Enhanced Perceptual Functioning in Autism: An Update, and Eight Principles of Autistic Perception

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We propose an "Enhanced Perceptual Functioning" model encompassing the main differences between autistic and non-autistic social and non-social perceptual processing: locally oriented visual and auditory perception, enhanced low-level discrimination, use of a more posterior network in "complex" visual tasks, enhanced perception of first order static stimuli, diminished perception of complex movement, autonomy of low-level information processing toward higher-order operations, and differential relation between perception and general intelligence. Increased perceptual expertise may be implicated in the choice of special ability in savant autistics, and in the variability of apparent presentations within PDD (autism with and without typical speech, Asperger syndrome) in non-savant autistics. The overfunctioning of brain regions typically involved in primary perceptual functions may explain the autistic perceptual endophenotype.

KEY WORDS: Perception; enhanced perceptual functioning; autism; Asperger syndrome; expertise; savant syndrome; local and global processing; fMRI.

INTRODUCTION

The aim of this paper is to update the Enhanced Perceptual Functioning (EPF) model originally proposed (Mottron & Burack, 2001) as a framework within which the perceptual characteristics of autistic persons could be understood. This model was proposed in alternative to the prevailing model of perceptual functioning in autism at the time, the Weak Central Coherence model (WCC, Happé & Frith, this issue). After 5 years, EPF is clearly a useful framework for the study of perception in autism, but also needs to be revisited in the light of new evidence both consistent and at odds with its basic tenets. We will review the contribution of the original model, and assess relevant work from the past 5 years, in presenting the revised EPF model in the context of eight principles of autistic perception.

Summary and Sources of the First EPF Model

The first conceptualization of EPF (Mottron & Burack, 2001) attempted to account for superior performance in both visual and auditory modalities in several types of domain-specific, "low-level"

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cognitive tasks; atypically high involvement of perception in the accomplishment of complex cognitive tasks; and the centrality of perception-related behaviors in typical every day situations. Superior performance in laboratory situations and superior importance in ecological situations were both attributed to the effect of an overall superior perceptual functioning. We suggested that the operations that are superior among autistic persons can be encompassed under the term "perception", as understood in the 1990s cognitive neuropsychology literature (Ellis & Young, 1988). This broader view of perception ranges from feature detection up to and including pattern recognition. This allowed the inclusion, within a single framework, of both superior performance in one-dimensional discrimination (e.g.: pitch) and superior ability to recognize visual patterns (e.g.: hyperlexia). According to the EPF model, superiority of perceptual flow of information in comparison to higher-order operations led to an atypical relationship between high and low order cognitive processes in autism, by making perceptual processes more difficult to control and more disruptive to the development of other behaviors and abilities. As a part of superior perceptual functioning, a superior perceptual trace was believed to be responsible for enhanced memory of the surface properties of visual and auditory patterns. Some positive symptoms, such as the apparent hypersensitivity to noise, represented the detrimental effect of discrepancies between autistic and non-autistic processing of perceptual information. Conversely, EPF was also viewed as adaptive in some cases, as in the example of Paradoxical Functional Facilitation (Kapur, 1996) where superior auditory perception has a compensatory role in sensory deprivation. Restricted interests in autism would therefore represent the adaptive aspect of EPF, as involving perceptual aspects shared by the class of objects which "root" a special ability (e.g. musical ability grounded in superior pitch perception).

Possible mechanisms for EPF were suggested, following *zeitgeists* of this time, and conforming to the dogma—now questioned by some—that even superior performance should be related to a pathological causal mechanism. These included atypical neuronal growth and connection; cortical rededication; inconstant or unpredictable inhibition by higher-order processes; compensation for a deficit; overtraining with certain materials; a recurring loop formed when an intact function replaces one which is absent or impaired, and in which increased training is perpetuated; and atypical functional persistence. We

favored, at the time, an imbalance, possibly compensatory and adaptive, between complex, high level and simple, perceptual processes. However, the variety of suspected mechanisms revealed our profound ignorance of the "cause" for EPF.

The sources for the original version of EPF were linked to savant syndrome. This followed from Mottron and Belleville's (1993) initial finding that the hierarchic (i.e., containing several embedded levels) processing and graphic construction of visual representation of EC, an autistic savant draftsman, favored local elements. To summarize the main findings of EC's study (local interference, random order of graphic construction and relative slowness in perceiving the global impossibility of a geometric figure), we proposed the "hierarchization deficit model". In this framework, the apparent local bias was not the result of a preference or an integration deficit, but the result, because local features are more numerous than global features, of non-hierarchical access to information favoring local targets. The unique postulated deficit was absence of the precedence for global elements demonstrated by non-autistics, and not the inability to integrate parts into wholes. Accordingly, EC's locally centered perception and graphic construction was associated with a preserved, in fact *outstanding*, ability to reproduce proportions.

The first attempt to generalize EC's particularities to non-savant autistic individuals produced conflicting results. We were not able to replicate atypical hierarchical properties at the perceptual level (Mottron, Burack, Stauder, & Robaey, 1999a; see also Ozonoff, Strayer, McMahon, & Filloux, 1994), although there were clear examples of locally oriented processing in tasks involving graphic construction (Mottron, Belleville, & Ménard, 1999b). Moreover, QC, a prodigious savant autistic musician, had no atypicalities in processing global aspects of musical information, in the presence of outstanding pitch memory (Mottron, Peretz, Belleville, & Rouleau, 1999c). This integrity of global perception echoed the conservation of proportion in EC's drawing.

The need to rework the hierarchization deficit model also became evident in the light of Plaisted, O'Riordan, and Baron-Cohen's (1998a) finding of enhanced visual discrimination in non-savant autistic persons. We realized that a *primary* superiority in perceptual analysis could possibly underlie both local biases in hierarchical perception and construction, and exceptionally accurate reproduction of surface properties of the world, like 3-D perspective or absolute pitch values in savants.

