seeing a hidden figure from among a larger figure) and show superior performance on the Block Design task (Shah & Frith, 1993), a subset of the Weschler Intelligent Scales (e.g., Weschler, 1991) which involves reproducing unsegmented block designs. Frith & Happé (1994) argue that the superior performances on these tasks is a result of weak central coherence since the autistic observers have selective access to local information and details, normally obscured by the global or holistic perception of the figure. This hypothesis can also explain autistic subjects' superior ability in matching inverted faces (Hobson, Ouston & Lee, 1988) since such a task requires local analysis of the parts of the faces and not the face as a whole. A similar argument is proposed by Snyder & Mitchell (1999). They propose that islets of ability of some autistic children may result from their privileged access to " lower-level " neural information before being integrated into a holistic percept, which ultimately, is what our perceptual systems have been adaptively developed for. Snyder & Mitchell argue that we are all processing the same raw information, but only some autistic observers are able to access it. Conversely, on tasks where the overall meaning and context of information is essential, weak central coherence would predict processing disadvantages. This is exemplified in cases of " conventional " face perception where individuals with autism demonstrate difficulty in recognizing visually presented faces and facial emotions (see Shultz et al., 1999, for a review). Functional imaging studies have demonstrated that these perceptual deficits are probably mediated by alternate cognitive pathways for face perception in autism (Pierce et al., 2001; Critchley et al., 2000), possibly defined by a more local-type analysis.

Proponents of the central coherence theory concede that this relatively recent account of autistic characteristics is tentative and limited (e.g. Frith & Happé, 1994). They also suggest defining and evaluating the levels at which coherence is weak in autism, a direction which will perhaps increase the robustness of the theory. Based on empirical findings, Happé (1999) has defined three provisional levels of processing that demonstrate weak central coherence. The first is *visuospatial-constructional coherence*, exemplified by the enhanced performance on tasks where local information analysis is advantageous. Such tasks include the processing on the Weschler Block Design (Shah & Frith, 1993), the Embedded Figures Test (Shah & Frith, 1983; Joliffe & Baron-Cohen, 1997), detail-by-detail drawing style (Mottron & Belleville, 1993) and a facility for reproducing globally incoherent figures (Mottron et al., 1999). The second level of coherence defined by Happé is *verbal-semantic coherence*. The advancement of this level stems from findings demonstrating that individuals with autism seem to have difficulty deriving context from the individual words they read, as when reading a sentence. For example, when asked to recall sentences and strings of unrelated words, individuals with autism took less advantage of context (e.g., sentences) and performed worse than non-autistic children for sentence recall (Hermelin & O'Conner, 1967) suggesting that autistic children make less use of semantic relations during recall. Such studies have demonstrated the possibility that holistic processing at a verbal-semantic level, necessary for efficient comprehension of contextual verbal information, is deficient in autism.

The last type of coherence defined by Happé (1999) is that of *perceptual coherence*, or the inability for individuals with autism to perceive their physical environment in terms of coherent objects. Happé based this level of coherence on findings of atypical lower-level perceptual analysis (visual and auditory) characterized by a bias towards local information processing resulting in the less efficient processing of global perceptual processing. Such atypical performances mentioned by Happé included a decreased susceptibility to visual illusions (Happé, 1996), a reduced McGurk effect (de Gelder et al., 1991), abnormal pitch processing (Heaton et al., 1998) and reduced visuo-motor response to optic flow motion (Gepner et al., 1995). Since then, there have been important demonstrations of atypical information processing in both visual and auditory modalities that have supported the concept of weak perceptual coherence (see Plaisted al., 2003 for review). Examples of superior processing of low-level local visual information (e.g., Shah & Frith, 1983; 1993; Happé, 1996; Plaisted et al., 1999; Ropar & Mitchell, 1999), deficits in the ability to efficiently process global or information in context (e.g., Jolliffe & Baron-Cohen, 1999) and / or difficulty with the hierarchical processing of perceptual information (Motron & Belleville, 1993; Mottron et al., 1999).

4.4. Using the motion model to assess *perceptual coherence* in autism

Apart from the interest to study motion perception in autism as one among the several visual aspects concerning abnormal visual processing, atypical motion processing may also be accountable for the clinical observation of frequent idiosyncratic interest of autistic individuals during their young age such as staring at spinning objects (fans, car wheels) or at objects animated by a periodic movement (waves, flickering lights). This fascination for moving objects raises several questions regarding motion perception in autism. One basic question is whether high-functioning autistic individuals have normal or atypical basic motion perception capabilities. Gepner et al. (1995) were the first to suggest that motion perception may be atypical in autism. They found that the postural stability of autistic children, as measured by a force platform on which observers stood during experimentation, was unaffected by the presentation of a radiating flow-field (optic flow). These researchers concluded that the lack of postural reactivity could either be the result of impairment in motion perception or a lack of visual attention to the radiating stimulus. Recently, many other studies have investigated motion perception in autism using a variety of dynamic stimuli (Gepner, 1999; Castelli et al., 2000; Spencer et al., 2000; Gepner et al., 2001; Castelli et al., 2002; Gepner & Mestre, 2002a, 2002b; Milne et al., 2002; Bertone et al., 2003; Blake et al., 2003), most of which have demonstrated atypical processing of visual motion in autism and how they may be associated with characteristic autistic behaviours.

In addition to such interpretations, the motion model may also be used to assess *perceptual coherence* in autism. Regarded to reflect cognitive functioning, visuo-perceptual capabilities can be evaluated by measuring an observer's ability to integrate visual information. The method most commonly used to do so is to measure sensitivity (ability to discriminate motion direction) to simple (e.g., local analysis) and complex (e.g., necessitating integrative analysis) motion stimuli using psychophysical methodology. In order to efficiently discriminate complex motion direction, local motion inputs must be integrated and therefore, decreased complex motion sensitivity is believed to reflect abnormal neural function. In this context, the motion model can be used to assess integrative functioning at a visuo-perceptual level in autism, or in other words, provide a theoretical framework to investigate perceptual coherence. However, past psychophysical studies using complex motion stimuli (e.g., Gepner et al., 1995; Spencer et al., 2000; Milne et al., 2002; Blake et al., 2003) did not measure performance using simple motion stimuli. Therefore, an inferior performance for autistic participants could be attributable to either a motion perception deficit or weak perceptual coherence, defined by less efficient neuro-integrative mechanisms operating at a perpetual level. Although these authors interpreted their findings of decreased sensitivity for complex motion stimuli as the consequence of impaired magnocellular or dorsal stream functioning, it is also possible that their results can be due to impaired integrative mechanisms mediating dynamic information processing. Therefore, the aforementioned studies were unable to dissociate a " motion " deficit from a " coherence / neuro-integrative " deficit in autism since performance was evaluated at only one level of motion complexity.

As mentioned above, past studies assessing visual motion processing in autism have used different types of complex motion stimuli including full-field radiating flow fields (Gepner et al., 1995), adapted global motion stimuli (Spencer et al., 2000), random dot kinemotograms (RDKs) (Milne et al., 2002) and biological motion stimuli (Spencer et al., 2003). All these stimuli are believed to be processed in extra-striate areas of the visual pathways and necessitate passive integrative operations in order to be perceived. A problem with such stimuli with respect to addressing the complexity issue is that comparable stimuli that are simple (e.g., processed in the striate cortex and do not necessitate integration) and perceptually equivalent simply do not exist. For this reason, even if the authors investigating motion perception in autism were interested in evaluating neuro-integrative processes in autism, they wouldn't be able to do so using their stimuli of choice. In order to evaluate motion processing *and* neuro-integrative functioning simultaneously in autism, and therefore, to be able to dissociate a motion specific deficit from a neuro-integrative deficit affecting complex motion perception, the second study of this thesis used first- and second-order motion stimuli for the following reasons. Firstly, as demonstrated by Bertone et al. (2003), first-order or luminance-defined motion patterns, whether unidirectional or multidirectional (e.g., radial or rotational), are processed very efficiently by the visual system. On the other hand, second-order motion stimuli of the same types necessitate pre-processing in the form of rectification and additional integration of second-order motion signals. Therefore, although normal and autistic observers perceive both first- and second-order motion patterns, second-order motion stimuli are considered to be complex, while first-order motion stimuli are simple. In this respect, the following study is the first assessment of motion processing in autism that uses motion stimuli that require neural processing mechanisms of varying complexity. Furthermore, at near threshold, it is impossible to dissociate a first-order stimuli from a second-order motion stimuli; they are perceptually equivalent. For this reason, the observer responds to each stimulus presentation, whether it is a first-order or a second-order pattern, in exactly the same manner. The only difference is that the neural processing involved in identifying their motion direction differs.

Chapter 5
Article 2

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5.1. Chapter overview

The goal of the proposed study was twofold. The first was to evaluate motion perception capabilities of high-functioning persons with autism by using motion stimuli varying in the amount of neural processing involved in discriminating their motion direction (e.g., simple and complex). Being the first study to do so, it meant that for the first time, one is able dissociate a " motion " deficit from a " neuro-integrative " deficit in autism. Secondly, to empirically evaluate integrative processes of autistic observers using a motion model in order to assess central coherence at a low-level of information processing (perceptual coherence). Possible implications of visuo-perceptual deficits on autistic behaviours are also forwarded.

5.2. Abstract

We present the first assessment of motion sensitivity for persons with autism and normal intelligence using motion patterns that require neural processing mechanisms of varying complexity. Compared to matched controls, our results demonstrate that the motion sensitivity of observers with autism is similar to that of non-autistic observers for different types of first-order (luminance-defined) motion stimuli, but significantly decreased for the same types of second-order (texture-defined) stimuli. The latter class of motion stimuli has been demonstrated to require additional neural computation to be processed adequately. This finding may reflect less efficient integrative functioning of the neural mechanisms that mediate visuo-perceptual processing in autism. The contribution of this finding with regards to abnormal perceptual integration in autism, its effect on cognitive operations and possible behavioural implications are discussed.

5.3. Introduction

Autism is a developmental disorder characterized by a triad of impairments affecting reciprocal social interactions, interpersonal communication and imagination (Wing & Gould, 1979). A third area of abnormality concerns non-triadic or non-social impairments (Frith & Happé, 1994; Happé, 1999), grouped under the "*Restricted repetitive and stereotyped patterns of behavior, interests and activities*" diagnostic description of autism in the DSM-IV (American Psychiatric Association, 1994). Non-triadic symptoms include abnormal preoccupations with parts of objects, islets of abilities, restricted repertoire of interests and idiosyncratic responses to sensory stimulation. A significant proportion of these non-triadic symptoms implicates the visual-perceptual domain and can be described as either negative or positive. Negative symptoms can be defined as the absence of a typical behavior in response to visual information (e.g., absence of eye contact during interpersonal interaction). Conversely, positive symptoms are behaviors rarely or never evident in typically developing individuals (e.g., preoccupation with certain types of flickering or spinning objects).

Empirical evidence of abnormal visual processing in autism is currently available. For example, individuals with autism exhibit *deficits* in recognizing visually presented faces and facial emotions, possibly due to an atypical locally-oriented processing (see Schultz, Romanski & Tsatsanis, 1999, for a review). Recent functional neuroimaging studies have demonstrated that these deficits are associated with an abnormal localization of brain activation during face perception (Schultz et al., 2000; Critchley et al., 2000; Pierce et al., 2001), suggesting that persons with autism develop alternative cognitive pathways for face and facial emotion recognition. However, the majority of the evidence demonstrating atypical visual processing in autism is related to an *enhanced* performance on visuo-spatial tasks implicating the detection or matching of simple geometric patterns among a more complex visual field. Accordingly, individuals with autism show an enhanced performance on the Block Design test (Shah & Frith, 1993), in reproducing impossible figures (Mottron, Belleville & Ménard, 1999) and in discriminating elementary visual information, within a visual search paradigm

(O'Riordan et al., 2001). Another illustration of superior perceptual functioning has been demonstrated using the Embedded Figures Test (EFT) of the Wechsler intelligence test where autistic individuals are better at identifying a simple shape embedded in a more complex shape (Shah & Frith, 1983; Jolliffe & Baron-Cohen, 1997). Using a functional neuroimaging technique, Ring et al. (1999) found different regions of cortical activation in participants with autism and a comparison group while performing an adapted version of the EFT. Based on the functional characteristics of the cortical areas activated for either group, these researchers concluded that the participants with autism were more dependent on perception than typically developing individuals and adopted a more "local" approach when performing the EFT.

This pattern of atypical performances has lead to the development of neurobehavioral theories of autism describing these anomalies as consequences of an abnormal multi-modal structure of information in the visual modality. Common to these theories is the notion that persons with autism do not integrate visual information in an optimal manner. Rather, the visual processing of complex stationary objects and visual scenes seems to be characterized by an atypical bias towards local processing, or Weak Central Coherence (WCC; Frith, 1989), an absence of hierarchy in feature processing (Mottron & Belleville, 1993). Alternatively, this processing may occur through an enhancement in the detection of its of visual features (Enhanced Perceptual Functioning or EPF model; Mottron & Burack, 2001). Weak Central Coherence is believed to result in superior performance on tasks for which locally-oriented processing is advantageous (i.e., EFT) but results in inferior performance when a holistic or global integration of visual features is necessary (i.e., face perception). Therefore, depending on the nature of the task, both the superior and inferior autistic performance on the aforementioned visuo-spatial tasks seem to be the result of a preference for local information processing. Furthermore, the differences in behavioural performance between autistic and control subjects seem to be associated to different underlying neural systems, suggesting that individuals with and without autism use different cognitive strategies when faced with the same task.

In the present study, a motion paradigm was used to evaluate the ability of autistic individuals to perceptually integrate visual information. The human motion pathway is hierarchical in structure and has relatively well-defined and well documented levels of neural processing that are characterized by their capacity to process moving stimuli defined by different attributes. Therefore, measuring sensitivity to motion information processed at different levels along the visual pathway allowed for a direct assessment of motion perception capabilities in persons with autism, and also furthers our understanding on how these capabilities are related to the neural complexity of the visual motion information being processed.

Relatively few studies have investigated motion processing among persons with autism. Gepner, Mestre, Masson & de Schonen (1995) found that the postural stability of children with autism, as measured by a force platform, was unaffected by the presentation of a radiating flow-field, suggesting that children with autism are less susceptible to visually induced movement relative to typically developing controls. These researchers concluded that the lack of postural reactivity may have resulted from either a motion perception impairment, or from a lack of visual attention to the radiating stimulus. This finding is important, as it demonstrates an abnormal reaction to visually presented information in an empirical setting that approximates the true ecological setting. However, it is difficult to conclude from this experiment that reduced reactivity of the children with autism results from a perceptual limitation, since higher-order operations (e.g., attention) or motor functioning (e.g., inadequate sensori-motor integration) may also be implicated. More recently, a study investigating motion and form perception in autism demonstrated that participants with autism were less sensitive to global motion compared to typically developing controls (Spencer et al., 2000). However, no difference was found between the two groups on the form perception task. The selective decrease in motion sensitivity was interpreted by these authors as a specific deficit of dorsal stream functioning in autism, since global motion perception may be mediated by this system (Ungerleider & Mishkin, 1982; see Merigan, Byrne & Maunsell, 1991 and Goodale & Milner, 1992, for an alternative view). However, an alternative hypothesis can be forwarded based on the "complexity" of the motion information used in their experiment. Specifically, to discriminate the direction of global motion patterns, the visual system must first integrate local motion signals. If persons with autism adopt a more local approach at the expense of global information processing, the results of Spencer et al. (2000) may be at least partially explained by a deficit in integrating complex information at a perceptual level, regardless of the system implicated in its processing.

In the current paper, we present a direct and systematic assessment of visual motion perception in persons with autism by using classes of moving stimuli. The motion sensitivity to translating, radiating and rotating motion patterns was measured for observers with autism as well as for matched non-autistic observers. Each type of motion pattern was either of the first- (luminance-defined) or second-order (texture-defined) motion class (Chubb & Sperling, 1988; Cavanagh & Mather, 1989). These two classes of motion were used because a large body of psychophysical evidence has demonstrated that they are initially processed by two distinct neural motion mechanisms, varying in neural complexity (Bertone & Faubert, 1999; see also Clifford & Vaina, 1999, for a review) and are sensitive to subtle neural dysfunctioning of visual information processing (Habak & Faubert, 2000; Bertone, Habak & Faubert, 2000). Contemporary motion models distinguish first- and second-order motion classes by the level at which they are processed along the motion pathway. First-order motion is initially processed by standard motion selective mechanisms operating in the primary visual cortex (or visual area V1). However, additional neural processing is required before second-order motion is perceived since standard motion analysis is unable to detect second-order information (e.g., Chubb & Sperling, 1988; Wilson & Ferrera, 1992). For this reason, second-order motion can be considered a more "complex" motion class than first order motion since it requires additional neural processing for integration. This is further evidenced by medical imaging data demonstrating initial first-order activation in area V1, whereas second-order motion activation appears further along the motion pathway, namely in areas V3 and VP (Smith, Greenlee Singh, Kraemer & Henning, 1998).

5.4. Results

Due to the different attributes which define the first- and second-order motion classes (e.g., luminance and texture modulation, respectively), comparing the mean differences of the absolute thresholds between the two motion classes is not informative. For this reason, the direction-identification threshold differences for the autistic and non-autistic observers of each type of motion (translational, radial and rotational) were analyzed separately for the first and second-order motion classes. The direction-identification thresholds were defined as the contrasts at which the direction of motion was correctly identified 75% of the time. For both the first-and second-order motion classes, the thresholds were expressed in terms of log motion sensitivity.

INSERT TABLE 1 HERE

5.4.1. First-order motion class.

Figure 1a shows the motion sensitivity for individuals with autism and the comparison group plotted as a function of motion type (translational, radial and rotational). A two way ANOVA (group X motion type) revealed no significant effect of group, F(1,22) = .274, p = .6057 demonstrating that persons with autism discriminated the direction of first-order motion as well as matched controls. A significant main effect of motion type (F(2,44) = 3.996, p = .0254) was found and a subsequent Tukey HSD analysis revealed that the direction of first-order radial motion was more difficult to discriminate relative to that of the translational and rotational motion types for both autistic and non-autistic observers. This finding may be a result of the perceived increase in speed of this type of motion, due to its apparent motion in depth (Bex & Makous, 1997). No significant group x motion type interaction was found (F(2,44) = .8721, p = .8721) for this motion class.

INSERT FIGURE 1 HERE

5.4.2. Second-order motion analysis.

As shown in Figure1b, the motion sensitivity of individuals with autism was significantly lower than that of the comparison group (F(1,22) = 5.550, p = .0278) across second-order motion types, demonstrating that persons with autism had more difficulty discriminating the direction of motion for the second-order motion patterns. As expected, a significant motion type effect was also found (F(2,44) = 27.702, p = .000). A Tukey HSD analysis revealed that both autistic and non-autistic observers were less sensitive to second-order radial ($p < .01$) or rotational motion ($p < .01$) relative to translational motion. This result is consistent with previous findings (Bertone & Faubert, 1999; Bertone, Habak & Faubert, 2000). Finally, no significant group x motion type interaction was found (F(2,44) = .131, p = .8778) for this motion class.

5.4.3. Age effects.

No significant correlation ($p > 0.05$) was found for both the control and autistic observers between age and motion sensitivity for any of the motion conditions.

5.5. Discussion

The present study used a motion discrimination paradigm to assess the ability of autistic individuals to perceptually integrate visual information. The findings revealed a dissociation in the sensitivity for two classes of motion necessitating different levels of neural processing. In addition, our results indicate that individuals with autism are less sensitive to second-order motion than typically developing individuals. However, they are capable of discriminating first-order motion as well as the comparison group. The possible role played by neural complexity in this dissociation, its relation to abnormal visuo-perceptual integration in autism and its effect on complex cognitive operations are discussed.

5.5.1. Motion perception in autism and its relation to integrative processing

Considering that an increased complexity of neural processing involved in the discrimination of motion direction is the unique factor that differentiates the first- and second-order motion perception, a selective decrease for second-order motion sensitivity is likely the result of less efficient integrative mechanisms operating at the visuo-perceptual level. According to this interpretation, the specialized mechanisms able to specifically and efficiently process first-order motion patterns (Regan & Beverly, 1978; Freeman & Harris, 1992; Morrone, Burr & Vaina, 1998; Bex et al., 1998), are less affected by a limited capacity of neural integration than those mediating the processing of complex motion information, such as second-order class stimuli.

These results are relevant for explaining why individuals with autism are less sensitive to another type of "complex" motion, global motion (Spencer et al., 2000). Spencer et al. interpret their findings as an evidence for a specific deficit in dorsal stream functioning in autism, since motion selective cortical areas are traditionally associated with dorsal pathway (e.g., the medial temporal area). However, our results demonstrate that persons with autism are capable of discriminating the direction of the different types of first-order motion as well as matched controls. Consequently, individuals with autism do not have a visual motion processing deficiency *per se,* indicative of a decreased dorsal pathway functioning, since the first-order motion patterns used in the present study are processed by specialized 'hard-wired' mechanisms located in this region. The fact that no specialized mechanisms are thought to exist for second-order motion (Bertone & Faubert, 1999; Badcock & Khuu, 2001) suggests that processing of any type of second-order pattern implicates a greater amount of neural circuitry and integrative processing for its direction to be discriminated. For this reason, we believe that our results are better explained by autistic observers' decreased capacity to integrate complex perceptual information rather than a specific inability to efficiently process motion information as such.

5.5.2. Integrative inefficiencies in autism: Possible origin and behavioral manifestations?

The dissociation in sensitivity among two classes of motion information that differ in the amount of neural computation involved in their respective processing supports the hypothesis of abnormal neural networks in autism. With the exception of abnormal neuronal oscillatory activity (Grice et al., 2001), previous support for this hypothesis in autism is speculative. For example, several authors have described how neural dysfunction in autism may originate from the hyperspecificity of neural representations (McClelland, 2000), excessive lateral synaptic inhibition (Gustafsson, 1997a & b) and abnormal amounts of neural connectivity (Cohen, 1994). Other support for abnormal neural functioning in autism is even more indirect and is based on discarding the implication of sub-cortical mechanisms to the benefit of cortical regions in a particular deficit (Minshew, 1997). Regardless of the exact nature of this neural dysfunction, it is highly probable that the ability of an autistic person to process perceptual information would be compromised to a greater extent if the information is complex, since more neural circuits would be involved.

The current finding that autistic observers are selectively less sensitive to complex motion information highlights a limitation in neural functioning even within an elementary perceptual process. Accordingly, the direction identification task used in the present study is cognitively simple, as the observers only have to choose between two possible motion directions after being presented with a moving stimulus. Although the amount of neural processing needed to correctly discriminate a motion direction is greater for the second-order motion stimuli, the cognitive load is maintained constant during the task. In this regard, this finding is in contrast with Minshew's (1997) proposition of intact early information processing in autism and impaired processing of "higher-level" operations. Instead, it suggests that neural mechanisms mediating perceptual processing in autism may be implicated in this condition, therefore at an earlier stage than previously believed.

Associating inefficient neural functioning at a perceptual level to higher-level cognitive deficits and atypical behaviors characterizing autism may be beyond the scope of this discussion. However, it is reasonable to hypothesize that at least some of the behavioural manifestations of autism are due to neural dysfunction that affect perceptual processing. An important function of perceptual systems is to provide the brain with accurate and meaningful internal representations of our external environment. Neural representations underlying our perception of events, and subsequent association of these events with appropriate affect, is necessary for higher-level cognitive functioning to occur. If the construction of internal representations based on complex perceptual information is compromised in autism, it is possible that subsequent social behaviors necessitating the recognition of internal representations may be affected and manifested by characteristic, "negative" autistic behaviors. Accordingly, the lack of involvement of young children with autism in reciprocal behavior implicating the visual modality, such as the production and decoding of pointing behaviors (Baron-Cohen, Jolliffe, Mortimore & Robertson, 1997), gaze following (Leekam, Hunnisett & Moore, 1998), and emotion and face recognition (Schultz et al., 2000) may originate from impaired perceptual information processing in autism.

5.5.3. Is the limitation in processing complex information specific to the visual domain?

Our suggestion of inefficient integrative functioning of the neural mechanisms mediating visuo-perceptual processing in autism is based on the assessment of a specific perceptual subsystem, namely, that which underlies visual motion perception. Consistent with this interpretation, a predisposition to local information processing has been shown for several other hierarchical tasks in autism in the visual domain (Jolliffe et al., 1997; Mottron, Belleville & Ménard, 1999; Ring et al., 1999; Rinehart et al., 2000). Therefore, it seems that the perception of different types of complex visual information (e.g., visuo-spatial, motion, etc.) is compromised in autism. However, locally-oriented information processing may also extend to hierarchical auditory information since it has been demonstrated that individuals with autism present an enhanced performance for processing elementary auditory stimuli (Mottron, Peretz & Ménard, 2000). It is therefore possible that individuals with autism use the same processing "strategy" when faced with complex information originating *within* each of the perceptual subsystems.

The construction of meaningful internal representations is contingent on the efficient integration of information originating from each perceptual subsystem. Unimpaired temporal lobe functioning would therefore be primordial in the construction of such representations, since the temporal lobe has the important role of integrating complex perceptual information between modalities (Gloor, 1997). Recent brain imaging findings demonstrating temporal lobe dysfunction in the form of hypometabolism (Zilbovicius et al., 2000) and neural rededication during face perception (Schultz et al., 2000; Critchley et al., 2000; Pierce et al., 2001), suggesting that the temporal lobe functioning in autism is abnormal. If this is the case, integrative processing *between* each perceptual subsystem may also be compromised during complex perceptual processing in that neural signals originating from each of the primary cortecies are not combined in an optimal manner. It is therefore possible that integrative mechanisms are less efficient both *within* a specific perceptual subsystem (i.e., as reflected by the present findings) as well as *between* subsystems in autism. This viewpoint is more ecologically viable since more than one perceptual attribute is involved in the construction of internal representations necessary for subsequent higher-order functioning (Faubert & Bellefeuille, 2002). Furthermore, anecdotal accounts of autism often describe a fragmented perception of the world which is not limited to one type of perceptual information but often implicates difficulties in integrating more than one type of perceptual attribute into a meaningful perception (Gerland, 1997).

5.6. Conclusion

The present study demonstrates that individuals with autism and normal intelligence process motion stimuli that require additional neural processing less efficiently than a comparison group, possibly due to less efficient integrative functioning of neural mechanisms at the perceptual level. In this context, we interpret the current findings not as a choice of a cognitive style which does not favor integrative information processing (Happé, 1999), but as a deficit that does not allow the autistic person to integrate information efficiently at a perceptual level and possibly at higher levels as well. Although this deficit may result in increased performance on tasks where local processing is advantageous (e.g., Frith, 1989; Mottron, Belleville & Ménard, 1999), the negative consequences of such a limitation may be manifested by the atypical cognitive performances in the visual modality in autism and more speculatively, by abnormal visually-related autistic behavior.

5.7. Methods

5.7.1. Participants

Twelve individuals with autism and normal intelligence (mean IQ = 100.8) were recruited from a specialized clinic for persons with autism. A diagnosis of autism was obtained using the algorithm of the Autism Diagnostic Interview (ADI) (Lord, Rutter & LeCouteur, 1994) combined with the Autistic Diagnostic Observation Schedule General (ADOS-G) (Lord et al., 1989), both of which were conducted by a trained researcher (LM) who obtained reliability on these instruments. All participants with autism had a score above the ADI / ADOS cut-off in the four areas relevant for diagnosis (social, communication, restricted interest and repetitive behaviors, and age of symptom onset). Twelve typically developing participants were recruited from the community as a comparison group. These were screened for a past or current history of psychiatric, neurological or other medical or and all had a typical academic background. The groups were matched as closely as possible in terms of laterality, gender and chronological age. The mean age of the control and autism groups was 13.13 and 12.18 years, respectively. All participants had normal or corrected-to-normal vision and were naive to the purpose of the study.

5.7.2. Apparatus

The stimulus presentation and data collection were controlled by a Power Macintosh 6100/66 microcomputer and presented on a 14-inch AppleVision color monitor refreshed at a rate of 67 cycles per second (Hz). The screen resolution was 640 x 480 pixels. The Pixx© graphics program controlled stimulus generation and animation. The luminance of the monitor was gamma-corrected to minimize the non-linearities in the display. Gamma-correction was implemented with a color calibration within the Pixx© graphics program. Calibration and luminance readings were taken using a Minolta CS-100 Chroma Meter colorimeter.

INSERT FIGURE 2 HERE

5.7.3. Stimuli

All motion stimuli were presented to subjects within a circular region at the center of the display that had a diameter of 5 deg when viewed from a distance of 114 cm. The mean luminance of the remainder of the display during testing was 20.03 cd/m^2 (u'= .1832, v'= .4608 in CIE (Commission Internationale de l'Eclairage) u' v' color space) where L_{min} and L_{max} were 0.07 & 40.01 cd/m^2, respectively.

The motion stimuli consisted of first- and second-order translating, radiating and rotating patterns. The first-order motion stimuli (**Fig. 2a**) were luminance-modulated noise patterns produced by adding static greyscale noise to modulating sinewaves of different profiles (e.g., a vertical sinusoid for translational motion, a radially symmetrical sinusoid for concentric motion and an angled sinusoid for rotational motion). The noise consisted of dots (1 pixel x 1 pixel, measuring approximately 2.235 arc min) with individual luminances randomly assigned as a function of sin (x), where (x) ranged from 0 to 2π. The contrast (luminance modulation depth) of the first-order patterns was varied to determine direction-identification thresholds by varying the amplitude of the modulating sinewave. The amplitude of the luminance modulation for the first-order patterns could be varied from 0.0 to 0.5 defined as:

$$\text{luminance modulation depth} = (L_{max} - L_{min}) / (L_{max} + L_{min})$$

where L_{max} and L_{min} refer to the average highest and lowest local luminances in the pattern. The first-order luminance modulation levels used in the constant stimuli presentations (0.04, 0.02, 0.01, 0.005, 0.0025 and 0.00125) were chosen based on pilot studies. The second-order stimuli (**Fig. 2b**) were texture-modulated noise patterns produced by multiplying rather than summing the same modulating sinewaves to the greyscale noise (Ledgeway & Smith, 1994). The depth of the texture modulation (contrast modulation depth) was also varied to find direction-identification thresholds by varying the amplitude of the modulating sinewave. The amplitude of the sinusoid therefore defined the contrast of the pattern and could be varied within a range of 0.0 and 1.0 defined as:

$$\text{contrast modulation depth} = (C_{max} - C_{min}) / (C_{max} + C_{min})$$

where C_{max} and C_{min} are the maximum and minimum local contrasts in the pattern. Second-order contrast modulation levels used during the constant stimuli procedures were 1.0, 0.333, 0.143, 0.111 and 0.059. For the translating and radiating patterns, the spatial and temporal frequency of the modulation was identical, at least for points along their horizontal radius. Their spatial and drift frequency were 1 cycle per degree (cpd) and 2 Hz, respectively. The angled modulation of the rotating pattern underwent eight cycles per 360 deg. Its angular velocity was $\pi/2$ rad per second.

5.7.4. Procedure

Participants were tested individually in a dimly lit room. In all conditions, they viewed the display binocularly from a distance of 114 cm, and their head movements were minimized using a chin rest. The stimuli were presented for 750 ms. To simplify responding instructions, the experimental session was comprised of three blocks, each of which defined by the type of motion stimuli presented (translational, radial or rotational). Therefore, only one motion type (e.g. translational) from both the first- and second-order motion class, was presented within each experimental block. Practice trials were completed before each block so that the participants could familiarize themselves with fixation, stimuli presentation and responding.

Procedural instructions were given verbally to each participant prior to each experimental block. Participants were required to identify the motion direction (e.g., left vs. right, expanding vs. contracting or clockwise vs. counterclockwise) of the stimuli by pressing one of two buttons on a keypad. During the experiment phase, the participants were reminded to fixate at the center of each pattern. The experimenter remained present throughout testing and initiated successive trials.

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5.10. Tables, Figures and Legends

Figure 1. Mean direction-identification thresholds expressed in terms of log motion sensitivity for first-order (a) and second-order (b) motion classes. Motion sensitivity was plotted as a function of motion type (translational, radial and rotational) for both autistic (white bars) and non-autistic (black bars) observers for each motion class. Standard error bars are included. If not shown, then the standard error is smaller than the symbols used to represent it for any given motion condition. The graphs for the first- and second-order motion classes are presented on different scales.

Figure 2. A schematic representation of the motion stimuli used in the present experiment. The upper panel (a) shows the luminance-defined or first-order translational, radial and rotational motion stimuli. The lower panel (b) shows the same types of contrast-defined or second-order stimuli.

Table 1. Mean direction-identification thresholds expressed in terms of log motion sensitivity (± SD) for each group and motion condition.

FIG 1. Bertone, Mottron, Jelenic & Faubert, 2003

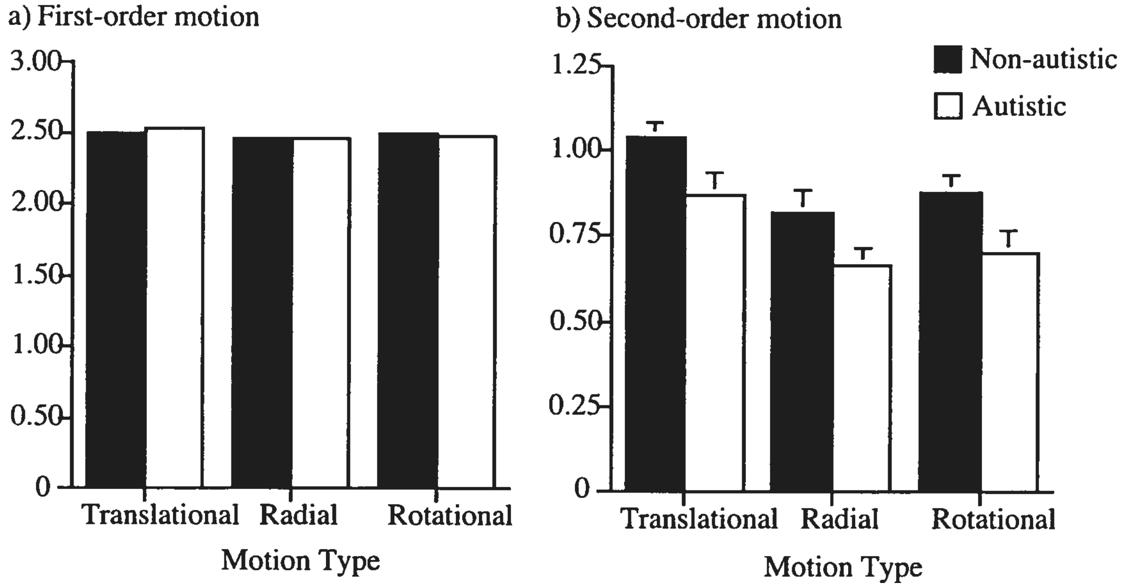

FIG. 2. Bertone, Mottron, Jelenic & Faubert

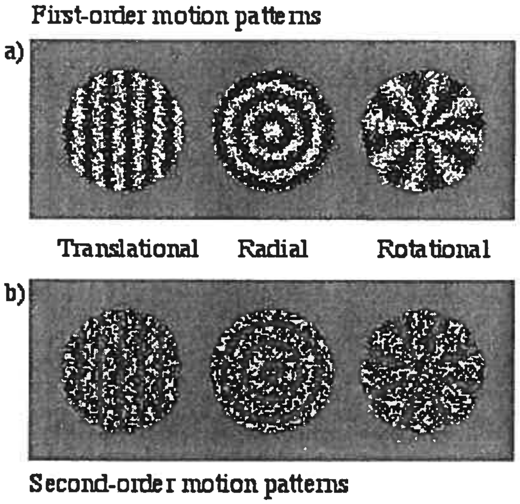

Table 1. Bertone, Mottron, Jelenic & Faubert

Motion Class	Translational	Radial	Rotational
	Motion Type		
First-order			
Autistic	2.527 (0.039)	2.457 (0.112)	2.483 (0.079)
Non-autistic	2.502 (0.104)	2.444 (0.097)	2.488 (0.053)
Second-order			
Autistic	0.873 (0.230)	0.632 (0.175)	0.708 (0.213)
Non-autistic	1.046 (0.139)	0.799 (0.224)	0.848 (0.153)

Chapter 6

Visuo-perceptual disturbances in autism, possible neurobiological origins and their relation to other conditions

Part of this chapter is an exact reproduction of two submitted invited commentaries to the Philips & Silverstein target article: Convergence of biological and psychological perspectives on cognitive coordination in schizophrenia. Behavioural and Brain Sciences, 26, 62-82.

6.1. Chapter overview

As previously suggested in section 5.5.2. entitled " Integrative inefficiencies in autism: Possible origin and behavioral manifestations?" of Bertone et al.'s study (2003), the possibility exists that characteristic autistic symptomology may be ultimately due to neural dysfunction affecting perceptual processing. Specifically, if internal representations of the external world are based on complex perceptual information processing, subsequent social behaviors requiring the recognition of such representations may be affected and manifested by autistic behaviors. These hypotheses are based on the suggestion that neural networks are abnormal in autism, as reflected by, among other things, the selective decrease in sensitivity to complex motion information. However, the nature of the abnormal neural dysfunction resulting in impaired perceptual information processing in autism remains elusive. As previously mentioned, different types of neural network models have been proposed and include abnormal neuronal oscillatory activity (Grice et al., 2001), hyperspecificity of neural representations (McClelland, 2000), excessive lateral synaptic inhibition (Gustafsson, 1997a & b) and abnormal amounts of neural connectivity (Cohen, 1994). More recently, additional theories have emerged that seem to be more closely associated with current neuro-cognitive theories of autism, such as the central coherence theory. A good example of this is the temporal binding deficit hypothesis, proposed by Brock et al. (2002). These researchers suggest that reduced integration in autism results form the limited growth of long-range connections in autism, caused by a reduction in synchronized gamma activity between local networks responsible for processing local perceptual features. Therefore, persons with autism will more often use a local approach during information processing, resulting in weak central coherence. Lamme (2003) proposes a similar hypothesis, suggesting that a disturbance in recurrent cortico-cortical interactions may underlie difficulties with integrating perceptual information into a global percept. The emergence of such neural network models of autism provide potential neural-based explanations for abnormal information processes and possibly, visually-related behaviour in autism.

Autism isn't the only condition that includes impaired visuo-perceptual integration, manifested at both experimental and symptomological levels. Schizophrenia is a complex syndrome that, like autism, presents a multitude of neuropsychological symptoms, including problems with perceptual organization that are manifested by an abnormal amount of focus on the details and elements of a visual scene. In their target *Behavioural and Brain Sciences* article, Phillips and Siverstein (2003) suggest that the perceptual abnormalities encountered by schizophrenic patients (e.g., abnormal performance on tasks requiring integrative visual analysis, anecdotal accounts of a perceptually fragmented world, etc.) are the result of impairments involving " cognitive coordination ", or the inability to coordinate the activity of local processing into a meaningful whole. Phillips and Silverstein (2003) suggest that NMDA-receptor dysfunction may be the fundamental neurobiological mechanism underlying and associating impaired holistic perception and cognitive coordination in schizophrenia. Given its theoretical similarity with the *weak central coherence account* of autism, is NMDA-receptor dysfunction the elusive neurobiological origin resulting in impaired perceptual information processing in autism? The following two invited commentaries attempt to address this question by comparing pertinent perceptual, behavioural, experimental and neuro-chemical hypothesis in autism, schizophrenia and aging.

6.1.A. Commentary A

[1]Bertone A, [2]Mottron L & [1]Faubert J. (2004). Autism and schizophrenia : similar perceptual consequence, different neurobiological etiology?
Behavioural and Brain Sciences **(in press)**

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6.A.2. Abstract

Phillips and Silverstein (P&S) propose that NMDA-receptor dysfunction may be the fundamental neurobiological mechanism underlying and associating impaired holistic perception and cognitive coordination with schizophrenic psychopathology. We discuss how the P & S hypothesis shares different aspects of the weak central coherence account of autism from both theoretical and experimental perspectives. Specifically, we believe that both persons with autism and schizophrenia do not integrate visuo-perceptual information efficiently, resulting in incongruous internal representations of their external world. However, although NMDA-hypofunction may be responsible for perceptual impairments in schizophrenia and possibly autism, we suggest that it is highly unlikely that NMDA-hypofunction is specifically responsible for the autistic behavioral symptomology, as described by P&S in their target article.