EPF's Development and other Theories of Autism

EPF has both similarities to and differences from the three other accounts of autism related to perception. First, from Frith and Happé's WCC (Frith, 1989; Frith & Happé, 1994; Happé, 1999; Shah & Frith, 1983, 1993), and from our own results (Mottron & Belleville, 1993; Mottron *et al.*, 1999b; Mottron, Peretz, & Ménard, 2000), we retained the idea of local bias. However, whereas WCC emphasized that local superiority was the result of some kind of deficit in constructing global aspects of global figures, we wanted to underline that a deficit in the processing of the global aspects of information may not be the reason for local bias in hierarchical material, and for superior performance in low-level perceptual operations. Instead, we attributed this local bias to a superiority *per se* of low-level perceptual operations. We also wanted to point out that perception as a level of processing may have a particular status among other cognitive operations, a status which becomes blurred in the non-specific (semantic and perceptual) character of WCC. In addition, we disagreed with the "facultative" aspect implicated by the term "cognitive style" ("not a deficit, but a cognitive style") that Happé had proposed in 1999, in reaction to the increasing number of papers demonstrating that global aspects could be typically processed in some conditions. Although the term "style" captures the unpredictable aspect of top-down processes in autism, we were convinced that cognitive differences between autistics and non-autistics had a "mandatory" basis, in the form of a profound and distributed difference in brain organization.

Second, Plaisted's (Plaisted *et al.*, 1998; Plaisted, 2001) idea of superior perceptual discrimination and diminished processing of common features was decisive in pointing to hyper-functioning of low-level perception. However, the EPF account underlined that discrimination was probably not the unique explanatory principle for the various cognitive superiorities exhibited by autistics. Instead, it was one among many other operations (detection, matching, reproduction, memory, categorization *and* discrimination) characterizing a level of processing called perception for non-autistics.

Third, we had been influenced by Minshew's (Minshew & Goldstein, 1993; Minshew, Goldstein, & Siegel, 1995, 1997) proposition that complexity may represent a way to account both for the level of impaired operations, and for their cross-modal aspect.

We mapped the simple vs. complex distinction on the negative vs. positive symptoms distinction: some kind of problem with processing complex material of any type may be responsible for mostly negative symptoms of autism. However, according to Minshew at the time, perception was considered as intact and therefore poorly informative in understanding autistic symptoms or etiology (Minshew *et al.*, 1997). In contrast, we introduced the idea that enhanced perception was at least partly responsible for positive symptoms of autism. Therefore, perception was informative in understanding autistic differences. Our contribution was to emphasize that perception was not intact, in the sense of "similar to that of non-autistics", but superior to that of non-autistics in absolute performance and relative involvement in laboratory and ecological settings.

Finally, WCC, enhanced discrimination, and diminished processing of complexity share the idea that a common mechanism (either a deficit or an over-functioning) may be implicated in the particularities evident in processing of social and non-social information by autistics. We agree with this, and that focusing exclusively on deficits in the processing of social material, as in alternative, "social first" models (e.g., current reviews in Schultz, 2005; Dawson, Webb, & McPartland, 2005) may miss the "pervasive" character of autistic differences. In comparison to approaches not dependent on a social/non-social distinction, "social brain"-based models appear to us too narrow to encompass the entire range of positive symptoms or the enhanced performance of savant and non-savant autistics. For example, it seems improbable that both superior processing of luminance-defined static stimuli (non-social domain; Bertone, Mottron, Jelenic, & Faubert 2005); and an enhanced ability to recognize faces with a one-part prime, coupled with typical configural face recognition (social domain; Lahaie *et al.*, 2005), result from an innate autistic deficit in social motivation.

The Updated EPF Model: Eight Principles of Autistic Perception

Our update of the original EPF model includes the contribution of 5 years of empirical findings of autistic perceptual functioning, resulting in a revised and expanded articulation of the model. Accordingly, we propose principles that both characterize autistic perception and provide a framework for its study. These principles will be presented in order from what

we estimate are the most consensual, to the most speculative.

Principle 1: The Default Setting of Autistic Perception is more Locally Oriented than that of Non-autistics

The multiple cognitive tasks that are used for the purpose of reproducing or explaining the locally oriented behavior of autistics are of two kinds–long exposure hierarchical tasks and short exposure hierarchical tasks.

Long exposure hierarchical tasks, imported from clinical testing, are those that allowed the initial serendipitous discovery of autistic peaks of ability. These tasks require tens of seconds to be completed, involve the visual perceptual component of distinguishing between local and global levels, but also attention, executive planning, and motor components. For example, this is the case of the classical block design (BD) task of the Wechsler scales (Shah & Frith, 1993) for which each trial involves a local level (a single block) and a global level (the figure to be reproduced) and is completed in approximately 5–60 seconds. This is also the case with graphic reproduction of possible and impossible figures (Mottron *et al.*, 1999b) and with the Embedded Figures Task (EFT; Joliffe & Baron-Cohen, 1997).

Autistics display a constant pattern of enhanced performance in these tasks. When the processing of a global aspect conflicts with a local analysis among typically developing persons (perceptual cohesiveness in BD, impossibility of a figure in graphic construction figure tasks, visual context in EFT), autistics perform at a level superior to their comparison groups. In contrast, when this conflict is diminished, for example by segmentation to diminish the perceptual cohesiveness in BD, or in copying possible vs. impossible figures, autistics are brought back to a level of performance equivalent to that of typical individuals. This indicates that autistics are not obliged to use a global strategy when a global approach to the task is detrimental to performance. For example, autistic persons are better able than typically developing persons to copy impossible figures (Mottron *et al.*, 1999b), and as able to identify that impossible figures are impossible (Brosnan, Scott, Fox, & Pye, 2004). In contrast, typical individuals cannot adjust to the situation of an impossible figure coinciding with a possible drawing. However, the use of gestalt principles is not mandatory: Brosnan *et al.* (2004), in an investigation of gestalt-type principles, found that with no time

constraints autistics were less likely to choose certain gestalt principles under some conditions, while clearly identifying and making use of gestalt principles under other conditions.