6.A.3. Commentary

Autism and schizophrenia are heterogeneous and complex neurobiological disorders defined by a continuum of subtypes that are differentiated by cognitive and behavioral manifestations. In line with the P&S statement that " [the] fragmentation of mental functions is the *prima facie* evidence of impaired cognitive function ", insight regarding the nature of cognitive dysfunction in these two conditions may be derived from an evaluation of visuo-perceptual capabilities necessitating different levels of neural information processing. The motive for such assessment and subsequent interpretation originates from the fact that persons affected by these disorders share a common perceptual manifestation, namely, impaired perceptual organization reflected by abnormal performance on tasks requiring Gestalt-like or holistic visual analysis. It is therefore not surprising that interest regarding perceptual processing in autism has increased significantly since the introduction of neurobehavioural theories suggesting that a portion of abnormal autistic cognition and behavior may explained in terms of the inefficient integration of visuo-perceptual information (i.e., Frith, 1989; Mottron & Belleville, 1993). Such theories share the notion that persons with autism do not integrate visuo-perceptual information efficiently into coherent percepts, characterized by a predominantly *local* approach to visual processing to the detriment of holistic information analysis. The *weak central coherence* (WCC) account of autism (Frith, 1989) is arguably the most flexible of these theories since it offers a theoretical framework describing inefficient integration of information at a different levels, including at a perceptual level, i.e, *perceptual coherence* (Happé, 1999). These theories encapsulate anecdotal accounts of a " fragmented visual world " described by persons with autism (i.e., Gerland, 1997; Gradin, 2000). Interestingly, accounts of " perceptual and apperceptual fragmentation " have also been described in schizophrenia (i.e, Arieti, 1966) which have preceeded experimental evidence of inefficient perceptual grouping in this disorder. Such impairments have been exemplified by demonstrations of impaired performance necessitating the integration or grouping complex static and dynamic visual information into meaningful percepts. As it has in autism, such evidence has lead to notions of " spatio-temporal disintegration " of visual perception (Isawa & Yamamoto,

2002) and anomalies regarding perceptual grouping schizophrenia (Place & Gilmore, 1980; Silverstein et al., 2000).

How then, can one evaluate the integrity of early or pre-attentive neuro-integrative mechanisms mediating perceptual grouping? One method is to investigate complex motion analysis capabilities of persons with autism and schizophrenia. Considered to be a form of dynamic grouping (Watt & Phillips, 2000), complex motion analysis exemplifies early neuro-integrative processing since local motion information must be integrated across space and time before a global or coherent motion direction can be discriminated. Results from recent psychophysical studies directly assessing complex motion analysis mediated by extra-striate motion-sensitive mechanisms (i.e., V2/V3, MT) have demonstrated a decreased sensitivity to complex motion in autism (i.e., Gepner, 2002; Spencer, et al., 2000; Milne et al., 2002; Bertone et al., 2003; Blake et al., 2003). Results from these studies have been by the most part interpreted as a dysfunction of the dorsal stream processing or as a localized neural impairment of motion-sensitive areas in autism (Gepner, 2002; Spencer, et al., 2000; Milne et al., 2002; Blake et al, 2003). In the only study investigating *both* simple and complex motion perception (Bertone et al., 2003), decreased sensitivity was evidenced for *only* complex motion types necessitating increased neural circuitry and integration to be resolved. For this reason, these findings were interpreted as a decreased capacity to integrate complex perceptual information rather than specific motion processing impairment per se (Bertone et al., 2003). The results from this study are very similar to those of Chen et al., (2003) who also demonstrated a decrease for complex, but not simple (or local) motion, in schizophrenia. Although the Chen et al. (2003) interpretation is more congruent with local neural dysfunction (i.e., dysfunction implicating motion-sensitive areas), they along with those of Bertone et al. (2003) provide clear evidence of impaired dynamic Gestalt organization in both schizophrenia and autism. As mentioned by P&S, these analogous results can be interpreted as exemplary evidence of impaired cognitive coordination, or analogously, weak central coherence, in either condition.

Persons with autism and schizophrenia therefore share the following perceptual consequences; predominant local analysis of visual information, inefficient neuro-integrative perceptual processing as well as anecdotal accounts of a " fragmented " perceptual world. The logically ensuing question is whether such common perceptual manifestations are the consequences of similar neurobiological etiology, specifically, NMDA-hypofunction? If one interprets inefficient complex motion analysis as manifestation of impaired cognitive coordination, then the tentative answer is yes. Since such analysis involves gestalt-like integration over time and space that is believed to be mediated by NMDA-receptor activity, it is possible that autism and schizophrenia share impaired analysis of complex information at a *perceptual* level due to NMDA-hypofunction. However, impaired complex motion analysis has been demonstrated and interpreted differently for a variety of conditions defined by different behavioral manifestations. Such conditions include normal aging (Habak & Faubert, 2000), dementia of the Alzheimer's type (Trick & Silverman, 1991; Gilmore et al. 1994), dyslexia (Cornelissen et al., 1998; Talcott et al., 2000) and Parkinson's disease (Trick et al., 1994). Therefore, a consistent association between perceptual dysfunction defined by impaired complex motion analysis and clinical symptomology is not evidenced.

P&S argument for associating NMDA-receptor hypofunction with perceptual, cognitive and behavioural manifestations in schizophrenia is based in part on the schizomimetic effects of NMDA-antgonists. Blocking NMDA-receptor channels in non-schizophrenic persons results in schizophrenia-like symptomology (referred to as PCP-psychosis), which according to P&S are congruous with symptoms of " cognitive disorganization " (Table 1 in Target article). Interestingly, Carlson (1998) has used a similar argument to explain autistic perceptual and behavioral symptomology, adding that like schizophrenia, abnormal glutamatergic interactions with other neurotransmitter systems (i.e., dopaminergic or serotonergic) may at least in part be responsible for the described autistic symptomology. Given the implication of NMDA-receptor activity in long-term potentiation (LTP), it can be argued that meaningful internal neural representations of their physical environment based on the efficient integration of perceptual information is compromised in both schizophrenia and autism. Consequently, appropriate behavior based on these representations would be abnormal and interpreted as being as part of the characteristic symptomology of either condition.

It can be argued that persons with autism and schizophrenia share (1) similar subjectively described and objectively measured manifestations of impaired Gestalt-like perception, probably the result of the inefficient integration of perceptual information, and (2) respective mimetic effects of NMDA-receptor antagonists. Given these similarities, can autism be considered to be a hypoglutamatergic disorder at a behavioral level if viewed within the context of P&S's working hypothesis? Probably the most important discrepancy between schizophrenia and autism regarding the possible implication of NMDA-hypofucntion in their respective psychopathology concerns the onset of clinical symptomology. Although both conditions are considered to be congenital, their clinical symptoms are initially evidenced at different ages : between adolescence and young adulthood in the case of schizophrenia and around the age of three for autism. Taking this into account, even if the perceptual consequences of both disorders implicate NMDA-hypofunction, the effects of these consequences on symptomology is less evident. For example, it can be argued that the nature of schizophrenic hallucinations and delusions, that are not typically manifested in autism, are based on previously constructed percepts that have some associated affective value. In most cases, persons with schizophrenia usually associate a predominantly adverse affect (i.e., terror or confusion) to their abnormal perceptual experience, much like what is experienced during a drug-induced psychosis. In the case of autism, it can be argued that such constructs are never fully developed and therefore, associations between perceptions and affects are never fully developed. Furthermore, persons with autism *grow up* with an abnormal perception of the world and therefore, although maladaptive, characteristic visually-related autistic behavior is usually void of negative affect (i.e., the pleasurable feeling experienced when fascinated with a specific part of an object). Therefore, one can argue that persons with schizophrenia and autism have different affective reactions to incongruent representations of their visual environment. Finally, one must take into account that at the onset of autistic symptomology, the neural development of the autistic perceptual system is incomplete (i.e., neural pruning) compared to that of persons with schizophrenia, making the behavioral link between NMDA-hypofunction and clinical manifestations in these two disorders that much more complicated. In conclusion, although the possibility that NMDA-hypofunction may underlie the *perceptual* consequence manifested in schizophrenia and autism, it is much less probable that NMDA-hypofunction is selectively responsible for *behavioral* symptomology, a general association made by P&S regarding schizophrenia.

6.A.4.References

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6.B.1. Commentary B

Faubert J. & Bertone A. (2004). A common link between
aging, schizophrenia and autism?
***Behavioural and Brain Sciences* (in press)**

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6.B.2. Abstract

Phillips and Silverstein (2003) propose that NMDA-receptor hypofunction is the central reason for impaired cognitive coordination and abnormal Gestalt-like perceptual processing in schizophrenia. We suggest that this model may also be applicable to non-pathological (or normal) aging given the compelling evidence of NMDA-receptor involvement during the aging process that results in age-related change in higher-level perceptual performance. Given that such deficits are present in other neurological disorders such as autism, an argument for a systematic assessment of perceptual functioning in these conditions may be posited.

6.B.3. Commentary

Phillips and Silverstein (P&S) propose that there are reduced numbers of NMDA-receptors in schizophrenia that results in abnormal Gestalt-like perceptual grouping. Fundamental to their argument is the implication of NMDA-receptor activity in long-term potentiation (LTP) which allows local events to be integrated into more global (or higher-level) perceptual constructs. As is the case for schizophrenia, there is abounding evidence of reduced LTP caused by NMDA-receptor dysfunction in the non-pathological (or normal) aging process that is accompanied by a decline in cognitive functioning (i.e., Wenk et al., 1991; Gazzaley et al., 1996; see Segovia et al. (2001) and Rosenzweig & Barnes (2003) for reviews). We suggest that there exists a parallel and selective decline in higher-level perceptual information processing in normal aging, supporting P&S's notion that NMDA-receptor activity is involved in perceptual organization. This suggestion is based on results from a series of recent studies demonstrating that the normal aging process has a much greater impact on mid- to high-level perceptual functioning which requires increased neural integration, than on lower-level perceptual processes (Faubert, 2002). As will be discussed, the differential efficacy of low and higher-level perceptual processing may also have consequences within certain types of cognitive functioning in aging, such as performance on visual working memory tasks.

As eluded by P&S, perception is not a monolithic process as it involves context integration and complexity constructs based on an infinite number of neural events. A series of recent studies have examined this exact process in normally aging observers in a number of visual modalities including motion and orientation (Habak & Faubert, 2000), texture (Herbert, Overbury, Singh & Faubert, 2002) and form perception (Faubert & Bellefeuille, 2002; Sara & Faubert, 2000). Findings from these studies have demonstrated that as the amount of neural processing required to generate complex perceptual constructs increases, so does age-related loss in performance (Faubert, 2002). The goal of the following commentary is to bring to light the similarities between normal aging and schizophrenia regarding inefficient higher-level integrative or Gestalt-like perception. In addition, we propose that P&S's hypothesis implicating NMDA-receptor hypofunctioning in abnormal higher-level perception in schizophrenia may also be applicable to normal aging given the comparable evidence of increasing NMDA-receptor dysfunction during the aging process.

Perceptual complexity can be exemplified by the differential amount of neural integration needed to resolve first- and second-order visual information (Cavanagh & Mather, 1989), the latter of which necessitates the activity of larger neural networks to be perceived (i.e., Wilson et al., 1992; Nishida et al., 1997; Chubb et al., 2001; Bertone & Faubert, 2003). Habak and Faubert (2000) demonstrated a larger age-related increase in motion and orientation discrimination thresholds when the stimuli were defined by second-order attributes (i.e., texture). These results suggest that the age-related loss in performance is due to perceptual complexity of the second-order information and not specific for visual attribute (i.e., motion or orientation). Since second-order image resolution implicates additional neural processing regardless of the type of information, it can be argued that decreased NMDA-mediated LTP may be the neurobiological mechanism responsible for the decrease in perceptual performance.

Gestalt-like perceptual grouping, as described by P&S, is exemplified by symmetry perception since it involves the spatial organization (i.e., symmetrically) of local stimulus elements (i.e., dots) into meaningful percepts. Therefore, perceiving symmetry involves the integration of local elements across the putative axis. Given the evidence of NMDA-receptor hypofunction in aging, we would expect an age-related loss in this type of spatial grouping task. In effect, a clear age-related deficit regarding the detection of bilateral symmetry detection has been demonstrated (Herbert, Overbury, Singh & Faubert, 2002).

The P&S NMDA-perception hypothesis predicts that long-range perceptual processes are affected in normal aging since NMDA depletion results in reduced LTP. Therefore, task performance based on the processing of information within a specific image attribute would be less affected by aging when compared to performance necessitating the processing and integration of information from two separate image attributes. A recent study by Faubert and Bellefeuille (2002) demonstrated that spatial frequency discriminations performed within an attribute condition (e.g. luminance vs. luminance or color vs. color) is less affected by age compared to intra-attribute discriminations (e.g. luminance vs. color) when compared with younger observers. Similar age-related deficits in long-range processing has been demonstrated for tasks necessitating the simultaneous integration of information within a large spatial area prior to efficient perceptual decision making (i.e., size discrimination) compared to when the information is presented in sequence (temporal forced choice in same location) (Sara & Faubert, 2000). Taken together, these findings suggest a selective age-related loss for tasks soliciting long range perceptual processing, as it has been proposed in schizophrenia by P&S. Again, these age-related decreases in performance are compatible with abnormal LTP.

As mentioned, the differential efficacy of low and higher-level perceptual functioning in aging may also have consequences when assessing performance on visual working memory tasks (Faubert, 2002). Recent studies have clearly demonstrated that normal aging has little effect on the capacity to retain either spatial frequency or size information defined by low-level perceptual information (Faubert & Bellefeuille, 2002; Sara & Faubert, 2000). This has lead Faubert (2002) to conclude that both perception and visual working memory are affected in similar ways during aging in that low-level information that does not require long-range processing (or complex networks as termed by Faubert) are minimally affected. However, perceptual or working memory processes that require more sophisticated neural network structures will show age-related decline. Faubert (2002) suggested that this is the result of the Simultaneous Access Network Deficit hypothesis (SAND) of aging, which as it appears to us, is comparable to the NMDA-perception hypothesis offered by P&S in both a functional and possibly, a neurobiological perspective.

In conclusion, we believe that there is comparable evidence of the impaired Gestalt-like visuo-perceptual grouping and accompanying neurobiological mechanism proposed by P&S in the normal aging process than in schizophrenia or possibly, other neurological disorders such as autism (please read commentary by Bertone, Mottron & Faubert). This suggestion is based on the fact that NMDA hypofunction and its relation to cognitive deficits appear to be relatively more elaborated and specific to the aging literature, particularly with respect to currently available animal and human models demonstrating reversibility of some age-related effects (i.e., Baxter et al., 1994; Held et al., 2002). Furthermore, if impaired cognitive coordination, as reflected by abnormal gestalt-like perceptual performance, is the consequence of reduced glutamatergic neurotransmission, then the aging model is more suitable for unidirectional hypotheses testing since glutaminergic NMDA receptor density decreases progressively with age. If NMDA hypofunction and gestalt-like information processing are functionally related, then one could not only predict a decline in higher-level perceptual information processing with increasing age, but also the rate with which such a decline in performance would occur (i.e., Trick & Silverman, 1991). These suggestions do not in any way detract from the proposal posited by P&S implicating NMDA hypofunction to abnormal holistic perceptual processing in schizophrenia. It simply states that if a link does exist between NMDA hypofunction, perceptual organization and higher-order cognitive processing, non-pathological aging seems to be just as compatible a neuro-behavioural model for the P&S hypothesis than does schizophrenia.

6.B.4. References

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Chapter 7
General discussion

7.1. Chapter overview

The idea that visuo-perceptual dysfunction may underlie abnormal behaviour in autism and other conditions (e.g., schizophrenia) has resulted in an increased use of applied psychophysical studies investigating perceptual information processing in these populations. The present thesis is exemplary of such and approach; a motion paradigm using stimuli processed differently by neural mechanisms (Bertone & Faubert, 2003) used to assess and infer how visuo-perceptual information is analyzed by persons with autism (Bertone et al., 2003). Probably the most common and enticing method of evaluating visuo-perceptual functioning in different patient populations has been the " global motion approach ". Reasons for the popularity of this approach are numerous and included the fact that global motion perception reflects early neuro-integrative processing and that this performance is mediated by specialized extra-striate moiton-sensitive areas (e.g., area MT), exemplifying of the dorsal visual stream functioning. Inferences can therefore be made concerning the integrity of the neural mechanisms mediating complex motion processing and neuro-integrative processing in general based on the participant's ability to perceive coherent motion at a specific level of coherence.

Because the neural mechanisms underlying global motion perception operating in MT represent both 1 - complex motion information processing dependant on efficient neuro-integrative processing, and 2 – dorsal stream functioning given the fact that motion-sensitive areas operate within the dorsal visual stream, decreased global motion sensitivity in autism can be interpreted in two different ways. The first possible interpretation is that persons with autism integrate complex motion information less efficiently than do persons without autism, suggesting *inefficient integration* at a perceptual level in autism. The second interpretation suggests a *specific dorsal pathway stream deficiency* in autism since motion-sensitive areas underlying decreased autistic performance operate within this visual pathway. Based on our results demonstrating a *selective* decrease in sensitivity for second-order motion (and not first-order motion), we suggest that the former of these interpretations is best (Bertone et al., 2003). Nevertheless, most studies demonstrating decreased global motion sensitivity in autism interpret their results in terms of dorsal stream dysfunction (Spencer et al., 2000; Milne et al., 2002; Blake et al., 2003). The following discussion is an attempt to demonstrate that such interpretations are derived from a suspect methodology, unable to dissociate a *pathway specific* from a *complexity specific* account of visuo-perceptual processing in autism.

7.2. Is there a dorsal visual stream deficit in autism?

Current neurobehavioural theories suggest that persons with autism do not integrate visuoperceptual information efficiently, using a *local* analysis approach to the detriment of holistic visual information processing (e.g., Frith, 1989; Mottron & Belleville, 1993; Teunisse, 2001). These theories have been used to interpret findings of both enhanced and inferior autistic performance on a variety of visual tasks, depending on the most advantageous approach (e.g., Shah & Frith, 1983; Shah & Frith, 1993; Joliffe & Baron-Cohen, 1997; Mottron et al., 1999; O'Riordan et al., 2001). The *weak central coherence* (WCC) theory of autism (Frith, 1989) is arguably the most flexible of these theories since it offers a theoretical framework describing inefficient integration of information at a different levels, including at a perceptual level, e.g, *perceptual coherence* (Happé, 1999).

The visual motion pathway is probably the best defined of all perceptual pathways in terms of its functional hierarchy and specialized analysis since much is known about its successive processing stages, characterized by increasingly complex neural mechanisms able to integrate increasingly elaborate types of motion (Zeki, 1994). It is therefore not surprising that the visual motion pathway has been the recent model of choice used to assess and interpret results regarding perceptual information processing in autism, particularly within the theoretical framework of the aforementioned theories describing inefficient integration of perceptual information (Gepner et al., 1995; Gepner, 1999; Castelli et al., 2000; Spencer et al., 2000; Gepner et al., 2001; Castelli et al., 2002; Gepner & Mestre, 2002a, 2002b; Milne et al., 2002; Bertone et al., 2003; Blake et al., 2003). Results from several recent psychophysical studies directly assessing *complex* motion analysis mediated by extra-striate motion-sensitive mechanisms have demonstrated decreased sensitivity to such complex stimuli (e.g., Gepner, 2002; Spencer et al., 2000; Milne et al., 2002; Bertone et al., 2003; Blake et al, 2003). Although founded on the assessment of a singular perceptual attribute (e.g., motion), these results support the WCC at a perceptual level when considered within a more general information processing context, possibly reflecting less efficient integrative mechanisms operating at the visuo-perceptual level in autism (Bertone et al., 2003).

Some authors have presented an alternative interpretation of the findings regarding decreased complex motion perception in autism based on the parallel nature of human visual information processing. Specifically, the motion-sensitive areas demonstrated to mediate the different types of complex motion stimuli used in the aforementioned studies (e.g., areas V2 / V3, the medial temporal (MT) area, the medial superior temporal (MST) and areas located proximal to the superior temporal sulcus (STS)) all operated within the dorsal visual pathway (Ungerleider & Mishkin, 1982; Merigan, Byrne & Maunsell, 1991; Merigan & Maunsell, 1993; Goodale & Milner, 1992; Milner & Goodale, 1995). Therefore, inferior autistic performance on complex motion tasks and on related behaviors may reflect a specific decrease of dorsal pathway functioning (e.g., Spencer et al., 2000; Gepner et al., 2001; Milne et al., 2002: Blake et al., 2003). The finding of decreased complex motion analysis in autism may consequently be interpreted in two different manners. The first plausible interpretation is that persons with autism integrate complex motion information less efficiently than do persons without autism, suggesting *inefficient integration* at a perceptual level in autism. The second interpretation suggests a *specific dorsal pathway stream deficiency* in autism since motion-sensitive areas underlying decreased autistic performance operate within this visual pathway. It is our opinion that the former of these interpretations is most consistent with the available results (Bertone et al., 2003). Regarding the latter hypothesis, we question whether evidence of decreased complex motion sensitivity is enough to suggest a dorsal visual stream deficiency in autism for the following reasons.

1. Although, the possibility that decreased sensitivity to complex motion may be the result of a less efficient dorsal stream functioning in autism, we have demonstrated that the perception of simple motion (e.g., first-order motion) also processed by the dorsal stream, is not affected in autism (Bertone et al., 2003). For this reason, we believe that decreased complex motion sensitivity in autism is more likely to be the result of diffuse or non-specific neural dysfunction of neuro-integrative mechanisms affecting complex

perceptual processing in general, and not the result of a dorsal stream dysfunction selectively affecting motion-sensitive areas responsible for complex motion perception per se.

2. In addition to results demonstrating decreased dorsal stream-mediated complex motion sensitivity in autism, studies have shown that ventral stream processing, measured by performance on complex form tasks, is intact in autism (Spencer et al., 2000; Blake et al., 2003). These authors have interpreted these results as corroborative evidence for a selective dorsal stream deficiency in autism. However, we argue that these complex spatial tasks used to demonstrate intact ventral stream processing may not access or necessitate the same level of neuro-integrative processing along the ventral pathway as the complex motion tasks do in the dorsal pathway. In this context, we suggest that although the complex motion and form tasks selectively assess dorsal and ventral stream processing respectively, they do not in effect assess functioning in either stream at the same level of neural complexity.

Support for the two aforementioned reasons against a selective dorsal visual stream deficiency in autism will be presented in the next sections.

7.3. Does decreased sensitivity to complex motion necessarily reflect a dorsal stream deficit in autism?

Psychophysical and electrophysiological studies have distinguished between local or simple motion processing – the sensitivity to the direction in a small region of the visual image, and global or complex motion processing, that allows for the discrimination of motion direction over extended regions of the visual scene that necessitates the integration of local motion signals into a coherent whole. The latter is usually identified with the integrative properties of MT neurons, while the former reflects the processing of motion detectors found in the primary visual cortex (Newsome & Paré, 1988). The stimuli of choice for investigating complex motion perception are referred to as random-dot patterns (or random-dot kinematograms (RDKs)). In such pattern, a proportion of dots move coherently in a certain direction while the remaining dots move in random directions. Considered to be a form of dynamic grouping (Watt & Phillips, 2000), global motion processing exemplifies early neuro-integrative processing since local motion information must be integrated across space and time before a global or coherent motion direction can be discriminated; the processing of individual or local dots cannot reveal the overall or global motion direction.

Given its acceptance as the prototypical complex visual stimuli and included as part of extra-striate dorsal visual stream functioning (e.g., area MT) (Newsome & Paré, 1988; Britten et al., 1992), it is not surprising that global motion processing has been evaluated in a number of different neurological conditions for various reasons. In addition to autism (Spencer et al, 2000; Milne et al, 2002), global motion perception has been evaluated in conditions including non-pathological aging (Trick et al, 1991), multiple sclerosis (Regan, 1991) mild cognitive impairment (Mapstone et al., 2003), Parkinson's disease (Trick et al, 1994), dementia of the Alzheimer's type (Gilmore et al., 1994), developmental dyslexia (Cornelissen, 1995; 1998), William's syndrome (Atkinson et al., 1997) and schizophrenia (Chen et al., 2003). Because global motion is mediated by visual area MT, considered to be an integral part of the magnocellular or dorsal visual stream, decreased sensitivity to global motion may be interpreted as the result of either dorsal stream dysfunction or of a selective deficit of motion-sensitive visual areas. Motivated by this " region of interest " approach, such an interpretation has been forwarded for a number of conditions demonstrating decreased sensitivity to global motion including multiple sclerosis (Regan, 1991), dementia of the Alzheimer's type (Gilmore et al., 1994), developmental dyslexia (Cornelissen, 1995; 1998), William's syndrome (Atkinson et al., 1997) and schizophrenia (Chen, 2003), and of course, autism (Spencer et al., 2000; Milne et al., 2002). On the other hand, given the fact that global motion is processed in the extra-striate region and has been shown to be a complex visual stimulus necessitating neuro-integrative processing, other researchers have interpreted decreased sensitivity to global motion as the result of diffuse degeneration of neural integrity affecting visuo-cortical areas. Such interpretations have been forwarded in the normal aging literature (Trick, 1991), for Parkinson's disease (Trick et al., 1994), as well as for mild cognitive impairment (Mapstone et al., 2003). So which is the correct one; the *pathway specific* or the *complexity specific* interpretation?

The initial hypothesis regarding which interpretation to adopt often depends on several factors including the current state of debate on the condition (e.g., is developmental dyslexia caused by deficient magnocellular functioning), anecdotal accounts of perceptual experiences (e.g., autistic and schizophrenic patient's describing their world as being fragmented), and the nature of the condition (e.g., developmental, degenerative, etc.). Nevertheless, the majority of studies demonstrating decreased global motion sensitivity, including those regarding autism, have opted for the *pathway specific* interpretation. For example, Braddick et al. (2003) argue that the visual processing of persons suffering from a range of developmental disorders (including William's syndrome and autism) is characterized by " dorsal-stream vulnerability " because the global motion sensitivity of these patients is decreased. Although it is *possible* that all the aforementioned conditions share a dorsal stream deficiency, it is in our opinion rather *unlikely* that this is indeed the case. The first reason for this is because when viewed as a whole, the populations assessed using a global motion task represent a very heterogeneous group that differ in many respects, including etiology, prevalence, behavioural manifestations, diagnostic features, onset and course. If a dorsal stream dysfunction is indeed common to all the aforementioned conditions, one would expect other common dorsal-functioning related features in addition to reduced sensitivity to global motion. Until now, this has not been demonstrated. On the other hand, despite their heterogeneity, these conditions are similar in that they share some form of neural abnormality or dysfunction (e.g., cortical atrophy, decreased temporal processing, etc.). Therefore, it is feasible that the neural networks implicated in complex dynamic information processing are less efficient in these conditions, possibly reflected by decreased sensitivity to global motion stimuli, that seem very sensitive for measuring neural dysfunction. The second and more important reason why it is difficult to accept that these conditions, including autism, are defined by a dorsal stream dysfunction has to do with the methodology used to derive their interpretations. The results and interpretation of Milne et al. (2002) will be used as a template to develop the following argument; a dorsal stream dysfunction cannot be confirmed, and therefore a complexity hypothesis rejected, unless at least two levels of motion processing (e.g., simple and complex) are evaluated along the dorsal visual pathway.

The purpose of Milne et al. (2002) study was twofold. The first purpose of the study was to evaluate global motion processing in a group of high-functioning autistic patients using an RDK motion stimulus. These authors suggested that an elevated motion-coherence threshold would indicate impairment in the magnocellular pathway functioning in autism, and/or areas within the visual system that receive input from the magnocellular system (e.g., the dorsal stream). Secondly, increased motion-coherence thresholds for the autistic group would also support the notion of weak central coherence at a perceptual level (or weak perpetual coherence; see Happé, 1999) since efficient global motion perception necessitates the integrative processing of dynamic information as a whole rather than analysis biased towards local information processing. Milne et al., (2002) found that the group of children with autism demonstrated significantly higher motion coherence thresholds when compared to typically developing children. They interpreted their results as evidence for both a magnocellular impairment in autism and evidence for weak central coherence for low-level visual processing. As shown in Figure 1, the motion coherence task used by Milne et al., (2002) evaluated dorsal stream functioning at extra-striate levels, referred to as a complex level of processing since performance is dependent of efficient integrative analysis of local motion signals to discriminate the overall direction of the global motion stimulus. Although the suggestions of Milne et al., (2002) are consistent with their results, the alternative 'complexity specific' interpretation cannot be ruled out because " simple " dorsal stream-mediated motion processing was not evaluated. In order to confirm a magnocellular / dorsal stream deficiency in autism, magnocellular / dorsal stream functioning at different levels along the pathway must be evaluated and shown to be deficient at all levels. It is our opinion that although complex motion stimuli, such as

Complexity

		simple	complex
Pathway	ventral		?
	dorsal	?	✓

Figure 1. A schematic representation of the research design and stimulus used by Milne et al. (2002). As shown, it is not possible dissociate whether the decreased global motion sensitivity is pathway- or complexity-specific since only one level of complexity is assessed along the dorsal visual stream.

global motion (Spencer et al., 2000; Milne et al., 2002), second-order motion (Bertone et al., 2003) and biological motion (Blake et al., 2003) stimuli are sensitive enough to assess even subtle neural deficits and isolate dorsal stream function, they cannot be used to dissociate a *pathway specific* from a *complexity specific* account of visuo-perceptual processing in autism if used in isolation, without complementary motion stimuli assessing dorsal stream functioning at other levels (e.g., striate mechanisms mediating simple motion). Until now, only one study has demonstrated that complex dorsal stream functioning is *selectively* affected in autism (Bertone et al., 2003). For this reason, we suggest that at the present, the *complexity specific* interpretation is the most congruent with available data evaluating complex dynamic information processing in autism.

7.4. Are " complex " dorsal and ventral visual tasks used to evaluate visual stream functioning in autism studies comparable?

As mentioned at the beginning of the chapter, global or complex motion processing is exemplary of dynamic grouping (Watt & Phillips, 2000), a perceptual processes involving the integration of local motion signals before a global motion can be discriminated over an extended region of the visual field. Another necessary aspect of visual grouping involves the process of identifying complex stationary structures in our visual environment by integrating and associating local *static* features with one another in order to recognize complex static images. This process is referred to as global form processing, a visual process associated with extra-striate ventral stream functioning (Zeki, 1994). Different forms of global form processing, demonstrated to possibly be mediated by area V4 (Gallant et al., 1993, 1996), are often compared and contrasted to global motion processing since either type of grouping is believed to selectively reflect extrastriate functioning in either visual stream by specialized visual areas (e.g., MT / dorsal / global motion versus V4 / ventral / global form) (e.g., Braddick et al., 2003). Tasks and stimuli that have been developed and used to assess complex form perception are generally based on the same premise as those assessing complex motion perception. Generally, such ventral-stream tasks consist of detecting or locating a target static region (e.g., concentrically aligned local line segments (or dots)) within a field of randomly oriented line segments. As is the case for global motion stimuli, the percentage of randomly aligned segments within the circle region can be varied to determine a signal-to-noise ratio, or form coherence threshold. In order to extract a global form percept, local form information must be integrated across space before a global form can be detected or located; the processing of individual or local line segments cannot yield the overall or global form of the stimuli. Although these type of stimuli have been used to evaluate complex form processing in autism and other conditions, we question whether they are the most appropriate for evaluating dorsal and ventral functioning in terms of their relative complexity.

7.4.1. The where argument

The complex spatial tasks used to demonstrate intact ventral stream processing in autism (e.g., Spencer et al., 2000; Blake et al., 2003), other developmental conditions such as William's syndrome (e.g., Atkinson et al., 1997) and typically-developing children (Kovacs et al., 1999) have used different variations of the " pathfinder " task. Initially introduced by Field et al. (1993) to evaluate how the visual system integrates local contour information along the length of a path, the task consists of identifying several locally-oriented elements (Gabor patches) aligned along a path that are embedded in an array of randomly oriented elements. Among other manipulations, the authors investigated the effect of the relative orientation between the successive local-path elements on the observers' ability to detect a path. They found that the most important stimulus property affecting path detection was the relative alignment between the locally-oriented elements (e.g., the observers' ability to detect the path is significantly affected if the relative difference in orientation between successive locally elements exceeds 30 deg). Based on this finding, Field et al. (1993) suggest that path segregation is better explained in terms of an " association field " which groups features based primarily on local processing, attributable to neural interconnections among orientation-selective neurons at early stages of visual processing within V1, rather than global grouping rules, as is the case for complex motion perception (e.g., Britten et al., 1993).

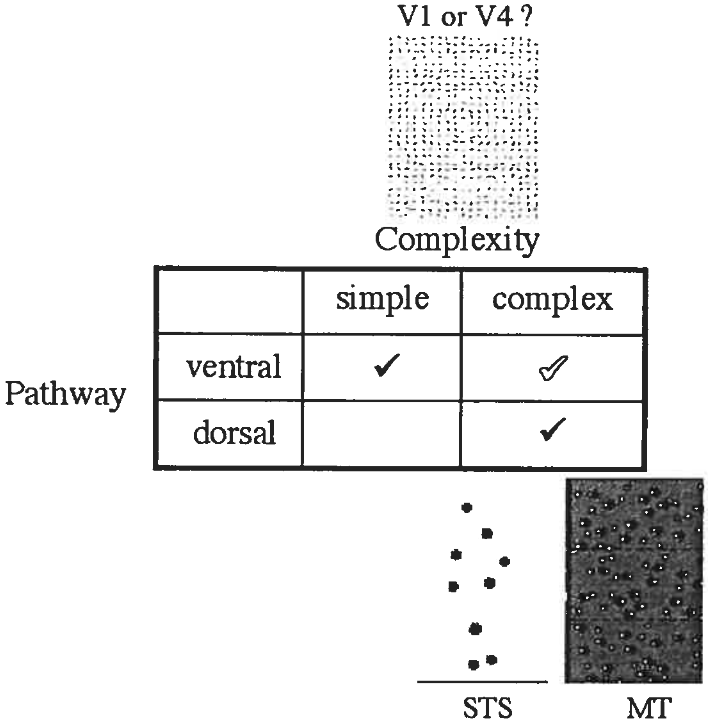
The two studies that have evaluated ventral stream functioning in autism (e.g., Spencer et al., 2000; Blake et al., 2003) have used modified versions of the pathfinder task in that the path of the stimuli was closed (e.g., circular) instead of opened (e.g., a curved path). In both these studies, observers were presented with an array of line segments, a proportion of which were tangentially oriented to lie on a concentric circle while the orientation of the others varied randomly. The proportion of these lines comprising the circle defined the form coherence threshold. In both studies, the results showed that global form processing, measured by these tasks, did not significantly differ between the autism and control groups. However, complex motion perception, measured by using either global motion stimuli (Spencer et al., 2000) or biological motion stimuli (Blake et al., 2003) was significantly reduced for the autistic participants. In both cases, the authors interpreted their results as evidence for a selective dorsal stream deficit in autism since global and biological motion are believed to be processed in extra-striate areas MT and areas near STS (superior temporal sulcus), respectively, both operating within the dorsal visual stream. In order for this interpretation to be correct, we argue that the tasks used to evaluate dorsal and ventral stream functioning must be underlied by the same amount of neuro-integrative processing, referred to in this thesis as " complexity ". If the complex spatial tasks used to demonstrate intact ventral stream processing do not access or necessitate the same level of neuro-integrative processing along the ventral pathway as the complex motion tasks do along the dorsal pathway, it is difficult to dissociate a *pathway specific* form a *complexity specific* dysfunction. This argument is based on the suggestion that the complex form tasks used in these studies may not be as complex as their dynamic counterparts and therefore, do not in effect assess functioning in either stream at the same level of neural complexity. This statement is based on the following observation; the pathfinder stimulus may be processed within the striate cortex.

In their paper, Field et al., (1993) speculate that path detection is mediated by interactions between multiple orientation-selective mechanisms operating locally within V1, where path segregation is based on local processes that group features locally (e.g., an association-field). This notion implies that path detection is probably not mediated by a single mechanism that integrates over local orientations of a certain global configuration as other extra-striate mechanisms are believed to operate (e.g., specialized motion mechanisms in MSTd). Although Field et al., (1993) speculate that the " association field " may represent a grouping model used by higher-level visual mechanisms, they do not suggest where this takes place. The mechanisms involved in the neuro-integrative processing of static spatial information were elucidated by Kovács & Julesz (1993). They found that when the locally-oriented elements comprising the path were in the form of a circle (e.g., closed paths or contours), the detection of the closed paths was much more efficient than those of the unclosed paths, even when both paths had the same length and average curvature. Basically, Kovács & Julesz (1993) found that the efficiency of the integration between the locally-oriented elements making up the closed path was increased by the global circular structure of its local elements. They suggested that although local integration within V1 is necessarily implicated in detecting the closed paths, " intermediate levels " of form analysis extracting the global shape of the contours is also probably involved (Kovács et al., 1999). This proposal has been recently supported by Achtman et al., (2003) who argue that a circular array of local Gabor elements is detected by a global process since sensitivity to these arrays was unaffected when various array (e.g., density) and element parameters (e.g., contrast, polarity) were changed; only the relative orientation (jitter) of the local elements affected performance. Electrophysiological (Gallant et al., 1993; 1996) medical imaging (Wilkinson et al., 2000) and neural modeling (Wilson et al., 1997; Wilson et al., 1998) data are consistent with the suggestion that mechanisms specialized for processing complex circular form operate in extra-striate area V4.

The question of *where* and *how* locally-oriented elements comprising a circular path is analyzed is important with respect to the interpretations of researchers using such stimuli to champion intact ventral stream and deficient dorsal stream processing in autism (e.g., Spencer et al., 2000; Blake et al., 2003). Figure 2 shows the stimuli used to evaluate ventral and dorsal stream functioning in these studies. Both Spencer et al., (2000) and Blake et al., (2003) used circular versions of the pathfinder task to assess ventral stream processing in autism. As mentioned, it is unclear if integrative mechanisms responsible for the perception of these stimuli operate within V1 (by integrating between the locally-oriented mechanisms) or V4 (by specialized analysis extracting the global shape of the contours). Nevertheless, Blake and his colleagues seem to suggest that these stimuli are processed within V1 since they explain in their paper :

> " *... the integration of contour information responsible for perception of targets in these pathfinder displays task is attributable to neural interconnections among orientation-selective neurons at early stages of visual processing (Field et al., 1993). ... given this interpretation, our results could be interpreted to mean that compromised neurophysiological function in autism spares the primary visual cortex, at least in terms of its integrative integrity.* "

This interpretation is an exemplary consequence of the stimulus-based methodological limitations that we suggest: the possibility that the circular pathfinder stimuli are processed in V1 while the complex biological motion stimuli cannot be processed in V1 (probably processed in area STS) make it difficult to dissociate a *pathway specific* from a the *complexity specific* account of visuo-perceptual processing in autism. As depicted in Figure 3, we suggest that although the complex motion and form tasks selectively assess dorsal and ventral stream processing respectively, they do not in effect assess functioning in either stream at the same level of neural complexity. The fact that Blake et al. (2003) suggest that V1 functioning is spared in autism (for ventrally mediated information) makes the case for a *complexity specific* hypothesis that much more appealing. In fact, if the circular pathfinder stimuli are indeed processed within V1, then we can interpret Blake et al. (2003) findings as evidence for a *complexity specific* deficiency since the more neuro-integrative processing in needed to perceive a stimulus, the more autistic children are less sensitive to it, regardless of which pathway is responsible for its analysis. This same argument is posited for the Spencer et al., (2000) study that used global motion stimuli, processed by extra-striate mechanisms operating beyond the primary visual cortex, in area MT.



	simple	complex
ventral	✔	✓
dorsal		✔

Figure 2. The complex form and motion stimuli used by Spencer et al., (2000) and Blake et al. (2003) to assess ventral and dorsal stream functioning in autism. The filled checks represent the level of complexity (striate vs extra-striate) at which the authors believe their stimuli is being processed; the white checks represent alternative levels of complexity.