Conversely, autistics are not rigidly stuck with a local strategy that would be beneficial only in a certain type of task. Accordingly, in a variant of BD, where using a global strategy was beneficial for pattern reproduction, Caron, Mottron, and Berthiaume (submitted) showed that a subgroup of autistics presenting with a peak in BD were superior on this task as compared to a group matched in non-verbal intelligence. This same group was also superior to a comparison group in a wide range of perceptual tasks, assessing long-term visual memory, visual search, perceptual discrimination, and a visual motor task. The absence of effect of increasing the perceptual cohesiveness of the figure to be reproduced dramatically contrasted between groups, as the execution time in typical individuals doubled, without influencing autistics with or without BD peak. However, the superiority of the autistic group in a global task, as well as in a series of tasks without hierarchical components, clearly discounts any explanation that this superiority derived from a deficit in analyzing global aspects of a figure, and instead favors an overall superiority in visual processing.

Short exposure hierarchical tasks include binary, forced choice responses, at the level of hundreds of ms. In comparison to long-exposure tasks, they are plausibly less influenced by conscious executive aspects and most motor components. Although some of these tasks are considered perceptual (e.g., Navon-type tasks) and others attentional (e.g., visual search), they all involve the low level, "pre-attentive" perceptual analysis of psychophysical dimensions that compose the visual display, the analysis of its local-global aspects (small vs. large letters; target vs. distracters), and the distribution of attention resources to both the relevant and irrelevant level of analysis.

In short exposure hierarchical tasks, autistic persons display the same enhanced ability to disembody targets from surrounding task-irrelevant stimuli that is evident in long exposure tasks. On these types of tasks, this enhanced ability takes the form of faster target detection in featural and conjunctive visual search (Jarrold, Gilchrist, & Bender, 2005; O'Riordan, Plaisted, Driver, & Baron-Cohen, 2001), more accurate local target detection of visual (Plaisted, Swettenham, & Rees, 1999) and auditory (Mottron, Peretz, & Ménard, 2000) hierarchical stimuli, more

accurate discrimination of elementary stimuli differing at the featural level (Plaisted, Saksida, Alcantara, & Weisblatt, 2003, exp. 1 & 2), diminished influence of increasing number of distracters in visual search tasks (O'Riordan et al., 2001), and diminished local-to-local interference to visual (Mottron, Burack, Iarocci, Belleville, & Enns, 2003) and auditory (Foxton et al., 2003) hierarchical stimuli. For social material (faces), local orientation is shown by a preference for local information in identity matching (Deruelle, Rondan, Gepner, & Tardif, 2004) and a superior priming effect of face parts (Lahaie et al., in press).

Another manifestation of locally oriented perception is evident in enhanced local to global interference. Reaction times to global level stimuli among autistics are more affected by incongruent stimuli at the local level than are those of typical individuals (Rinehart, Bradshaw, Moss, Brereton, & Tonge, 2000). A similar local to global interference for incongruent stimuli in the presence of a preserved global detection for congruent stimuli (greater slowing in the inconsistent case when global identification is required) was found by Behrmann et al. (2005, exp. 2).

A consistent result in these types of tasks is that autistics perform at a typical level for various aspects of multi-feature, global, or holistic perception. The ability to detect a target defined by a combination of properties seems unremarkable (O'Riordan et al., 2001). Perceptual recombination of features is generally preserved, except in specific cases that cannot be considered as representative of the autistic population (Mottron et al., 1997). Visual illusions, which are used to assess perceptual recombination at various levels of hierarchical processing, appear probably normal (Ropar & Mitchell, 1999). Typical holistic processing is manifested by standard effect of "good form" on visual target detection (Mottron et al., 1999a, exp. 2); typical global advantage in the auditory modality (Mottron et al., 2000); typical global advantage under various visual angles (Mottron et al., 2003); faster response to global as compared to local, configurations (i.e. global advantage; Mottron et al., 1999a; 2003); and slower response to local stimuli in global incongruence condition (global interference; Rinehart et al., 2000).

The default setting of hierarchical autistic perception can also be assessed within short exposure hierarchical tasks, by prompting local or global processing by priming the participant to the likelihood of the occurrence of the stimulus at one level or the other. For "many" primes, autistics present a shorter response time for element similarity than for global similarity, contrary to the comparison group. However, accuracy was identical for both groups (Behrmann et al., 2005, exp 3; but see Plaisted, Dobler, Bell and Davis, this issue). Similarly, autistics are influenced by structural global bias, although to a lesser extent than typically developing individuals (Iarocci et al., this issue). For faces, integrity of global level analysis is demonstrated by typical gains from the addition of configural information, typical inversion effect (Lahaie et al., in press), and by superior recognition of an embedded facial target compared to an isolated one (Joseph & Tanaka, 2002).

In sum, these findings, often described as contradictory, instead appear surprisingly consistent considering the variety of the paradigms in use, and their presence in visual as well as auditory modalities, for short as well as long exposure tasks. The default setting of the autistic perceptual system toward local information contrasts with typical hierarchical processing (Robertson & Lamb, 1991) that combines "global advantage", the superior relative speed and accuracy of global target detection, with "global interference", the asymmetric influence of global processing on the detection of the local stimuli.

Principle 2: Increased Gradient of Neural Complexity is Inversely Related to Level of Performance in Low-Level Perceptual Tasks

Only a small number of studies have investigated dimensional aspects of autistic perception, independently of the confounding factor of attention, the putative effects of a different understanding of task instruction, and the intrinsic ambiguity of finding interpretation in multidimensional tasks. This situation is realized in discrimination tasks. In the visual modality, unidimensional investigations have been mostly done for complex movement perception (see Bertone & Faubert, this issue), with the conclusion that discrimination thresholds for global motion (Milne et al., 2002; Pellicano, Gibson, Maybery, Durkin, & Badcock, 2005), second-order movement (Bertone, Mottron, Jelenic, & Faubert, 2003), and biological motion (Blake, Turner, Smoski, Pozdol, & Stine, 2003) were elevated in autism. Thresholds for flickering stimuli, indicative of ventral magnocellular stream functioning, were found unremarkable by Pellicano et al. (2005) and by Bertone et al. (2005). There is currently no indication that autistics might be superior in any dynamic task but, on the other hand, some doubt that it is movement *per se* which is misperceived (Bertone, Mottron, & Faubert, in press).