In addition, Braddick et al. (2000) demonstrated that the same form and motion coherence stimuli used by Spencer et al. (2000) activate independent but not dorsal / ventral segregated networks in the human brain. There results further emphasize the *where* argument and demonstrate that the precise role of human area V4 with regards to the analysis of global form is unresolved.

7.4.2. The how argument

The argument presented in the previous section discussed *where* complex static information is processed along the ventral visual pathway under the assumption that extra-striate processing necessarily implicates increased level of neuro-integrative processing. However, this isn't always necessarily the case. For this reason, it is also important to consider *how* complex static information is integrated by the visual system. The pathfinder stimulus (Field et al., 1993) will be used for explaining the distinction between *where* and *how* complex static information is integrated and how the nature of such integration can affect performance on global form tasks for persons with and without autism.

As already mentioned, when path elements are arranged in an opened array configuration (non-circular), the integration of local elements can be attributed to local interconnections among orientation-selective neurons operating within the primary visual cortex, and not by extra-striate grouping mechanisms specialized for processing paths of different forms (Field et al., 1993). It can therefore be argued that opened contour paths may be mediated by the sequential integration within V1 of individual locally-oriented elements before they can be detected. Kovacs & Julesz (1993) demonstrated that path detection was much more efficient when the same locally-oriented elements, differing only in their relative orientations, were presented in a circular configuration. Based on their finding, they suggested that the only stimulus factor contributing to increased detection performance for the circular path task was the global configuration of the stimulus (Kovacs et al., 1999). They explain their increase in performance by the contribution of specialized higher-level operations, in addition to integrative processing within V1 for the circular path elements (see Achtman et al., 2003). Therefore, the configuration of the local static elements characterizing the form stimuli used to evaluate ventral stream processing in autism is important with regards to; 1 - *how* they are processed (e.g., sequential or specialized integration) and consequently, 2 - on how efficiently they are detected (e.g., sensitivity relative to opened configurations).

In addition to circular versions of the pathfinder stimuli, psychophysical evidence for specialized complex from processing has for the most part been demonstrated using Glass patterns (Glass, 1969; Glass & Pérez, 1973). Considered to be ideal stimuli for investigating the effect of structure in global form, Glass patterns are composed of a field of dipoles (dots pairs) whose orientations are set such that each dipole is tangent to the contours of a global pattern. In order to detect the global pattern in these displays, the observer must first group the local dipoles and then integrate their local orientations inter a global percept revealing the overall pattern of the image, e.g., circular, rotational, hyperbolic or parallel. Using Glass patterns, Wilson et al. (1997) demonstrated that observers were much more sensitive to circular global structure compared to parallel structures (e.g., vertical structure). This was a surprising result since the circular and parallel Glass patterns had similar local characteristics. Wilson et al. (1997) interpreted these results as evidence for global summation of circularly arranged local orientations but not for local orientations arranged in parallel. This suggests that circularly configured local static elements are efficiently integrated by specialized " hard-wired" extra-striate mechanisms whereas complex static forms arranged in parallel are processed less efficiently, possibly mediated by a more local analysis of orientations. Wilkinson et al. (1998) provided additional support for " extreme " sensitivity for circular static form information using radial frequency patterns, demonstrating that observers are very good at detecting small deviations from circularity. Although it is unclear whether the mechanisms underlying the detection of different types of complex form stimuli are similar or not (Achtman et al., 2003), local orientation information is grouped much more efficiently when configured in a circular manner. Comparable specialized analysis of complex visual information has also been demonstrated for dynamic information. Using random dot flow patterns, Freeman and Harris (1992) showed that sensitivity to translating (unidirectional) motion was below that of both circular and rotational motion. They interpreted their results as evidence for specialized mechanisms (called relative motion system (RMS)) that are preferentially selective for local motion configurations that characterize rotating and expanding global motion. Collaborative evidence for such specialized motion mechanisms has been demonstrated by others (e.g., Morrone et al., 1995; Morrone et al., 1999), who along with Freeman & Harris (1992), suggest that such processing is analogous to extra-striate mechanisms operating in area MST (e.g., Duffy & Wurtz, 1991; Graziano, Andersen & Snowden, 1994; Tanaka & Saito, 1989). Suffice it to say, visual grouping, whether static or dynamic, is qualitatively different and more efficient when local information is organized in a circular manner.

This brings us back to the *how* argument. Specifically, how the complex form (circular pathfinder task) and complex motion (unidirectional or translational global motion) stimuli used to demonstrate dorsal stream dysfunction in autism are processed (e.g., Spencer et al., 2000) (see Figure 2). Although both stimuli and considered to be complex in that 1 - they require the integration of local elements to be perceived, and 2 - are processed by extra striate mechanisms operating in either visual stream, *how* each complex stimuli is processed may have implications regarding Spencer et al. (2000) interpretations for the following reason. The complex form stimulus is processed very efficiently by specialized " hard-wired " analysis whereas the translational global motion stimulus seems to be processed by a relatively less efficient manner. Unlike the complex circular form stimuli, translational global motion processing depends to a greater extent on local signal parameters (see Scase et al., 1996; Watamaniuk & Sekuler, 1992; Baker & Hess; 1998), possible reflecting a relatively less specialized analysis, relying instead on an increased amount of local neuro-integrative processing. If persons with autism do indeed present abnormal neural networks implicated in neuro-integrative functioning at a visuo-perceptual level (Cohen, 1994; Gustafsson, 1997a; 1997b; Grice et al., 2001; Brock et al., 2002; Bertone et al., 2003), it can be argued that perceptual analysis mediated by specialized mechanisms will be less affected compared to perceptual analysis necessitating the involvement of less specific neural circuitry. The fact that unidirectional global motion used by both Spencer et al. (2000) and Milne et al. (2002) seems to be very sensitive to a variety of neurological disorders suggests that performance on tasks using these stimuli may be more sensitive to neural dysfunction than either circular form or motion stimuli mediated by specialized analysis. For this reason, it can be argued that the selective dorsal stream deficit found by Spencer et al., (2000) in autism may have something to do with *how* the ventral and dorsal stimuli used in their study are differentially processed; specialized grouping vs non-specialized analysis, respectively. This argument may also explain findings of dorsal stream dysfunction in other conditions using the same stimuli in order evaluate ventral and dorsal stream functioning (Atkinson et al., 1997).

In conclusion, we argue that based on the presented *how* argument, it is difficult to dissociate a *pathway specific* from a *complexity specific* account of visuo-perceptual processing in autism by using the complex stimuli used by Spencer et al., (2000) and Blake et al. (2003) because they are not processed in the same manner. Therefore, the same level of neuro-integrative dysfunction, if diffuse and non-selective to a specific visual stream, may manifest itself differently (performance on form and motion tasks) based exclusively on *how* the stimuli are integrated. For this reason, the selective demonstration of dorsal stream deficiency in autism may be stimulus dependent, and not be caused by a *pathway specific* dysfunction.

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Chapter 8

Conclusions and future directions

8.1. Conclusions

The general goal of the present thesis was to evaluate and elaborate on the nature of abnormal visuo-perceptual processing in autism using a psychophysical approach. This was carried out by evaluating the sensitivity of autistic participants to different types of simple (first-order) and complex (second-order) motion stimuli (Bertone & Faubert, 2003). In this respect, the applied study by Bertone et al. (2003) was the first assessment of motion processing in autism to use motion stimuli that require neural processing mechanisms of varying complexity. The finding that only second-order motion sensitivity was significantly decreased in autistic participants has important implications. First, it can be concluded that persons with autism do not have a " motion perception impairment " (Gepner et al., 1995), since they perceive simple motion (first-order) as efficiently as persons without autism. Because motion perception has been used to assess the integrity and reflect of dorsal visual stream functioning, it can also be concluded that our results are better explained in terms of a neuro-integrative deficit affecting perceptual performance in autism, rather than a selective dorsal stream deficit (Spencer et al., 2000; Milne et al., 2002; Blake et al., 2003). Although the neurobiological origins underlying abnormal neural connectivity in autism remain elusive, several " neural network " hypotheses suggesting abnormal integrative functioning at a perceptual level have been forwarded (Gustaffson, 1997a, 1997b; McClelland, 2000; Grice et al., 2001; Brock et al., 2002; Lamme, 2003). We conclude that such hypotheses, that describe possible neural abnormalities as not restricted to a specific brain region or visual pathway, are most congruent with experimental findings that demonstrate impaired wholistic processing in autism. Furthermore, we believe these " neural network " hypotheses present the most congruous neurophysiological explanations for abnormal information processing in autism, exemplified by the *weak central coherence* theory.

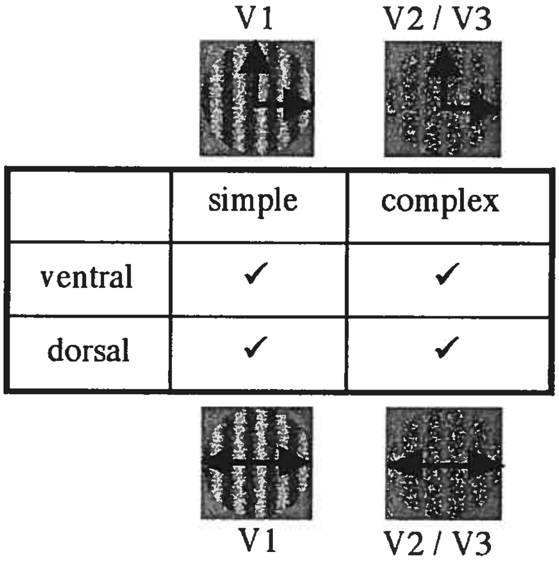
Numerous applied studies have investigated complex motion perception (usually global motion) in a variety of conditions defined by neural change or dysfunction, the majority of which found reduced sensitivity to complex motion for their respective clinical populations. Given the fact that only one level of motion complexity was evaluated in these studies, we conclude that decreased sensitivity to complex motion in these studies can be interpreted as the result of either *pathway specific* (dorsal visual stream deficit) or *complexity specific* (neuro-integrative deficit) deficiency. In addition to the Bertone et al. (2003) autism study presented as part of this thesis, only a few other applied studies have evaluated ***both*** simple ***and*** complex motion perception [non-pathological aging (Habak & Faubert, 2000); schizophrenia (Chen et al., 2003); mild cognitive impairment (Mapstone et al., 2003)]. Similar to our findings (Bertone et al., 2003), only the sensitivity to complex motion was decreased compared to control participants in these studies. Taken together, this indicates that measuring the sensitivity to complex motion (and not simple motion) is an approach that is sensitive enough to demonstrate subtle neural dysfunction, but not selective enough to suggest dorsal stream pathology.

As discussed in the previous chapter, studies have attempted to evaluate dorsal and ventral stream functioning autism by measuring the sensitivity to complex form and motion stimuli, respectively (Spencer et al., 2000; Blake et al., 2003). Results from these studies demonstrated a selective decrease for complex motion sensitivity, interpreted by these researchers as evidence for a dorsal visual stream deficiency. Although there is a possibility that visuo-perceptual abnormalities in autism are indeed mediated by such a *pathway specific* deficit, we argue that the stimuli used in these studies do not evaluate each visual stream at comparable levels of neuro-integrative complexity. For this reason, the alternative *complexity specific* hypothesis can also be forwarded. This suggestion is based on the *where* and *how* arguments presented in sections 7.4.1. & 7.4.2. of the general discussion. In the next section, we present an alternative experimental paradigm that addresses these limitations, as well as studies using this paradigm in both autistic and Fragile-X populations.

8.2. Addressing methodological limitations using an alternative experimental paradigm.

As contended in Chapter 7, the findings of recent studies proposing a dorsal stream deficit in autism (Spencer et al., 2000; Blake et al., 2003) may be the result of the different type of analysis necessitated to process complex form and motion stimuli. Basically, we contend that the stimuli used to assess dorsal and ventral visual stream integrity may differ in two ways. The first is in terms of their relative complexity ; the complex spatial tasks used to demonstrate intact ventral stream processing may not access or necessitate the same level of neuro-integrative processing along the ventral pathway as do the complex motion tasks (the *where* argument). Secondly, the complex circular form stimuli used to assess ventral pathway functioning may differ from the complex motion stimuli in terms of the manner with which the local information is integrated, either by specialized or non-specialized mechanisms (the *how* argument). Either one of these arguments may have an effect on the efficiency with which the stimuli are detected, especially if the origin of abnormal perception in autism is not specific to one visual pathway. The *how* and *where* arguments reinforce the suggestion that the stimuli and research designs previously used to evaluate the origin of visuo-perceptual abnormalities in autism (Spencer et al., 2000; Milne et al., 2002; Blake et al., 2003) may have methodological limitations. Consequently, dissociating between a *pathway specific* and a *complexity specific* account of visuo-perceptual processing in autism is difficult.

We propose an alternative experimental approach that we believe is better suited for evaluating dorsal and ventral visual stream integrity at comparable levels of complexity. This approach was initially used by Habak & Faubert (2000) to assess perceptual functioning in non-pathological aging. In order to do this, they measured the sensitivity to static and dynamic stimuli (e.g., either stationary or drifting gratings) defined by first- and second-order attributes. Specifically, static visual information processing, which is mediated by ventral visual stream, was evaluated using an orientation-identification task where participants are asked whether first- and second-order grating are oriented vertically or horizontally (see Figure 1, top two cells). Conversely, dynamic information processing, mediated by dorsal stream functioning, was evaluated using a direction-identification task using similar stimuli that drifted either to the left or right (see Figure 1, bottom two cells). We suggest that using this alternative method for investigating the origin of visuo-perceptual abnormalities in autism is advantageous relative to those previously used (Spencer et al., 2000; Milne et al., 2002; Blake et al., 2003) for several reasons.



	simple	complex
ventral	✓	✓
dorsal	✓	✓

Figure 1. Proposed stimuli and research design, initially used by Habak & Faubert (2000) to assess perceptual functioning in non-pathological aging. The perpendicular arrows represent an orientation-identification task and the oppositely-oriented arrows represent a direction-identification task.

The primary reason is that this approach addresses both the *where* and *how* arguments. It is well accepted that both static and dynamic forms of first- and second-order information are initially processed in parallel by separate passive mechanisms using similar principles of detection (e.g., Chubb & Sperling, 1988; Wilson et al., 1992; Baker, 1999). This processing is exemplified by filter-rectify-filter analysis where the first stage filters, operating within V1, extract first-order orientation or motion direction whereas second-order orientation or motion information is detected at a second-stage of filtering at a coarser spatial scale (in areas V2/V3), but only after rectification of the second-order signals (e.g., Chubb & Sperling, 1988; Wilson et al., 1992; Sperling et al., 1994; Smith et al., 1998; Wilson, 1998; Nishida et al., 1997; Baker, 1999; Bertone & Faubert, 2003). For this reason, first-order information can be considered to be a " simple " type of visual information whereas second-order visual information is considered to be more " complex " because it recruits more extensive neural circuitry as well as additional processing prior to detection. In terms of their relative complexity, the first- and second-order tasks access dorsal and ventral visual stream processing at the same level of complexity, defined by the physiological limitations of the mechanisms operating within each candidate level initially responsible for their detection (e.g., V1 and V2/V3). In conclusion, with respect to the *where* argument, this experimental approach offers a more precise method of assessing the functioning of each visual pathway at comparable levels of complexity.

The aforementioned *how* argument obviates the importance of considering *how* complex static information is processed by the visual system (e.g., specialized vs. sequential or " less-specialized " analysis), and how such processing may differ from complex dynamic processing, such as that mediating global motion perception. Integrating complex visual information, whether static or dynamic, is more efficient when local information is organized in a circular manner. This underlying increase in integrative efficiency, and consequently, enhanced performance on tasks requiring the detection of circular stimuli, is probably the result of specialized analysis. Within the context of experimental approaches used by Spencer et al., (2000) and Blake et al., (2003), we argued that reports of a static and dynamic stimuli used to assess ventral and dorsal stream processing in autism were not processed in the same manner. For this reason, we argue that the findings of selective dorsal stream dysfunction in these studies may have been stimulus dependant. This being said, the second reason why we believe that this alternative method is advantageous is as follows; the complex (second-order) static and dynamic stimuli used to assess either visual pathway are processed in the *same* manner. As mentioned, both the orientation- and direction-identification of complex second-order gratings are functionally defined by the same filter-rectify-filter models used to describe second-order motion perception. Therefore, visuo-perceptual functioning in each visual pathway is assessed before the point where specialized mechanisms operate (e.g., V4 or MT). Taken together, the neuro-integrative complexity of both the static and dynamic stimuli used in the proposed experimental approach are more comparable in terms of *where* and *how* they are processed in either visual stream. As a result, we believe that results obtained using this experimental approach will be less subject to interpretive debate than results using previous experimental approaches in autism (Spencer et al., 2000; Blake et al., 2003) and other conditions (Atkinson et al., 1997).

The next question is whether the proposed experimental approach is sensitive enough to dissociate a *pathway specific* from a *complexity specific* account of visuo-perceptual processing in autism. Habak and Faubert (2000) used this experimental approach to evaluate the effect of diffuse cortical change (e.g., loss of neural function and/or reduction) during the normal aging process. They found that older individual had a larger threshold increase for second-order information relative to first-order information. The magnitude of the threshold increase for second-order information was similar for both static and dynamic conditions, and therefore not pathway specific. Based on their findings, Habak and Faubert (2000) concluded that complex second-order visual information perception is more affected by the less efficient neuro-integrative mechanisms characterizing the neural aging process. Therefore, much like other types of complex " motion models " (e.g., complex global motion; Trick & Silverman, 1991), second-order motion is sensitive enough to detect even subtle types of neural dysfunction characterized by neuro-integrative dysfunction. We have already supported a *complexity specific* account of visuo-perceptual processing in autism by demonstrating a selective decrease for second-order motion information in autism (Bertone et al., 2003). However, to further support the *complexity specific* account in autism, and consequently, to provide additional evidence against the *pathway specific* account, an assessment of ventral stream processing using first- and second-order stimuli is necessary. We have evaluated ventral stream processing in autism using the proposed first- and second-order orientation task (Bertone et al., 2004), demonstrating a pattern of result specific to autism (see Chapter 9). We had the opportunity to use our experimental paradigm to evaluate visual processing in Fragile-X syndrome (FXS), a condition that sometimes manifests a behavioral phenotype comparable to that of autism. FXS is the most common cause of inherited mental retardation, caused by the transcriptional inactivation of the Fragile-X Mental Retardation 1 (FMR1) gene (Turner et al., 1996; Verkerk et al., 1996). Kogan et al., (2004a) have recently investigated the consequence of FMR1 gene dysfunction on both LGN physiology and consequent visuo-perceptual functioning. Using immunohistochemical staining, they demonstrated anatomical and morphological evidence of selective M-layer dysfunction in lateral geniculate nucleus (LGN) of persons with FXS. As expected Kogan et al., (2004a), demonstrated selective visual deficits related to magnocellular / dorsal stream functioning in FXS using complex form and motion tasks similar to those of Spencer et al., (2000) (as described by Atkinson et al., 1997). In doing so, they demonstrated a direct association between M-layer pathology and reduced performance on tasks requiring intact dorsal visual stream functioning (global motion perception). Based on their physiological findings, we have *a priori* reason to expect a decreased performance on direction-identification tasks (but not on orientation-identification) of our experimental paradigm for the FXS group relative to control participants. Such results would confirm a selective dorsal visual stream deficit for FXS patients using an alternate method as well as demonstrate that the proposed experimental paradigm is sensitive to *pathway specific* perceptual dysfunction. In effect, this is what was found (see chapter 10).

In addition to the important theoretical implication that these results have on visuo-perceptual processing and behaviour in FXS, we have demonstrated that the proposed paradigm using first- and second-order static and dynamic stimuli is sensitive enough to dissociate between *pathway-* and *complexity specific* accounts of visuo-perceptual deficits in non-pathological aging (Habak & Faubert, 2000), autism (Bertone et al., 2003; 2004) and FXS (Kogan et al., 2004b) populations. In conclusion, these results suggest that this proposed experimental paradigm is a valid alternative to those used previously for evaluating the origin of abnormal visual perception in a variety of neurological conditions.

8.3. References

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Chapter 9
Article 3

This chapter is an exact reproduction of the following published article:

[1]Bertone A, [2]Mottron L, [2]Jelenic P & [1]Faubert J (2004).
Enhanced and diminished visuo-spatial information processing in autism depends on stimulus complexity.
Submitted to *Brain*

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9.1. Abstract

We present the first demonstration of concurrent enhanced and decreased performance in autism on the same visuo-spatial task; the only factor dichotomizing performance being stimulus complexity. The ability of persons with autism was found to be *superior* for discriminating the orientation of simple, luminance-defined (or first-order) gratings but *inferior* for complex, texture-defined (or second-order) gratings. Together, these results are interpreted as a clear indication of altered low-level perceptual information analysis in autism and have important implications regarding both the neural origin of enhanced autistic performance on visuo-spatial tasks, and the dissociation between pathway- versus complexity-specific accounts of perceptual abnormalities in autism. Using a « systems » rather than a « region of interest » type approach for understanding the physiology of autistic perceptual dysfunction, the results are discussed in terms of a hypothetical neural network model suggesting abnormal synaptic connectivity mediating lateral inhibition in autism.

9.2. Introduction

Autism is a pervasive developmental disorder with a neurogenetic basis, defined by a triad of symptoms affecting social interaction, communication and imagination (American Psychological Association, 1994). In addition to socio-behavioral difficulties, atypical processing of visuo-perceptual information is also a characterizing feature of this condition (Happé, 1999). Visual information processing in autism presents a dichotomous picture, with intact or *enhanced* performance on tasks necessitating static spatial information, and *inferior* performance in dynamic information analysis.

The performance of persons with autism on tasks necessitating the detection of a static visual target embedded in larger field has been found to be either enhanced (Plaisted, Sweetenham & Reese, 1999; O'Riordan *et al.*, 2001; Caron *et al.*, 2004) or more locally oriented (Shah & Frith, 1983; Shah & Frith, 1993; Jolliffe & Baron-Cohen, 1997; Mottron, Belleville & Ménard, 1999) when compared to typically developing observers. Hypotheses explaining such perceptual assets in autism include superior processing of low-level static information (Plaisted, O'Riordan & Baron-Cohen, 1998; Mottron & Burack, 2001) or a by-product of defective integration of low-level information in higher-order operations (Frith, 2003).

In contrast, persons with autism are consistently less sensitive to a variety of complex motion stimuli that include full-field radiating flow field (Gepner et *al.*, 1995), adapted global motion stimuli (Spencer *et al.*, 2000), random dot kinemotograms (Milne *et al.*, 2002), biological motion stimuli (Blake *et al.*, 2003) and texture-defined motion patterns (Bertone *et al.*, 2003). All the aforementioned complex motion stimuli are processed in motion-sensitive, extra-striate areas located within the dorsal visual pathway (Goodale & Milner, 1992) and necessitate passive integrative processing to be perceived (Watamaniuk & Sekular, 1992; Wilson, Ferrera & Yo, 1992; Neri, Morrone & Burr, 1998; Bertone & Faubert, 2003). These findings of decreased complex motion have been attributed for the most part to a motion processing impairment or a dorsal stream dysfunction (*the pathway specific hypothesis*) (Gepner et *al.*, 1995; Spencer *et al.*, 2000; Milne *et al.*, 2002; Blake *et al.*, 2003). Concurrent explanations of defective global form analysis (mediated by the ventral visual stream), have been discarded by demonstration of a preserved perception of the global aspect of hierarchical stimuli in autism (Plaisted, Sweetenham & Reese, 1999; Spencer *et al.*, 2000; Blake *et al.*, 2003; Ozonoff *et al.*, 1994; Mottron *et al.*, 2003).

Bertone *et al.* (2003) suggested that decreased complex motion sensitivity in autism may be better explained by less efficient neuro-integrative mechanisms operating at a perceptual level in autism (*the complexity specific hypothesis*), regardless of the type of information (static or dynamic) being analyzed. They assessed motion processing at two levels along the dorsal visual pathway in autism, defined by the amount of neuro-integrative analysis required to perceive the motion. They found a selective decrease for complex second-order (or texture-defined) motion perception (Chubb & Sperling, 1988; Cavanagh & Mather, 1989). In contrast, simple first-order motion (luminance-defined) perception was unaffected for persons with autism. Since simple motion (V1-mediated analysis) perception is also mediated by dorsal stream functioning, Bertone et al. (2003) suggested that their results, and possibly those of other studies demonstrating inferior autistic sensitivity to complex motion, might be explained by a *complexity* account of visuo-perceptual processing in autism rather than by a dorsal pathway dysfunction defining the *pathway specific hypothesis*.

In order to further dissociate between these two hypotheses, the present study assesses ventral stream functioning in autism at two different levels by manipulating the level of complexity of the presented static information. This was accomplished by measuring orientation-discrimination thresholds for simple and complex *static* stimuli for both high-functioning persons with autism (HFA) and typically developing (TD) observers. The *pathway specific hypothesis* would predict intact ventral stream functioning in autism, reflected by similar performance for both simple and complex orientation conditions between groups. Conversely, the *complexity specific* account of visuo-perceptual processing in autism (Bertone et al., 2003) would predict a selective decrease for second-order performance since it contends that inefficient neuro-integrative functioning at a perceptual level in autism preferentially affects complex information analysis, regardless of whether the information is static or dynamic.

9.3. Results

9.3.1. Enhanced and diminished autistic performance on orientation-discrimination task depends on stimulus complexity

Orientation-discrimination thresholds for HFA and TD participants were measured using static gratings differing only in the attribute defining their orientation; luminance for the first-order condition and texture for the second-order condition (Fig. 1). Results revealed two very different patterns of HFA performance, contingent on the complexity of the stimuli used during each condition.

INSERT FIGURE 1 HERE

As shown in Figure 2, HFA orientation-discrimination thresholds were significantly *lower* for the first-order condition when compared to the typically-developing (TD) participants ($F_{1,24}$ = 7.872, p = 0.0098). These findings represent another demonstration of superior performance in tasks necessitating visuo-spatial information processing (i.e., position discrimination, visual search, etc.), albeit at a lower level of processing. In contrast, HFA thresholds were significantly *higher* for the exact same task using complex second-order stimuli ($F_{1,24}$ = 5.042, p = 0.0342), representing the first demonstration of a perceptual visual deficit for a static task in autism. Taken as a whole, these findings suggest that *enhanced* autistic performance on visuo-spatial tasks is complexity dependant, and that persons with autism are selectively less sensitive to complex visual information, whether it is static or dynamic in nature. These results will be discussed in the context of a *complexity-specific* account of visuo-perceptual processing in autism in later sections.

INSERT FIGURE 2 HERE

9.3.2. Unaffected magno- and parvocellular functioning in autism

In order to further assess the *pathway-specific* account of perceptual abnormalities in autism, we also measured flicker contrast sensitivity using stimuli that preferentially evaluate magnocellular and parvocellular functioning at early levels (i.e, LGN and V1) along each visual pathway (Fig. 3). We measured the minimum contrast needed to detect a counterphasing stimulus defined by either high-temporal, low spatial characteristics (mediated by magnocellular functioning) or by low-temporal, high-spatial characteristics (mediated by parvocellular functioning) (Merigan & Maunsell, 1993). Contrast thresholds were transformed into contrast flicker sensitivity measures for each condition (Fig. 3).

INSERT FIGURE 3 HERE

Flicker contrast sensitivity did not differ significantly between HFA and TD participants for either magnocellular ($F_{1,24} = 1.729$, p = 0.2009) or parvocellular ($F_{1,24} = 0.451$, p = 0.5810) conditions. In addition to the demonstration of intact simple motion perception in autism (Bertone *et al.*, 2003), this finding does not support a *pathway-specific* account of perceptual abnormalities in autism. Given the fact that parvocellular functioning was also found to be unaffected in the HFA group (i.e., not enhanced), findings of enhanced and diminished performance on the orientation-discrimination task seem to be the result of atypical processing at a cortical level in autism and not the result of abnormal pre-cortical visual input.

9.4. Discussion

The present study represents the first evaluation of ventral stream processing in autism at two levels of neural complexity, assessed by measuring orientation-discrimination thresholds for simple luminance- and complex texture-defined stimuli for both HFA and TD observers. By demonstrating that complex static information processing is selectively impaired in autism, we propose that atypical visual information analysis in autism is best described by a *complexity specific* account. Specifically, regardless of whether the visual information is dynamic (Bertone *et al.*, 2003) or static (current findings), diminished neuro-integrative functioning at a perceptual level will preferentially affect complex information analysis. It can therefore be argued that previous demonstrations of decreased complex motion sensitivity, interpreted as being the result of either motion impairments or dorsal stream dysfunction (Gepner *et al.*, 1995; Spencer *et al.*, 2000; Milne *et al.*, 2002; Blake *et al.*, 2003), may rather be explained the *complexity specific* hypothesis. We are able to forward this suggestion because our group has evaluated both ventral (current study) and dorsal visual stream functioning at two levels in autism, using static and dynamic stimuli of comparable complexity. In addition, we present compelling evidence against the *pathway specific* hypothesis in autism by demonstrating that flicker contrast sensitivity to stimuli mediated by both magno- and parvocellular functioning is unaffected in the HFA group. The *pathway specific* hypothesis would predict a selective increase in flicker sensitivity for the counterphasing stimuli defined by high-temporal, low spatial characteristics, a result not found in the present study. Finally, by demonstrating unaffected magno- and parvocellular functioning in autism and superior processing of visual information mediated by primary visual cortex, we suggest that both enhanced and inferior autistic performance on visuo-perceptual tasks is due to atypical information processing originating at the neural level, and not the result of impaired pre-cortical information processing (Milne *et al.*, 2002).

Previous studies have advanced that ventral stream processing is intact in autism by demonstrating unaffected autistic detection of circular forms of locally-oriented line segments (Spencer *et al.*, 2000; Blake *et al.*, 2003). Similar types of complex static stimuli are reported to be processed extremely efficiently by specialized "hard-wired' mechanisms, (i.e., less dependant on local signal characteristics) (Wilkinson, Wilson & Habak, 1998; Achtman, Hess & Wang, 2003). Therefore, we argue that these spatial stimuli are not equivalent to their dynamic complex motion stimuli counterparts in terms of processing requirements. If persons with autism present atypical neuro-integrative functioning as early as at a perceptual level, decreased autistic performance would be most likely manifested perceptually for the dynamic condition only, a dissociation inaccurately interpreted as the result of a dorsal stream dysfunction (Spencer *et al.*, 2000; Blake *et al.*, 2003).

Our results demonstrate that the performance of HFA participants is *inferior* at discriminating the orientation of complex, second-order gratings but *superior* for simple, first-order gratings. This dichotomous performance reflects how the *same* atypical neural systems mediating low-level visual processing in autism (orientation discrimination) differentially affects simple and complex static information processing. We therefore propose that the dichotomous performance on our spatial task is best explained by a « system » rather than a « region of interest » dysfunction, characterized by abnormal neural connectivity mediating the extraction of low-level information within the visual processing hierarchy in autism (Cohen, 1994; Gustafsson, 1997a; Gustafsson, 1997b; McLelland, 2000; Grice *et al.*, 2001; Brock *et al.*, 2002). The type of abnormal connectivity most congruent with the finding of enhanced sensitivity to simple luminance-defined gratings for the HFA group is that of strong or excessive lateral inhibition, as first suggested by Gustafsson (1997a, 1997b). Gustafsson's model is based on a « feature map » model of cortical functioning where neurons selective to specific visual features are arranged in columns and are optimally activated (increased neuronal activity within each column) when a specific visual attribute is present (Kohonen, 1995). Lateral inhibition allows proximal columns to be activated by similar stimulus features. Hypothetically, increasing lateral inhibition would result in the « narrowing » of the range of a particular stimulus feature that activates each column. This would result in a neural network theoretically capable of improved ability for discriminating between two stimuli differing slightly along a certain stimulus attribute (i.e., orientation, contrast, etc). Resulting in a form of enhanced edge detection, increased lateral inhibition would therefore predict increased performance on the orientation-discrimination task using simple luminance-defined stimuli for the HFA group, as was found in the present study. This model is particularly appealing since it is in agreement with evidence of columnar narrowing in the autistic brain (Casanova *et al.*, 2002), a possible morphological consequence of abnormal neural connectivity characterized by increased lateral inhibition.

As already mentioned, the dichotomous performance of the HFA group was contingent on stimulus complexity. We therefore propose that abnormal lateral inhibition did not enhance the sensitivity to complex texture-defined information for HFA group due to the following reason. Neurons comprising feature-specific columns selectively respond to oriented edges defined by changes in luminance, such as the simple luminance-defined, first-order stimuli used in our task (Fig. 1). In contrast, enhanced edge detection mediated by lateral inhibition for complex texture-defined information has been demonstrated, but only after additional information processing (i.e., full-wave rectification, see legend of Fig. 1) (Lu & Sperling, 1996). After such processing, the resulting texture-defined spatial information is much coarser. It is therefore less likely that the « narrowing » of the orientation-selective, luminance-driven columns in the primary visual cortex would significantly improve orientation-discrimination of complex texture-defined stimuli for HFA group. Therefore, although abnormal neural connectivity resulting in the narrowing of feature-specific columns may have been responsible for enhanced performance for discriminating simple orientation-information, in may in fact hinder the processing for more complex types of visual information necessitating a larger neural circuitry to be perceived.

The present results are interpreted as behavioral evidence of altered « local » neural networks in autism, possibly affecting the low-level processing of elementary stimulus features such as spatial frequency, orientation and contrast. Given the fact that these abnormal networks are the initial components of standard larger-scale networks responsible for higher-order information analysis, it can be argued that subsequent larger-scale networks integrating across specific stimulus features would also be compromised in autism (McLelland, 2000; Grice *et al.*, 2001; Brock *et al.*, 2002; Bertone *et al.*, 2003; Just *et al.*, 2004). At least in the context of the present experimental paradigm, excessive lateral inhibition seems to be a candidate type of abnormal neural connectivity that is congruent with *both* superior visuo-static information processing and a potential origin of neuro-integrative dysfunction in autism. Other « systems » -based explanations have been forwarded to account for dichotomous abilities in autism for both perceptual (*Temporal binding deficit hypothesis*) (Brock *et al.*, 2002) and language domains (*Underconnectivity hypothesis*) (Just *et al.*, 2004). Although different with respect to their defining nature of synaptic dysfunction, both hypotheses predict impaired information processing if it is contingent on integrating information *between* specialized networks located in different brain regions, and enhanced processing is limited *within* local networks. However, unlike these theories, our results suggest that integrative dysfunction can affect different levels of processing within the same « local » network and is not selective to inter-network connectivity. We therefore propose that abnormal neural connectivity in autism may be manifested at much lower-levels than previously suggested, affecting initial stages of neural processing of visual information.

In addition to being most congruent with the present results, enhanced edge detection caused by increased lateral inhibition may also be at least in part responsible for other findings of improved autistic performance on spatial tasks involving the discrimination of luminance-defined stimuli mediated by low-level perceptual processing (Plaisted, Sweetenham & Reese, 1999; O'Riordan *et al.*, 2001; Caron *et al.*, 2004). Although such tasks involve higher-level operations (i.e., attention), enhanced processing of low-level spatial information may positively affect subsequent analysis, resulting in increased autistic performance. Furthermore, the narrowing of feature-specific columns may provide a plausible physiological explanation for the locally-oriented analysis of visual information in autism (Shah & Frith, 1983; Shah & Frith, 1993; Jolliffe & Baron-Cohen, 1997; Mottron, Belleville & Ménard, 1999; Ring et al., 1999; Hubl et al., 2003). It has been proposed that persons with autism *actively* attend to local, rather than global levels of information during a task if allowed the choice (Plaisted, Sweetenham & Reese, 1999) Given that enhanced edge detection is a « local » process, one can speculate that persons with autism *passively* orient their attention toward local information to best complete the task since they are advantaged in doing so.

Enhanced low-level functioning has been reliably demonstrated in the visual as well as auditory modality (Mottron & Burack, 2001). Although our results and interpretations are based on performance on a visuo-perceptual task, it is nevertheless plausible that abnormal lateral inhibition may also be the neural origin of enhanced low-level auditory perception in autism. This is a possibility since neural organization within the primary auditory cortex has a columnar arrangement similar to that of the primary visual cortex (Abeles & Goldstein, 1970). Increased lateral inhibition between frequency-specific columns may therefore result in an increased temporal resolution, with the benefit of enhanced pitch sensitivity in autism (Bonnel *et al.*, 2003) and diminished local-to-local interference (Foxton *et al.*, 2003).

In addition to autism, decreased complex motion sensitivity has been demonstrated for a variety of neurological conditions. Although it is a sensitive method for demonstrating perceptual dysfunction, measuring complex motion sensitivity in isolation does not allow for dissociation between *pathway* and *complexity* specific hypotheses that best characterize visuo-perceptual anomalies in a variety of conditions. As we have done presently for autism, we have measured simple and complex information processing along each visual pathway to successfully characterize the perceptual functioning in other neurological conditions characterized by visually-related anomalies (Habak & Faubert, 2000; Bertone et al., 2003; Kogan et al., 2004). As shown in Table 1, such investigations using the same stimuli and experimental paradigm have resulted in different patterns of performance specific to each condition and consistent with their respective neuropathology.

INSERT FIGURE 4 HERE

Most pertinent to the present discussion, the finding of enhanced sensitivity to simple static information is specific to autism and therefore, hypothesis regarding abnormal neural connectivity differentiating autism form other conditions manifesting decreased complex motion sensitivity can be forwarded. In addition to being consistent with other findings of enhanced performance on visuo-spatial tasks, we suggest that this result is neither stimulus nor paradigm dependent since a similar pattern of performance was not demonstrated for other neurological conditions using the same stimuli and experimental methodology.

9.5. Methods

9.5.1. Participants.

Thirteen high-functioning persons with autism (HFA) and normal intelligence (mean IQ = 100.4, SD = 13.6) were recruited from a specialized clinic for persons with autism. A diagnosis of autism was obtained using the algorithm of the Autism Diagnostic Interview (ADI) (Lord, Rutter & LeCouteur, 1994) combined with the Autistic Diagnostic Observation Schedule General (ADOS-G) (Lord *et al.*, 1989), both of which were conducted by a trained researcher (LM) who obtained reliability on these instruments. All HFA had a score above the ADI / ADOS cut-off in the four areas relevant for diagnosis (social, communication, restricted interest and repetitive behaviors, and age of symptom onset). Thirteen typically developing (TD) participants were recruited from the community as a comparison group. These were screened for a past or current history of psychiatric, neurological or other medical disorders and all had a typical academic background and development (mean IQ = 108.2, SD = 13.1). The groups were matched as closely as possible in terms of laterality, gender and chronological age and full-scale IQ. The mean age of the control and autism groups was 22.3 (SD = 6.1) and 20.5 years (SD = 4.3), respectively. All observers participated in psychophysical Studies in the past and had normal or corrected-to-normal vision. Informed written consent was obtained from all participants.

9.5.2. Apparatus

For all testing, stimulus presentation and data collection were controlled by a Power Macintosh G4 microcomputer and presented on a 14-inch AppleVision color monitor refreshed at a rate of 75 cycles per second (Hz). The screen resolution was 1152 x 870 pixels. The VPixx© (ww.vpixx.com) graphics program controlled stimulus generation and animation. The luminance of the monitor was gamma-corrected (implemented with a color calibration within the VPixx © program) to minimize the non-linearities in the display. Calibration and luminance readings verified using a Minolta CS-100 Chroma Meter colorimeter on a regular basis.