This pattern of findings displays a striking contrast with the evidence of superior performance by autistic persons on static, "simple" discrimination tasks. For example, Plaisted *et al.* (1998a) demonstrated enhanced discrimination of novel, highly similar stimuli (seven circles randomly positioned on a screen). In this task, the stimuli to be discriminated differed only in their place relationships, which involve some kind of relational analysis among, at least, pairs of features. Therefore, these stimuli cannot be considered as "one-dimensional", and are not different, in this regard, from configural stimuli. Bertone *et al.* (2005) studied orientation-identification thresholds for first- and second-order gratings. As compared to typically developing persons, high-functioning autistics (HFA) were better able to identify the orientation of simple, first-order gratings, but less able to identify the orientation of complex, second-order gratings. This unusual threshold profile is not concordant with a straightforward intact vs. impaired dichotomy as it depicts a different "default setting" of discrimination performance according to the level of complexity of visual information. Superiority in discriminating low-level visual input was also observed in a random pattern discrimination task, where a subgroup of HFAs selected on the basis of presenting a BD peak required less exposure time than typically developing individuals to obtain a comparable performance in discrimination, while their absolute discrimination threshold was similar to that of typically developing participants (Caron, Mottron, & Berthiaume, submitted). This notion that one-dimensional, low-level visual processing is different in autism is further supported by the finding of less positive occipital ERP activity associated with high spatial frequencies during the passive viewing of visual stimuli filtered for high or low spatial frequencies (Boeschoten, Kemner, Kenemans, & Engeland, submitted; Jemel *et al.*, 2005; see Kemner & van Engeland, this issue). In consequence, the finding of unremarkable central vs. peripheral representation of the visual field in a group of persons with various pervasive developmental disorders (Hadjikhani *et al.*, 2004) is not sufficient to assert, as do these authors, that "low-level visual processing is intact in high ability individuals with autism, and that social-communication deficits in autism are probably not the result of primary visuo-perceptual deficits".

Similar to what is observed in the visual modality, a complexity gradient between neurally defined simple vs. complex tasks may explain the differential level of performance in the auditory modality (Samson *et al.*, this issue). Enhanced discrimination of pure tones in the auditory modality (Bonnel *et al.*, 2003) may be considered as the visual counterpart of hyper-discrimination of first-order gratings. Pitch identification and discrimination, which are the simplest tasks according to a hierarchical neural organization of auditory perception, are enhanced among autistics and are tasks for which savant abilities spontaneously occur. In contrast, tasks involving temporal and spectral complexity are those for which autistics display deficits or inferior brain activation. Commonalities between the definitions of "primary" sensory areas in both visual and auditory modalities, such as small receptive fields, tonotopia or retinotopia, and feed-forward flow of information, may be implicated in this pattern of performance.

Neurally "simple" perceptual brain regions overlap with the concept of superior local overconnectivity recently forwarded by Belmonte *et al.* (2004) to summarize the "higher functional connectivity", "hyperspecialized" centers and "abnormal specialization of the neocortical processing centers" suggested by Just, Cherkassky, Keller, and Minshew (2004). The concept of local overconnectivity, embedded in the underconnectivity hypothesis (UCH), is based on Minshew's complexity hypothesis, and on CD Frith's (2003) hypothesis of diminished connectivity between frontal and temporal regions (Castelli, Frith, Happe, & Frith, 2002; Courchesne & Peirce, 2005; Frith, 2003; Just *et al.*, 2004; Koshino *et al.*, 2005). As the UCH aims to account for superior perception in autism, its current explanatory value for perceptual patterns of performance will be examined here.

According to the UCH, long range connections, required for higher level processes, would be impaired in autism. Long connections are predominantly used both in frontal lobes and in any task requiring the cooperative action of several interconnected regions. In contrast, short range intraregional connections, within one brain region dedicated to a domain-specific operation like those composing low-level perception, would be preserved or even superior in autism (local overconnectivity). The main empirical basis for this model is the diminished level of synchrony of activation among brain regions typically implicated in complex tasks, in opposition to a preserved or increased activation and synchrony in posterior regions.

The UCH predicts local overconnectivity as a developmental result of generalized interconnectivity. According to Just *et al.* (2004), "A processing center

that has inadequate connectivity to another center with which it would normally collaborate might develop processing algorithms that are less dependent on collaborative input and hence might become hyperspecialized'. The causality of the deficit could also be in the opposite direction, such that centers that inherently develop more self-reliant algorithms might also develop weaker connections to other centers."

However, several theoretical and empirical gaps have still to be filled before the UCH becomes a satisfying explanation for the autistic perceptual pattern of performance, and specifically, of superior perceptual performances. First, the neural basis of the UCH is represented by a limited ratio (10 of 186, in Just *et al.*, 2004) of significant diminished synchrony of activation among brain regions that were involved in a task, and there is some current latitude between a generalized (Just *et al.*, 2004) vs. a localized (Koshino *et al.*, 2005) interpretation of the broad concept of underconnectivity. A related consequence of this uncertainty is that predictions derived from the UCH are contradictory at least for frontal lobes (underconnectivity in Just *et al.*, 2005; over-synchrony in Courchesne & Pierce, 2005). Second, there is still an inferential leap between functional diminished synchrony and hardwired diminished connectivity. Third, autistics present at least one example of superior long-range connectivity (between the left dorso-lateral prefrontal cortex and the right inferior temporal lobe, Koshino *et al.*, 2005), that is inconsistent with a generalized UCH. Fourth, the frequently outstanding performance of autistics in the Raven matrices, a complex and general test of fluid intelligence that requires high-level abstract reasoning (Dawson, Mottron, Jelenic, & Soulières, 2005), is difficult to reconcile with a general limitation of long-range connectivity. Fifth, *increased* brain volume in white matter in autism (Herbert *et al.*, 2004; Schultz *et al.*, 2005) still needs to be related to *inferior* physical connectivity. Sixth, the observation of a diminished synchrony on tasks in which autistics show dramatically shorter reaction times without a significant decrement in accuracy (Just *et al.*, 2004), suggests that underconnectivity has no detrimental influence on some higher-order complex tasks. These criticisms diminish the explanatory power of the UCH for negative symptoms of autism.