9.5.3. Orientation-discrimination task.

9.5.3.1 Stimuli. Static stimuli were presented to the participants within a circular region at the center of the display that had a diameter of 10 deg when viewed from a distance of 57 cm. The mean luminance of the remainder of the display during testing was 15.00 cd/m^2 (u' = 0.1912, v' = 0.4456 in CIE (Commission Internationale de l'Eclairage) u' v' color space) where L_{min} and L_{max} were 0.02 & 30.02 cd/m^2, respectively. The static stimuli consisted of first- and second-order grating presented either vertically or horizontally. The first-order motion stimuli (Fig. 1) were luminance-defined noise stimuli produced by adding static greyscale noise to a modulating sinewave. The noise consisted of dots (1 pixel x 1 pixel, measuring approximately 2.235 arc min) with individual luminances randomly assigned as a function of sin (x), where (x) ranged from 0 to 2π. The luminance-contrast of the first-order stimuli was varied to determine orientation-discrimination thresholds by varying the amplitude of the modulating sinewave. The amplitude of the luminance modulation for the first-order patterns could be varied from 0.0 to 0.5 defined as:

$$\text{luminance modulation depth} = (L_{max} - L_{min}) / (L_{max} + L_{min})$$

where L_{max} and L_{min} refer to the average highest and lowest local luminances in the pattern. The first-order luminance modulation levels used in the constant stimuli presentations (0.10, 0.05, 0.035, 0.02, 0.0125 and 0.00625) were chosen based on pilot studies. The second-order stimuli (Fig. 1) were texture-modulated noise stimuli produced by multiplying rather than summing the same modulating sinewaves to the greyscale noise . The texture-contrast (contrast modulation depth) was also varied to find orientation-discrimination thresholds by varying the amplitude of the modulating sinewave. The amplitude of the texture-modulation that defined the contrast of the second-order stimuli could be varied within a range of 0.0 and 1.0 defined as:

$$\text{contrast modulation depth} = (C_{max} - C_{min}) / (C_{max} + C_{min})$$

where C_{max} and C_{min} are the maximum and minimum local contrasts in the pattern. Second-order contrast modulation levels used during the constant stimuli procedures were 1.0, 0.429, 0.250, 0.143, 0.067 and 0.032. All first- and second-order static stimuli had a spatial frequency of 0.75 cycles per degree (cpd) and a drift frequency of 0 cycles per second (Hz).

9.5.3.2. Procedure. Participants were tested individually in a dimly lit room. Procedural instructions were given verbally to each participant prior to each experimental block. Before the actual testing, practice trials were completed so that the participants could familiarize themselves with fixation, stimuli presentation and responding. Each participant was then presented with trials consisting of static first- and second-order stimuli oriented either vertically or horizontally for 750 msec. They were then required to identify the orientation of each stimuli by pressing one of two buttons on a keypad (2 alternative forced-choice). For each testing session, first- and second-order stimuli were presented in random order ten times in either orientation at each level of modulation (for a total of twenty trials at each level of modulation). Psychometric functions were then fitted to the responses for each condition in order to obtain orientation-identification thresholds at a 75% correct level of performance. Throughout testing, the participants were reminded to fixate at the center of each pattern. The experimenter remained present throughout testing and initiated successive trials.

9.5.4.Flicker sensitivity task

9.5.4.1. Stimuli. As was the case for the orientation-discrimination task, flicker stimuli were presented to the participants within a circular region at the center of the display that had a diameter of 10 deg when viewed from a distance of 57 cm. The mean luminance of the remainder of the display during testing was 17.70 cd/m^2 (u' = 0.1912, v' = 0.4456) where L_{min} and L_{max} were 0.01 & 35.40 cd/m^2, respectively. Flicker contrast sensitivity was measured using stimuli that preferentially evaluated magnocellular and parvocellular functioning. In separate sessions, a two-alternative temporal forced choice paradigm was used to measure the minimum contrast needed to detect a a 0.5 cpd grating counterphasing at a rate of 6Hz (magnocellular condition) and a 6 cpd grating counterphasing at a rate of 1 Hz (parvocellular condition).

9.5.4.2. Procedure. For both magno- and parvocellular conditions, participants were presented with trials consisting of counterphasing stimuli of a certain luminance contrast for 750 msec., followed (or preceded) by a stimuli containing no counterphasing information. Participants were required to identify the trial that contained the counterphasing stimuli (i.e., first or second presentation). Luminance contrast was the physical variable being manipulated for each condition using an adaptive PEST (Parameter Estimation by Sequential Testing) procedure controlled by the VPixx program. A session ended when the PEST routine converged on the 81 % level on a psychometric Weibull function, representing the flicker contrast thresholds for each condition, which were then transformed into contrast flicker sensitivity measures. A preset level of accuracy (95% confidence interval hat the true threshold was within 0.1 log units of the PESTed threshold) had to be met in order for the PEST routine to end for each condition. Maximum number of trials was fixed at one-hundred for each condition, which was never met.

The total time taken for each participant to complete both orientation-discrimination and flicker sensitivity tasks took on average, approximately 60 minutes.

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9.8. Tables, Figures and Legends

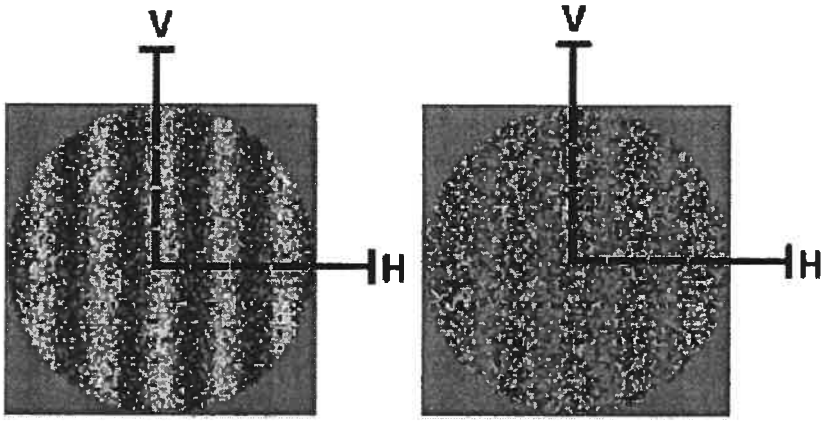
Figure 1. Schematic representation of static stimuli used for experiment 1. First- and second-order stimuli are presented in their vertical (V) orientation. Both static and dynamic forms of first- and second-order information are initially processed in parallel by separate passive mechanisms using similar principles of detection. Specifically, first stage filters, operating within V1, extract first-order orientation or motion direction whereas second-order information is detected at a second stage of filtering at a coarser spatial scale (in areas V2/V3), but only after full-wave rectification of the second-order signals (Wilson, Fererra & Yo, 1992; Chubb & Sperling, 1988; Cavanagh & Mather, 1989; Sperling, Chubb & Solomon, 1994; Baker, 1999). For this reason, first-order information can be considered to be a simple and second-order information complex because the latter type recruits more extensive neural circuitry as well as additional processing prior to detection.

Figure 2. Orientation-discrimination thresholds as a function of stimulus complexity for high-functioning persons with autism (HFA) and typically-developing participants (TD). Since first- and second-order stimuli are constructed using different image attributes, the absolute difference between first- and second-order thresholds is uninformative. Error bars represent 1 standard deviation.

Figure 3. Contrast flicker sensitivity measures for parvocellular and magnocellular functioning for HFA and TD groups. Error bars represent 1 standard deviation.

Figure 4. Schematic representation of the sensitivity compared to control participants for normally-aging persons (Habak & Faubert, 2000), persons with fragile x syndrome (FXS) (Kogan *et al.*, 2004) and HFA (dorsal (Bertone *et al.*, 2003) and present results) using the same task. Single arrows (↓,↑), double arrows (↓↓,↑↑) and equal sign (=), represent significant small difference, significant larger difference and no difference (respectively) in sensitivity between control and clinical groups.

Figure 1. Bertone et al., 2004



First-order Second-order

Figure 2. Bertone et al., 2004

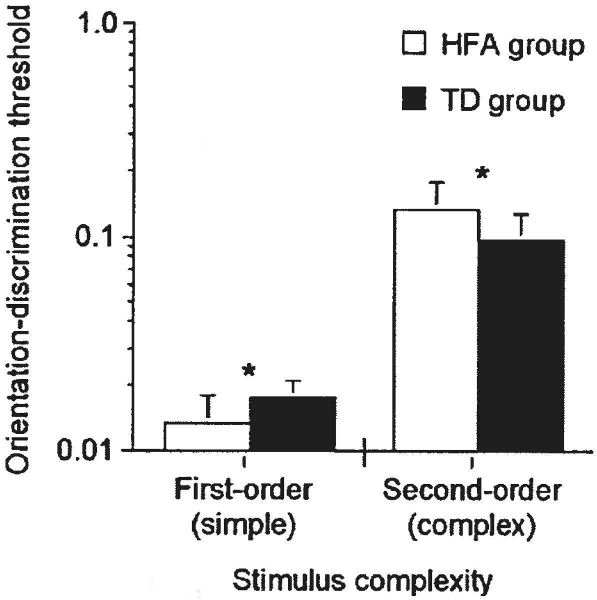


Figure 3. Bertone et al., 2004

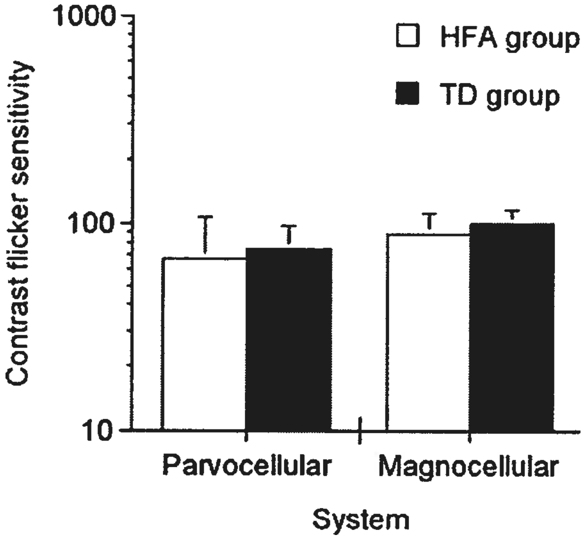


Figure 4. Bertone et al., 2004

	Normal aging		FXS		HFA	
	Simple	Complex	Simple	Complex	Simple	Complex
Ventral	↓	↓↓	=	↓↓	↑↑	↓↓
Dorsal	↓	↓↓	↓↓	↓↓	=	↓↓

Chapter 10
Article 4

This chapter is an exact reproduction of the following published article:

[1]Kogan CS, [2]Bertone A, [3]Cornish K, [1]Boutet I, [3]DerKaloustian VM, [4]Andermann E, [2]Faubert J & [1]Chaudhuri A (2004).
Integrative cortical dysfunction and a pervasive motion perception deficit in fragile X syndrome.
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10.1. Abstract

Background: Fragile X syndrome (FXS) is associated with neurological deficits recently attributed to the magnocellular pathway of the lateral geniculate nucleus. *Objective:* To test the hypotheses that FXS individuals: 1) have a pervasive visual motion perception impairment affecting neocortical circuits in the parietal lobe and 2) have deficits in integrative neocortical mechanisms necessary for perception of complex stimuli. *Methods:* Psychophysical tests of visual motion and form perception defined by either first-order (luminance) or second-order (texture) attributes were used to probe early and later occipito-temporal and occiptio-parietal functioning. *Results:* When compared to developmental- and age-matched controls, FXS individuals displayed severe impairments in first- and second-order motion perception. This deficit was accompanied by near normal perception for first-order form stimuli but not second-order form stimuli. *Conclusions:* Impaired visual motion processing for first- and second-order stimuli suggests that both early- and later-level neurological function of the parietal lobe are affected in FXS. Furthermore, this deficit likely stems from abnormal input from the magnocellular compartment of the lateral geniculate nucleus. Impaired visual form and motion processing for complex visual stimuli with normal processing for simple (i.e., first-order) form stimuli suggests that FXS individuals have normal early form processing accompanied by a generalized impairment in neurological mechanisms necessary for integrating all early visual input.

10.2. Introduction

Fragile X syndrome (FXS) is the most common cause of heritable mental retardation and is unique because the condition results from the silencing of a single gene, Fragile-X Mental Retardation 1 (*FMR1*)[1, 2]. The silencing is caused by methylation of the gene promoter in response to expansion of an upstream trinucleotide repeat region. In affected individuals, repeat expansion appears to accumulate across generations, reaching a so-called full mutation beyond a critical threshold (> 200 repeats)[3]. Due to X chromosome hemizygosity, men possessing the full mutation either lack or have a significant reduction in the *FMR1* protein product, Fragile X Mental Retardation protein (FMRP).

A unique constellation of strengths and weaknesses comprising the neurobehavioural and neurocognitive phenotype of FXS serves to distinguish this condition from other forms of mental retardation[4-6]. A striking aspect of the syndrome is the observed deficit of skills that require integration of visual information for effective motor control[7-9]. One possible explanation for the specific nature of these deficits is that an underlying impairment may exist in processing visual information critical for guiding adaptive motor behavior.

In support of this idea, convergent neurobiological and behavioral experiments have demonstrated that FXS is associated with a specific impairment in the magnocellular (M) portion of the thalamus10, which belongs to one of two main subcortical channels for transmission of visual information to the cerebral cortex. The neurobiological data presented in that study showed FMRP to be selectively expressed in M pathway neurons and less so in thalamic compartments that are part of the other main subcortical channel, the parvocellular (P) pathway. Of particular importance was the finding that the M portion of the thalamus showed striking neuromorphological abnormalities in FXS human brain samples as compared to controls.

The hypothesis that M pathway function may be compromised in FXS has also been supported by behavioral data10. FXS men were found to have elevated thresholds for visual stimuli that are selectively processed by the M pathway. These same patients, however, displayed normal visual function for stimuli that selectively engage the P pathway. The authors reasoned that a functional deficit of the M channel may also affect visual processing at higher cortical centers that reside in the parietal lobe and which are known to receive a dominant M pathway input[11-14]. The parietal stream is known to be crucial for processing dynamic aspects of the visual scene as well as the spatial relationships of objects for the visual control of action. In contrast, visual structures in the temporal lobe, which receive a dominant input from the P pathway, are known to be involved in object identification and visual awareness[11, 13, 14]. These functions appear to be relatively spared in patients with FXS.

The results of the behavioural and neurobiological experiments examining visual perceptual deficits in FXS raised important new questions as to whether the neurobehavioral deficits in FXS are due solely to impairments in low-level neurological processing or instead are caused by deficits in higher cortical mechanisms that integrate low-level visual information. For example, it may be that only the mere encoding of visual signals is compromised at the early stages of processing or alternatively, the low-level neurological impact may be compounded by further deficits of an integrative nature at higher levels. One way to distinguish between these alternative possibilities is to employ visual stimuli and tasks that preferentially engage the two different levels of information processing. The strategy for differentiating these two levels relies on use of two separate classes of visual stimuli—first-order *versus* second-order stimuli. First-order stimuli are defined on the basis of luminance differences and are useful for probing low-level cortical function. Second-order stimuli are defined by isoluminant contrast, texture, or depth and have been shown to be largely processed at higher-level cortical areas[15-19].

In this study, we have employed the strategy of selective probing of both early- and later-level neurological function in patients with FXS using first- and second-order visual stimuli. We provide evidence for deficits in parietal stream function at both levels. This finding suggests that the previously identified M pathway impairment has a pervasive effect on higher cortical processes as well. Furthermore, a concomitant deficit in response to first-order stimuli was not apparent in a test that probed low-level temporal lobe function. However, evidence was found for a deficit with more complex second-order stimuli that probed high-level temporal lobe function. This finding suggests that in addition to the deficit in visual motion perception, FXS individuals have a generalized impairment in neurological mechanisms necessary for integrating early visual input. The significance of these data is that it now offers a more coherent picture of the specific neural functions that are disrupted in FXS that in turn may produce the observed neurocognitive and neurobehavioural phenotype characteristic of this condition.

10.3. Methods.

10.3.1. Participants.

Eleven men or adolescents with FXS (mean chronological age (CA) = 17.61 ± 3.47 years; mean verbal mental age (MA) = 7.43 ± 1.28 years) were recruited in the United Kingdom through the UK Fragile X Society and in Canada through the Department of Pediatrics and Human Genetics at the Montreal Children's Hospital. All patients had a DNA confirmed diagnosis of a FXS full mutation, Eleven age-matched control participant men or adolescent (CA = 17.28 ± 3.17 years) and eleven developmental-matched control participant boys (MA = 7.18 ± 2.39 years) were recruited through newspaper advertisements. The MA controls were matched according to their verbal mental age and therefore were chronologically younger than the patients with FXS. The CA and MA groups were selected to control for the separate influences of chronological age on visual perception (i.e. the CA controls) and cognitive ability on performance of the psychophysical tasks (i.e. the MA controls). Participants or their caregivers gave their or their ward's/children's written consent to take part in this study and were paid for their participation. The ethics committees of the Department of Psychology, McGill University, the Montreal Neurological Hospital and Institute, and the Montreal Children's Hospital approved the study.

10.3.2. Cognitive Assessment

Participants in the MA-matched comparison group were selected according to their achievement of overall similar performance as the FXS participants on a test of verbal mental ability. Patients with FXS and the MA-matched control participants were assessed using the Peabody Picture Vocabulary Test[20] (PPVT-R, Form L) for English-speaking participants or its French translation, the Échelle de Vocabulaire en Images Peabody[21] (EVIP, Forme A) for French-speaking participants. The PPVT and EVIP are individually administered tests that consist of 175 vocabulary items of increasing difficulty used to assess breadth of receptive language.

10.3.3. Apparatus

For data collected at the Visual Psychophysics and Perception Laboratory of the Université de Montréal (Canada), stimulus presentation and data collection were controlled by a Power Macintosh G3 computer and presented on a 16-inch AppleVision 1710 monitor (frame refresh rate of 75 Hz), which was gamma-corrected using a color look-up table. The screen resolution was 832 x 624 pixels. Stimuli were generated and animated by the VPixx© graphics program (www.vpixx.com). The mean luminance of the display was 32.1 cd/m^2 (u'= .1888, v'= .4349 in CIE (Commission Internationale de l'Eclairage) u' v' color space) where L_{min} was 0.206 and L_{max} was 64.4 cd/m^2. Color calibration and luminance readings were taken using a Minolta Chromameter. For data collected at the Queen's Medical Centre in Nottingham (United Kingdom), stimulus presentation and data collection were controlled by a Power Macintosh G3 laptop computer and presented on a 15-inch Hansol 710A monitor (frame refresh rate of 75 Hz), which was gamma-corrected using a color look-up table. In order to ensure physical equivalencies between the stimuli presented in Canada and those in the United Kingdom, a Minolta Chromameter was used to match the mean luminance, L_{max} and L_{min}, as well as the color of the gray values used (i.e., u' and v' values) to define the stimuli. Stimuli were generated and animated as described above for the data collected in Canada.

10.3.4. Visual stimuli—motion condition

The stimuli used for the motion direction-identification task are shown in Figure 1. They consisted of first- and second-order translating patterns, constructed by either adding or multiplying static grayscale noise to a modulating vertically-oriented sinewave[22, 23]. The stimuli were presented within a hard-edged circular region at the center of the display subtending a visual angle of 10 deg in diameter when viewed from a distance of 114 cm. The noise consisted of dots (1 pixel x 1 pixel, measuring approximately 2.235 min arc) whose individual luminances were randomly assigned as a function of sin (x), where (x) ranged from 0 to 2π. The average contrast of the noise was set at half its maximal value. All motion stimuli had a spatial frequency of 1 cycle per degree (cpd) and a drift frequency of 2 cycles per second (Hz). Direction-identification thresholds for the first-order patterns were found by varying the contrast (luminance modulation or luminance modulation depth), defined as the amplitude of the modulating sinewave, which ranged between 0.0 and 0.5:

$$\text{luminance modulation depth} = (L_{max} - L_{min}) / (L_{max} + L_{min})$$

where L_{max} and L_{min} refer to the average highest and lowest local luminances in the pattern. The first-order patterns were presented at five levels of luminance modulation (0.04, 0.02, 0.01, 0.005, and 0.0025).

Second-order patterns were produced by multiplying the same modulating sinewaves with grayscale noise. Direction-identification thresholds for the second-order patterns were found by varying the contrast modulation (contrast modulation depth) of the motion patterns, defined as the amplitude of the modulating sinewave, which ranged between 0.0 and 1.0:

$$\text{contrast modulation depth} = (C_{max} - C_{min}) / C_{max} + C_{min})$$

where C_{max} and C_{min} are the maximum and minimum local contrasts in the pattern. The second-order patterns were also presented at five levels of contrast modulation (1.0, 0.333, 0.143, 0.111 and 0.059).

10.3.5. Visual stimuli—form condition

The physical properties and parameters of the static stimuli used for the orientation-identification task were identical to the motion patterns used in the dynamic condition except that they were stationary (i.e., drift frequency of 0 Hz). They were constructed by either adding or multiplying static grayscale noise to either a vertically or horizontally oriented stationary sinewave grating (Figure 1). Therefore, the stimuli used in both the dynamic and static conditions were physically identical except for their defining attribute; motion (i.e., left-right) in one case and orientation (i.e., vertical-horizontal) in the other.