To summarize, the finding of a dissociation within perception opposing performance in neurally defined "simple" and "complex" tasks indicates that neural complexity may be implicated both in relatively superior or inferior perceptual performances. However, this does not imply that superior performances result from inferior ones, as in the compensatory mechanism proposed by WCC and the original EPF model. Other explanations for this dissociation could be that some basic information learning and storage properties (e.g. lateral inhibition) may be formatted differently with a consequence on both types of operations, associated or not with "expertise effects" (see principles 6 & 7).

Principle 3: Early Atypical Behaviors have a Regulatory Function Toward Perceptual Input

The notion that autistic children present atypical visual behavior toward social information is one of the most documented abnormalities evident in young children with autism (e.g. Chawarska, Klin, & Volkmar, 2003 for a recent review). However, atypical visual exploratory behaviors for inanimate objects also date to the first description of autism (Kanner, 1943) and are now integrated in the clinical knowledge of autism. In a recent prospective longitudinal study of children considered likely to develop autism, Zwaigenbaum *et al.* (2005) found that longer fixation on objects could discriminate autistic from non-autistic children as early as one year of age. We found that the most frequent atypical visual behaviors among 15 autistic toddlers aged 9–48 months were lateral glances, mostly oriented toward moving stimuli (the child's own fingers, a manipulated object, or a surrounding moving object). This behavior consists of staring at an object with the pupils in the corner of the eyes, while maintaining the head either in the direction of the object, straight ahead, or in a direction opposite to the object. Lateral vision is associated with the filtering of high spatial frequency (detail perception) information and the facilitation of high temporal frequencies (movement perception) in higher vertebrates. Detail perception being enhanced (principle 1) and movement perception being diminished (principle 2) in autistic adults, we interpreted the high prevalence of lateral glances among autistic toddlers as an early attempt to limit otherwise excessive amounts of information and/or to focus on optimal information for a given task (Mottron *et al.*, in press).

Principle 4: Perceptual Primary and Associative Brain Regions are Atypically Activated During Social and Non-Social Tasks

Findings from functional imaging studies consistently indicate that, despite typical levels of performance, autistics display an enhanced activation of visuo-perceptual regions (occipital or occipito-temporal) in association with a diminished activation in regions that are devoted to "higher order" (frontal) or "socially relevant" (e.g.: fusiform face area or FFA) tasks among non-autistics (but see Hadjikhani et al., 2004; and Pierce, Haist, Sedaghat & Courchesne, 2004, for evidence of typical levels of FFA activation). This pattern of findings is observed in both perceptual and non-perceptual tasks and for both social and non-social stimuli.

For non-social tasks, the first result in this direction was that of Ring et al. (1999), using functional magnetic resonance imaging (fMRI) to record activation during an EFT. The right lateral occipital cortex (Brodmann Area [BA] 17, 18 and 19) was more activated in the autistic group, whereas left occipital cortex, bilateral parietal cortex, and right prefrontal cortex were more activated in the comparison group. Further studies indicated that this pattern was very common. Schultz (unpublished data) found a significant hyper-responsiveness to patterns (vs. objects) in autistics in more posterior regions of the right lateral and mesial fusiform gyrus (BA 19). Belmonte and Yurgelun-Todd (2003) found ventral occipital activity, whereas activation in superior parietal lobes evident in typically developing controls was absent in the autistic group. The task was a visuospatial, covert attention shifting task during fMRI. Using PET, Hazlett et al. (2004) reported a non-significant increased occipital (BA 19) and parietal (BA 39 and 7b) activity during a word learning task. A better performance was correlated with higher frontal activation in controls, but the reverse was true for autistics. Similarly, in a spatial attention task, Haist, Adamo, Westerfield, Courchesne, and Townsend (2005) reported activations related to physical eye movements located within right occipital gyri and bilateral lingual gyrus in an autistic group, whereas the comparison group activated more frontal regions. Luna et al. (2002) observed a bilateral activation of visual cortex in the autistic and non-autistic group during visually guided saccades, whereas the typical activation in left frontal cortex was almost absent in the autistic group. During an N-Back task, an autistic group had more

activation and local temporal synchrony in fMRI than the comparison group in the inferior temporal and occipital posterior regions (Koshino et al., 2005). Lastly, an autistic group displayed more parieto-occipital activation and frontal (BA 8 and 10) than a comparison group during the fMRI recording of a visuo-motor learning task (Müller, Kleinhans, Kemmotsu, Pierce, & Courchesne, 2003).

The same pattern of superior posterior activation was found in several social tasks. Using complex vocal sounds in an auditory oddball paradigm, Kemner, Verbaten, Cuperus, Camfferman, and van Engeland (1995) found an enhanced P300 in the occipital site (O1). As compared to typically developing persons, Hubl et al. (2003) observed reduced fusiform gyrus activity in 10 autistic participants during face processing, but an enhanced activation in the medial occipital gyrus (lateral occipital complex). Pierce, Müller, Ambrose, Allen, and Courchesne (2001) identified an autistic participant who displayed a unique occipital activation during a face decision task. In explicit and implicit processing of emotional faces, Critchley et al. (2000) found greater activity in autistics than in controls in the left superior temporal gyrus and left peristriate visual cortex. Hall, Szechtman, and Nahmias (2003) found that when autistic persons attended to a pair of facial stimuli while a prosodic voice was presented, they were unique in activating BA 17 (V1) in emotion perception compared to gender perception. The comparison group in Hadjikhani et al. (2004) showed less activation in the infero-occipital gyrus than the PDD group during passive observation of faces. In a theory of mind task (Baron-Cohen et al., 1999), frontal and amygdala activation were "replaced" in autistics with superior temporal gyrus activation. The autistic group investigated by Castelli et al. (2002) displayed a minor, non-significant superior activation of extrastriate areas, but also an inferior synchrony of the latter areas with the superior temporal sulcus while looking at animated shapes which represent social interaction for non-autistics. Overactivation of posterior, visuo-perceptual regions during a large array of tasks and material processing therefore appears robust enough to resist the variety of methodology in use.

Principle 5: Higher-order Processing is Optional in Autism and Mandatory in Non-Autistics

Most cognitive research in neurodevelopmental disorders is based on the assumption that the

between-group differences revealed by empirical work are stable and intrinsic to the condition under study. However, when exposed to a cognitive task, autistic individuals present multiple sources of response variability that differ from those observed in typical individuals. For example, commenting on Ropar and Mitchell's (1999) conflicting findings about autistic perception of visual illusions, Brosnan *et al.* (2004) remarked that individuals with autism are sensitive to visual illusions (for example the Muller–Lyer illusion) when asked "which line looks longer" but not when asked "which line is longer". The latter authors suggest that autistics have access to physically accurate or psychologically distorted representations dependent upon the cue in the question. This variability is especially important for the study of autistic perception as the versatility of the influence that high level perception exercises on low-level perception in autism contrasts with the mandatory laws of global precedence, gestalt laws, or categorization effects observed among typical individuals.

This optional property of higher-order interventions in lower-order operations is found at one of the most elementary levels of cognition, perceptual categorization. Categorical perception occurs when there is a qualitative difference in the perceived similarity between stimuli according to whether they are in the same category. Categories therefore have a top-down influence on the discrimination of their members. Soulières, Mottron, Saumier, and Larochelle (in press) used a discrimination task and a classification task with a continuum of thin to wide ellipses. The representation of the categories was similar in both groups, as demonstrated by indistinguishable classification curves. However, the autistic participants displayed no facilitation of discrimination ("discrimination peak") near the boundary of the categories in a discrimination task, which suggests a reduced top-down influence of categories on discrimination. In a second study on the processes involved in category learning, Soulières, Mottron, Giguère, and Larochelle (submitted) used feedback to train participants to distinguish between two categories of imaginary animals after a same-different and a discrimination task. In the discrimination component, the autistic participants were less affected than non-autistic participants by increasing the number of attributes differing among the stimuli. In the categorization component, the autistic participants were slower to reach their maximum level of accuracy, which was however identical in both groups.

Categorization of relatively complex visual information is therefore successfully performed by autistics, though perhaps by using a reduced number of dimensions. Together, the results from these studies, and those from Molesworth, Bowler, and Hampton (in press) showing typical performance in two categorization tasks, suggest that autistic individuals can achieve categorization at a similar level as non-autistic individuals. However, autistics may focus on fewer dimensions to categorize, or may not automatically categorize, which can result in slower category learning.

Another example of access to perceptual information without influence from non-perceptual information is in the "slant circle" experiment by Ropar and Mitchell (2002). The task consists of adjusting a computerized ellipse to the apparent shape of a target ellipse, in various conditions of contextual cues and knowledge about this ellipse. There are two conditions, one where contextual cues indicate that the presented ellipse is actually a slanted circle, and one where these cues are eliminated. In the latter condition, participants were or were not made aware that this ellipse corresponds to a slanted circle. The autistic participants exaggerated circularity similarly to their comparison group when given contextual cues, but to a lesser degree specifically in the condition without contextual cues. This indicates that autistics had a superior access to the "perceptual reality" of the ellipses, without being influenced by their previous knowledge. To summarize, autistics present with a greater autonomy of discrimination processes from the top-down influence of categorization, and a greater autonomy of perception as a whole toward higher-level functions—which is notably different from a deficit.

Principle 6: Perceptual Expertise Underlies Savant Syndrome

A remarkable aspect of "savant" performances is that domains of information (e.g., calendar) and types of cognitive operations performed on this material (e.g., list memory) are restricted, and highly similar among observers. The result is a small number of savant capabilities, including calendar calculators, list memory, 3-D drawing, detection of prime numbers, mental computation and music memory and improvisation. In our previous EPF account of savant performances, savant musicians were invoked as heuristic tools to understand the role of perception in savant abilities. A superior pitch processing ability,

demonstrated in musically naïve autistics, was supposed to favor the choice of musical material through the initial encounter of this material. This initiated a restricted interest for music, a consecutive over-exposure to musical regularities, with the consecutive implicit learning of musical laws. We predicted that other savant abilities (e.g. 3-D drawing) were also grounded on superior low-level abilities.

This approach will now be refined, while maintaining the special status of perception in the birth and development of savant ability. Savant abilities may represent the autistic equivalent of what "expertise" is for non-autistic individuals. Special abilities would use a bottom-up instead of a top-down choice of domain of application, involve different domains of information, substitute self-reward for social reward, make a different use of perception and memory, and rely on implicit rule extraction vs. explicit learning. Savant abilities rely also on different relations among the various cognitive operations involved in their accomplishment, and entertain a unique relation with general intelligence. We now hypothesize that the development of savant ability requires five distinct components, including an encounter with a *perceptually defined class of units*, a *brain-behavior cycle*, *expertise effects*, *implicit learning*, and *generalization to new material*.

Special abilities operate on series of perceptually defined units that are rigidly defined for each savant but present the same phenomenalistic properties for all savants. Even if special abilities may sometimes reach a high level of abstraction, we contend that they are all "rooted" by their composition in series of perceptually recognizable elements. The choice of these units is plausibly constrained for the entire autistic population, as indicated by the very high level of similarity of special abilities all over the world. These units appear to satisfy the following phenomenal criteria: they are presented in organized patterns (books, calendars, phonebooks, mechanical objects; tonal melodies, prayers, lists); they share a high level of perceptual similarity across time and space (letters for hyperlexia, digits for calculators, letters and digits for calendar calculators, 2-D of 3-D visuo-perceptual properties for savant mechanists and draftsmen, pitches for savant musicians); and they belong to a defined combinatorial series (digits, letters, "geons", chromatic scale).

At the individual level, a logical sequence leading to savant abilities includes an encounter with a certain material within a critical period during which the class of units is "chosen" on the basis of their phenomenalistic properties[1] and of their exposure to the individual. This step represents the *imprinting stage* of the special ability—similar to that which has been demonstrated in the development of non-autistic absolute pitch possessors (Zatorre, 2003). Support for this stage is found in the traces of a temporally defined encounter, still visible at the mature stage of the special ability. These traces may be responsible for the apparently arbitrary selection of the class of objects, usually referred to as being "restricted". This can be seen in the case of calculation span for calendar calculators. For example, DBC presented hyperlexic behaviors before practicing calendar calculation, which indicates that interest for units composing calendars (letters and digits) preceded his interest for calendars. DBC may therefore have arrived at calendars due to their phenomenal and formal properties, corresponding more to the type of information an autistic individual processes the best. In addition, the boundaries of DBC's calendar knowledge (Mottron, Lemmens, Gagnon, & Seron, in press), as frequently observed (Miller, 1999), corresponded approximately to his years of special interest for calendars. It suggests that the encoding of calendars actually encountered is an essential component of calendar calculation ability.