10.3.6. Psychophysical testing

Participants were tested individually in a dimly lit laboratory room and viewed the display binocularly from a distance of 114 cm for each of two separate testing sessions (i.e., dynamic and static testing sessions). Procedural instructions were given verbally prior to each session, followed by a series of practice trials to familiarize participants with the procedure and to assure the experimenters that the participants understood the task at hand by being able to respond correctly to the stimuli before actual testing began. To ensure full comprehension of the task, participants had to obtain a criterion level of ten consecutive correct responses during each of the practice sessions before continuing on to the thresholds estimation phase of the experiment. The experimenter was present throughout the testing and initiated successive trials only when he was sure that he participant's gaze was oriented towards the point of fixation.

Within a dynamic testing session, each participant was presented with trials consisting of first- and second-order stimuli moving in either of two possible directions (i.e., left vs. right) by making a two alternative forced choice (2AFC). The motion stimuli were presented for 1 sec, after which each participant responded verbally or by using a hand gesture (i.e., pointing in a certain direction), depending on what was less demanding. The experimenter entered the responses after each trial. For the static testing session, each participant was presented with trials consisting of stationary first- and second-order stimuli oriented either vertically or horizontally for 1 sec. Similarly, the participants responded to the orientation of the stimuli either verbally or with hand gestures.

The method of constant stimuli was used to measure direction- and orientation-identification thresholds for each experimental condition and included five levels of luminance modulation for the first-order stimuli and five levels of contrast modulation for the second-order stimuli. Testing order of static and dynamic conditions was counterbalanced across participants. Moreover, within each testing condition first- and second-order stimuli were presented in random order. Stimuli were presented ten times in either direction/orientation at each level of modulation (for a total of twenty trials at each level of modulation for each of the experimental conditions). Where possible, Weibull[24] functions were fitted to the responses for each condition in order to derive direction- and orientation-identification thresholds at a 75% correct level of performance.

10.4. Results

10.4.1. Motion condition.

All of the FXS participants tested were capable of discriminating the direction of motion during practice sessions where luminance and contrast modulation depth for first- and second-order stimuli were set at their respective maximal values. However, we were able to obtain direction-of-motion thresholds for only a fraction of these individuals (Table 1), which cannot be attributed to non-specific effects (e.g., lack of attention) because all of the FXS participants were able to complete at least one of the testing conditions. Although thresholds were not calculable for many of the patients with FXS, group performance at the highest levels of luminance modulation for the first-order task and contrast modulation for the second-order task were determined, using one-sample t-tests, to be significantly greater than chance (first-order motion: $t = 7.069$, $p < 0.05$; second-order motion: $t = 2.906$, $p < 0.05$). This indicates that the FXS participants understood the task instructions. In contrast, we were able to obtain direction-of-motion thresholds for all control participants using both types of dynamic stimuli. The severity of the visual motion processing deficit in FXS participants precluded the use of standard parametric statistical analyses. Therefore, we conducted two non-parametric Kruskal-Wallis one-way analysis of variance (ANOVA) tests, one for each of the motion conditions (first- and second-order), to compare group medians, with Group (FXS, Age-matched, Developmental-matched) as the independent measures variable (Figure 2). Separate analyses were necessary because the attributes defining the first- and second-order motion stimuli (i.e., luminance *versus* contrast) are qualitatively different, making a direct comparison of threshold values across stimuli type uninformative. A comparison of the median threshold values for the first-order static stimuli revealed a significant main effect of Group ($\chi^2 = 19.458$, $p = 0.005$). Post hoc pairwise comparisons using Mann-Whitney U tests with Bonferonni correction ($\alpha = 0.05/3 = 0.017$) confirmed that the FXS group had significantly elevated luminance thresholds when compared to both the age-matched comparison group ($p = 0.002$) and the developmental-matched comparison group ($p = 0.002$).

A similar pattern of results was found for the second-order motion stimuli with a significant main effect of Group ($\chi^2 = 7.858$, $p = 0.02$). Post hoc pairwise comparisons using Mann-Whitney *U* tests with Bonferonni correction ($\alpha = 0.05/3 = 0.017$) confirmed that the FXS group had significantly elevated contrast thresholds when compared to both the age-matched comparison group ($p = 0.010$) and the developmental-matched comparison group ($p = 0.010$). Thus, there are significant differences between the median threshold values for both first- and second-order dynamic stimuli between the FXS group and the two comparison groups. Furthermore, comparing the success rates on the respective dynamic tasks (Table 1), a majority of FXS individuals had difficulty perceiving simple motion stimuli and an even greater numberhad difficulty perceiving complex motion.

10.4.2. Form condition

Static luminance and contrast modulation depth thresholds were obtained for all participants with the exception of three of the FXS participants when tested with the first-order static stimuli (Table 1). We conducted two one-way ANOVA tests, one for each of the static conditions (first- and second-order), with Group (FXS, Age-matched, Developmental-matched) as the independent measures variable (Figure 3). Separate ANOVAs were necessary for the same reason that separate analyses were conducted on the data obtained for the first- and second-order motion stimuli. That is, because the attributes defining the first- and second-order static stimuli (i.e., luminance *versus* contrast) are qualitatively different.

A comparison of the mean threshold values for the first-order static stimuli revealed a significant main effect of Group ($F_{2,33} = 10.76$, $p < 0.01$). Post hoc pairwise comparisons using Tukey's honestly significant difference (HSD) confirmed that both the FXS group ($p < 0.05$) and the developmental-matched comparison group ($p < 0.05$) had significantly elevated luminance thresholds when compared to the age-matched comparison group. That differences could not be found in performance between the FXS and developmental-matched participants for first-order stimuli indicates a mental age-dependent difference in the ability to perform the method of constant stimuli threshold task and highlights the need for the developmental-matched comparison group. Thus, compared to the dynamic conditions, the FXS participants' perception of the first-order static stimuli appears to be intact.

A similar pattern of results was found for the second-order static stimuli with a significant main effect of Group ($F_{2,35} = 8.67$, $p < 0.05$). However, unlike the first-order findings, post hoc pairwise comparisons using Tukey's HSD revealed that the FXS group had significantly elevated contrast thresholds when compared to both the age-matched comparison group ($p < 0.05$) and the developmental-matched comparison group ($p < 0.05$). This result suggests that the FXS group had difficulties integrating local elements in the more complex second-order form task in order to perceive the orientation of the stimuli.

10.5. Discussion.

In the present study, we evaluated the integrity of the parietal and temporal streams in patients with FXS by comparing motion and form perception using physically identical stimuli that differed only in terms of their defining attribute (static or dynamic) and the degree of stimulus complexity (first- or second-order). Our results can be briefly summarized as follows: 1) the majority of FXS participants performed poorly on dynamic tasks and were unable to discriminate the direction of motion for first- and second-order stimuli, 2) FXS individuals who were able to complete the both first- and second-order tasks had significantly elevated thresholds for direction of motion when compared to age- and developmental-matched control participants, 3) a majority of FXS participants were able to discriminate the orientation of static first- and second-order stimuli, 4) FXS individuals who were able to complete the first-order task had thresholds that were similar to those of the developmental-matched control participants, and 5) static second-order thresholds were significantly elevated in FXS individuals relative to both comparison groups.

These results support the hypothesis that the M pathway deficit previously reported in patients with FXS10 also yields a parietal stream deficit regardless of whether the occipital-parietal axis is probed at early (first-order stimuli) or later levels (second-order stimuli). This reflects a clear pervasive impairment of motion perception in FXS. Furthermore, the deficit seen only with second-order form processing reveals a later-level temporal processing impairment without a concomitant early-level deficit. We take this finding as evidence of a generalized cortical dysfunction in integrative mechanisms of early visual input regardless of its source.

Our use of first- and second-order motion and form stimuli ensured an equitable comparison of functional integrity of the two cortical visual streams at both early and later levels. It is generally believed that first- and second-order stimuli are processed at different levels within the cortical hierarchy[25, 26]. An important consideration in the design of perceptual experiments is to ensure that high-level cognitive factors have little differential impact on the dependent measure. We therefore used an identical instruction set for the motion and form tasks, whether defined by first- or second-order attributes, so as to minimize differences in the cognitive load needed to comprehend the task objective.

Our finding that patients with FXS have elevated thresholds for first- and second-order motion stimuli but normal thresholds for first-order static stimuli can be understood in the context of current knowledge of hierarchical cortical processing. A functional imaging study showed that first-order motion activation appears initially in area V1 whereas second-order motion shows that activation first arises in later areas, such as areas V3 and VP. Both types of motion are further processed in area V5 (also known as area MT)[26]. The preferential input that these areas receive from the M pathway leads to the conjecture that the previously observed impairment of that pathway affects later parietal stream areas in FXS[10]. Indeed, the results of this study strongly support the hypothesis that a pervasive parietal stream deficit is present at both early and later levels within the occipito-parietal axis. Our finding that form perception is affected only at later stages of temporal visual stream processing highlights both the specificity of the parietal impairment as a dysfunction of afferent input (i.e., M pathway impairment) and points to an additional deficit in FXS in cortical integrative processing of all early visual input.

We found an effect of complexity for both parietal and temporal streams. The impairment in motion perception was more pronounced for second- than for first-order stimuli (i.e., fewer patients with FXS were able to complete the second-order task). Similarly, the impairment in form perception was evident only with second-order stimuli. Contemporary models and empirical findings differentiate first- and second-order stimuli by the level at which they are processed along the cortical visual pathways. First-order information is processed by neural circuits in area V1 where local luminance variations are used to detect motion and orientation. For this reason, first-order stimuli are considered to be simpler. However, additional nonlinear processing is required with second-order signals in order to resolve the direction or orientation of this class of visual information, something that is presumed to occur in later visual areas[18, 27]. Second-order visual information is therefore considered to be of a more complex nature because it requires recruitment of more extensive neural circuitry as well as additional processing prior to perception.

The perception of complex second-order stimuli may be more susceptible to neurological abnormalities because there is a greater computational requirement for integration and coordination of low-level inputs. In fact, complexity has been used as a measure of neural integrity and should be considered independently of the functional specialization of the parietal and temporal streams. First- and second-order stimuli have been used to investigate the effects of aging on visual perception[28]. The findings were of a larger decrease in sensitivity for both static and dynamic second-order stimuli but not for their first-order counterparts. These results suggest that the perceptual deficits in older adults are due to diffuse and non-specific cell death in the aging brain[29, 30]. Similarly, we take the deficit in FXS for second-order stimuli that probe both parietal and temporal lobes to suggest that a generalized later– *versus* early-level deficit occurs in this syndrome. However, for the parietal visual stream we propose an additional mechanism whereby the selective deficit in the M pathway is compounded or amplified in later parietal areas that are reliant upon a dominant M input. Such a pervasive deficit in motion perception may account for some of the observable relative performance deficits for neuropsychological tasks with a visual motor component[7-9].

A study investigating putative motion perception deficits in autism revealed normal first-order detection of motion thresholds alongside elevated second-order ones[23]. The authors proposed a deficit in integrative mechanisms acting at higher levels within the cortex rather than a motion perception deficit *per se*. Similarly, we suggest that the elevated thresholds for the more complex second-order form stimulus reflect a neurological deficit in integrative mechanisms in FXS rather than a specific form perception impairment.

Pervasive parietal stream impairment may not be unique to FXS. In fact, several studies have demonstrated deficits in global motion processing in individuals affected by a wide array of etiologically diverse conditions including, autism[31], Williams Syndrome[32], dyslexia[33], and hemiplegia[34], raising the interesting possibility that this stream is more vulnerable during development as compared to its temporal counterpart[35]. Given the importance of including complexity as an independent variable, its absence in prior studies opens up the possibility that integrative deficits may also play a role in other neurological conditions[23].

Patients with FXS show pervasive and selective parietal visual stream impairment at both early- and later-levels of processing. These impairments are accompanied by a sparing of early-level but interestingly, a deficit in later-level form processing. The selectivity of this impairment suggests that early-level form processing is spared but that later integrative mechanisms are compromised in the form-processing pathway as well. We propose that the observed deficits in motion perception in FXS arise as a result of abnormalities acting at two levels. First, pathological features at the neuroanatomical level have beenpreviously reported. Specifically, autopsy material from one FXS patient showed that the entire LGN was almainar and that M-LGN neurons displayed significantly reduced size[10] . Second, patients with FXS at the functional level have selectively elevated thresholds for high-temporal frequency stimuli, information normally relayed by the M portion of the retino-thalamo-cortical pathway.

Our results show the importance of task selection for tests of visuo-perceptual function, especially with regard to parietal versus temporal pathway integrity. The use of first- and second-order visual stimuli may be especially important in identifying the level at which disruption in neurological processing is presumed to occur. And finally, our findings highlight the importance of pinpointing the nature of the perceptual deficits in neurological syndromes and offer potential insight into the development of targeted medical or pedagogical interventions.

10.6. References

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10.8. Tables, Figures & Legends

Figure 1. Examples of the first-order (FO) and second-order (SO) motion and form stimuli employed to obtain motion- and orientation-identification thresholds. When shown, arrows superimposed on the grating represent the direction of motion (i.e., left or right). The physical properties of the form stimuli were identical to the motion stimuli except that they remained stationary (i.e., presented at 0 Hz).

Figure 2. Visual motion thresholds (ordinate) for first- and second-order stimuli and for three participant groups. (A) Only a fraction of the fragile X (FXS) affected participants (5 of 11) were able to perceive the direction of motion of the first-order stimuli while developmental-matched (MA) and age-matched (CA) controls maintained similar thresholds. Patients with FXS for whom thresholds were calculable had significantly elevated luminance thresholds when compared to the MA and CA control groups. (B) Similarly, only a fraction of the FXS affected participants (3 of 11) were able to perceive the direction of motion of the second-order stimuli while MA and CA controls maintained similar thresholds. Patients with FXS for whom thresholds were calculable had significantly elevated contrast thresholds when compared to the MA and CA control groups. An asterisk indicated significance at the 0.017 level.

Figure 3. Visual form thresholds (ordinate) for first- and second-order stimuli and for the three participant groups. (A) A majority of FXS affected participants were able to complete the first-order form task and had similar thresholds when compared to the developmental-matched controls (MA) but not the age-matched controls (CA). (B) All FXS affected participants were able to complete the second-order task. However, when compared to the MA and CA controls, the FXS group had a significantly elevated mean threshold. An asterisk indicates significance at the 0.05 level.

Table 1. Number of participants successfully completing the task.

Figure 1. Kogan et al., 2004

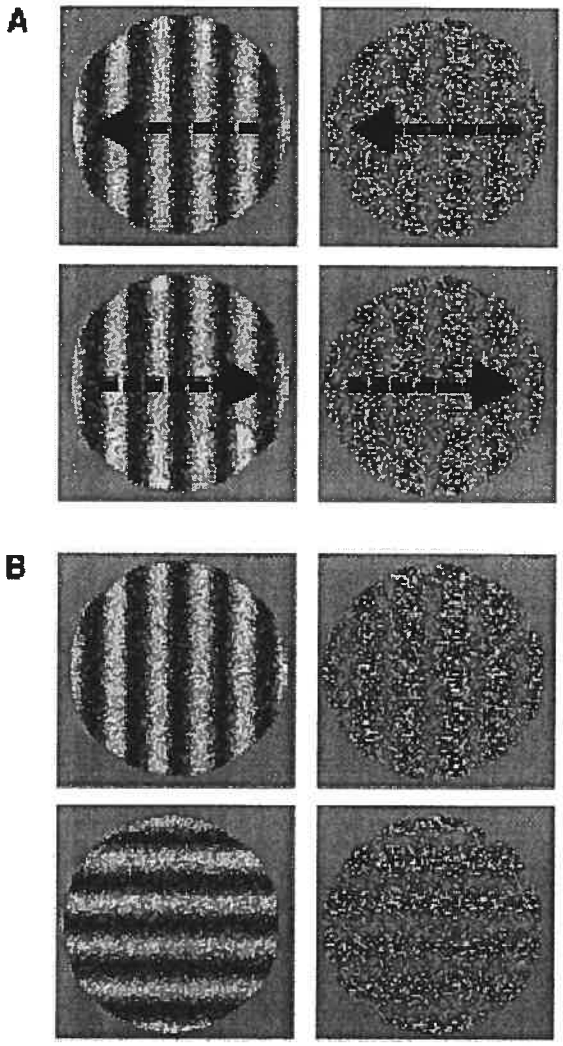

Figure 2. Kogan et al., 2004

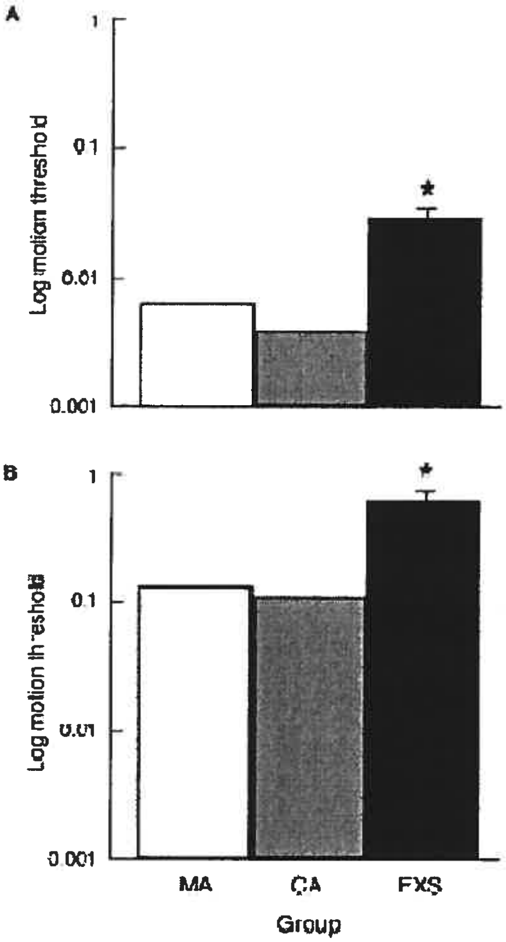

Figure 3. Kogan et al., 2004

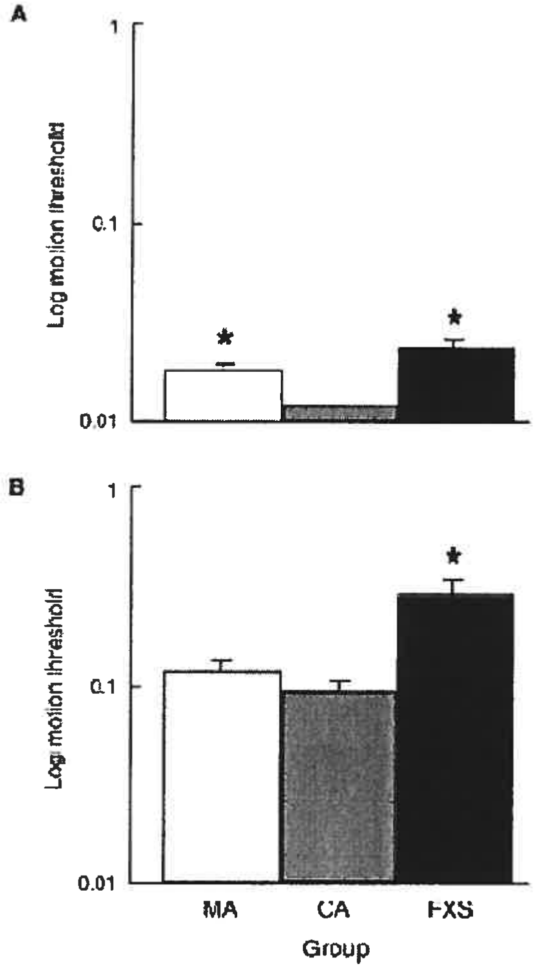

Table 1. Kogan et al., 2004

Task type	Complexity	Fragile X (N=11)	Age-matched (N=11)	Developmental matched (N=11)
Dynamic	First-order	n=5	n=11	n=11
	Second-order	n=3	n=11	n=11
Static	First-order	n=8	n=11	n=11
	Second-order	n=11	n=11	n=11

Chapter 11

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