Our hypothesis is that the encounter of a phenomenal regularity forms the "perceptual root" of the savant ability. This perceptual root of savant ability would be responsible for the apparent "material specificity" of autistic peaks of ability, which is not the equivalent of the modularist approach to autistic cognition defended by Johnson, Halit, Grice, and Karmiloff-Smith (2005). Accordingly, we hypothesize that it is because low-level perception works differently and with a superior level of discrimination that materials possessing a certain perceptual feature (as music for pitches, mechanics to movements or 3D features), become the object of a "restricted" interest.

The development of savant ability can be understood within the context of a *brain-behavior cycle* in which repetitive behaviors in a specific area of functioning "train" a processing system to expertise, but may impede the development of other special abilities. This is evident as savant abilities always involve a behavioral pattern of a single restricted and repetitive interest for a certain class of stimuli, such as pitches, words, or letters. This leads to a "stoppage

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[1] According to the autistic member of our team, M. Dawson, "We do what we can with what's around."

rule" with the majority of "savant" individuals having only one, or exceptionally two or three domains of savant capabilities. The behaviorally obvious positive emotions that are linked to the manipulation of the relevant material may form a self-rewarding loop that fuels the special ability (Mercier, Mottron, & Belleville, 2000). The negative outcome of the special ability is that the restricted interest may lead to the neglect of entire domains of information.

Devoting a large amount of time to the manipulation of a specific material may produce *expertise effects* in autistics in several ways. One, it would reinforce the perceptual traces of units that compose a specific material (e.g. pitches, letters, digits) in a specific modality, thereby making these units easily and more quickly manipulated ("frequency" effect; Segui, Mehler, Frauenfelder, & Morton, 1982). For example, Heavey, Pring, and Hermelin (1999) showed that savant calendar calculators are better able than IQ-matched typically developing persons to remember calendar information, presented in a different format than that of typical calendars. Pring and Hermelin (2002) showed that a savant autistic calendar calculator was superior to a typically developing comparison individual in remembering new letter-digit associations. Similarly, NM, a proper name memorizer, displayed outstanding memory for lists of proper names, but not common names (Mottron, Belleville, & Stip, 1996). Bus number memorizers show superior memory of new number associations, but not of fruits and vegetables (O'Connor & Hermelin, 1989). If FFA functions overlap in autistics and non-autistics, these expertise effects may help understand why FFA, implicated in the processing of classes of stimuli for which non-autistics have an expertise, is activated by exposure to the domain of special interest (Grelotti et al., 2005). Moreover, the fusiform gyrus, which includes the FFA, is apparently the brain structure which, on average, displays the largest volume increase in autistic individuals aged 15 years and up, unselected for special ability, as compared to non-autistics (Schultz et al., 2005). This would indicate that autistic expertise may not coincide with "overt" savant expertise–and possibly, extends to an entire modality, resulting in a "covert" expertise and peaks of ability.

An initially perceptual delineation of the object class to which a special ability is devoted may determine a feed-forward direction of expertise learning, resulting in *implicit learning*. The repeated exposure to structured displays composed of these units would allow the implicit learning of the contextual regularities characterizing these units, such as harmony rules for pitches, 3-D rules for spatial features, calendar regularities for letter and digits, graphic contextual rules for written code, and syntax for language. Across various anecdotal reports, the mastering of complex rules for structured material does not follow the same time course in autistics and non-autistics. The process begins abruptly after an exposure period and is apparently devoid of practice for autistics, but is progressive and includes considerable training and overt manipulation among non-autistics.

The special ability at its peak level would entail the creative manipulation of large sets of these units that are structured by implicitly learned rules. Some aspects of this manipulation may be considered as a memory performance, as is the case for the "redintegration" (Schweickert, 1993) of missing pieces of information from a recall cue (e.g. recovering day-date correspondence in calendars to which the person has been exposed). Non-algorithmic retrieval, random errors, equivalent retrieval according to semantic categories, and multi-directionality of access, demonstrated for calendar calculation (Mottron et al. in press), would characterize these types of operations. However, savant performance largely exceeds memory, and is a manifestation of autistic intelligence (Dawson, 2004). The generalization of the material in memory to new material structured by the same rules, such as retrieving dates by extending the rules of the calendar to past or future years, the graphic creation of a town by combination of elementary 3D "geons", mathematical inventiveness, and musical improvisation, is the ultimate stage of savant ability. At this stage, the merging of savant abilities with typical uses of explicit rules, including mathematical algorithms, musical notation, and explicit syntactic rules, is possible. An example of this integration of non-autistic notation is attested to by some calendar savants who display a secondary use of typical algorithms. This may also explain the counterintuitive observation that levels of savant performance are correlated with IQ level (O'Connor, Cowan, & Zamella, 2000), as are peaks of ability (Mottron, 2004).

Principle 7: Savant Syndrome is an Autistic Model for Subtyping PDDs

There are currently two major sources of heterogeneity in primary PDDs, i.e. individuals presenting

with an autistic phenotype unrelated to other diagnosable conditions and/or gross neurological abnormalities. The first distinction, currently labelled the Asperger vs. autism distinction, opposes individuals with a precocious use of speech, unremarkable visuo-spatial abilities, and frequent motor clumsiness, to individuals with superior visuo-spatial abilities and late or absent use of expressive speech. Within the latter autistic group, a secondary source of variability opposes the individuals who use oral language to those who don't. Use of overt speech has to be distinguished from a high vs. low functioning distinction, considering the high IQs (measured by, e.g., PPVT or Raven's Progressive Matrices) of certain "mute" autistics, and their frequent ability to read and to communicate via text. The other distinction is that some members of the autistic group develop considerable expertise in certain materials and are labelled "autistic savants".

There are no available convincing data that autism with vs. without overt peaks of ability, with vs. without overt speech, or overall autism vs. Asperger syndrome, differs at a genetic level. Even language abilities cannot be used to distinguish autism from Asperger syndrome, as written language experts are as representative of autism as oral language experts are representative of Asperger's. Although attractive, the endophenotype explanation of differences within autistic cognitive profiles produced conflicting findings (Nurmi *et al.*, 2003; Ma *et al.*, 2005). Also, the search for anomalies in the genes implicated in dysphasia in available autistic samples was unsuccessful (Gauthier *et al.*, 2003; MRC, 2001; Tager-Flusberg, Joseph, & Folstein, 2001; Volkmar, Lord, Bailey, Schultz, & Klin, 2004). The sole phenotypic distinction which is currently supported by data is that which separates primary (Pavone *et al.*, 2004) or "essential" (Miles *et al.*, 2005) autism, which is characterized by higher IQ, high heritability, low epilepsy rate, and absence of brain macroscopic abnormalities, vs. secondary (or "complex") autism, with higher incidence of mental retardation, epilepsy and brain abnormalities, and lower heritability.

In the absence of genetic subtyping, the explanation of PDD subtypes by a post-natal overspecialization processes have to be also considered, inasmuch as savant syndrome provides an autistic model for the subtyping of PDD. The heterogeneity of the autistic phenotype at older ages would result from an overspecialization to a certain perceptual material inherent to the developmental course of autism. Autistic subtypes with and without a visuo-spatial peak, autism with or without overt speech, and even the autism vs. Asperger distinction may be at least partially produced by differences in objects of expertise, in opportunity or lack thereof to enact perceptual specialization and expertise, and by the related "stoppage rule" associated with this specialization when it is allowed the means to develop. A precocious (Asperger), late (autistic with competent speech), or either slight or futile (autistic with sparse speech) investment in oral language as a perceptually defined material of interest should play a major role in eventual phenotypic heterogeneity. Conversely, the nature of apparent neglect for "unchosen" domains may be identical for savant syndrome, autism and possibly Asperger syndrome. Although this hypothesis may appear unconventional and speculative, we contend that importing a model within PDD to explain PDD is less risky than the common use of importing brain-injured models of non-autistic individuals to account for an autistic difference. For example, use of frontally injured, typically developing patients to construct the executive deficit hypothesis is based on superficial analogies (Pennington & Ozonoff, 1996) and on a "residual normalcy" (Thomas & Karmiloff-Smith, 2002) assumption. Similarly, the use of typically developing temporally injured patients has produced dead-end models, like our "agnosia" hypothesis of autism (Mottron *et al.*, 1997).

Exposure to speech is clearly not the unique source of the early vs. late vs. sparse overt language use, as most PDD individuals are exposed to speech in a similar way—at least according to non-autistic criteria. In the same way, most autistic individuals are exposed to music, and not all become savants. For this reason, determining the phenomenal properties that orient the choice of a special interest in a young autistic individual (the type of material and the period of time at which this "perceptual root" occurs) represents a topic of considerable importance to facilitate the ideal outcome of a successful autistic person.

Principle 8: Enhanced Functioning of Primary Perceptual Brain Regions may Account for Autistic Perceptual Atypicalities

How can a more local default orientation, superior discrimination of physical dimensions, enhanced autonomy of perceptual processes, and superior expertise effects be grounded in brain allocation and organization? The recent systematization

of the organization of the visual perpetual cortex (Grill-Spector & Malach, 2004) provides a possible, unified explanation for the various principles characterizing autistic perception.

In typical individuals, feed-forward visual processing follows a double hierarchical pattern. More posterior regions of the occipital lobe are devoted to extraction of unique dimensions and to small areas of the visual field, and more anterior regions to both large areas of the visual field and increasingly abstract, higher-order operations (e.g. global processing, categorization). An orthogonal, dorso-ventral hierarchy opposes central to peripheral preferential response in the early visual cortex. Specialized identification (face and objects) and high magnification factor are related to posterior and central occipital areas, while less specialized representations and low magnification factor are related to higher-level cortex. In addition, the activity of these regions is under the dependence of feedback from non-material-specific attention and executive processes (Grill-Spector & Malach, 2004).

This organization of visual cortex suggests that the characteristics that differentiate autistic from non-autistic perception plausibly correspond to an overall superior functioning, involvement, and autonomy of posterior regions of the perceptual visual cortex (for the hierarchical, antero-posterior axis) and of the central part of this cortex (for the dorso-ventral, specialization axis). Locally oriented processing *(Pr. 1)*, superior involvement of posterior regions in multiple tasks *(Pr. 4)*, and enhanced autonomy toward higher-order influences *(Pr. 5)*, would therefore correspond to a skewing of "hierarchical axis" toward more posterior regions. Enhanced low-level processing *(Pr. 2)*, and specifically first vs. second-order dissociation, would correspond to a superior performance of the functions deserved by the most posterior regions of the visual brain. Early lateral glances *(Pr. 3)* may be interpreted as early regulation of excessive input of high spatial frequencies, related to an enhanced input from posterior visual cortex. Lastly, enhanced specialization or expertise level, as exemplified by the restricted nature of autistic interest culminating in savant-syndrome *(Pr. 6)* and possibly determining subgroups of PDDs *(Pr. 7)*, would correspond to a skewing of the "specialization axis" toward central regions of the visual cortex, and the equivalent skewing of auditory processing toward primary auditory cortex.

CONCLUSION

Five years of research have strengthened the notion, stated in the original EPF model, that perception plays a different and superior role in autistic cognition. Recent studies in the visual and auditory modalities indicate a skewing of brain activation toward primary and early associative areas in autistics in most tasks involving higher-order or socially relevant information in non-autistics. Therefore, it becomes increasingly difficult for "social-first" models to explain why most of the cognitive operations performed by autistics differ from their equivalent in non-autistics. A new version of the EPF re-asserts, with a larger empirical basis, the principle of locally oriented and enhanced perceptual functioning. Two new propositions aiming to explain aspects of autistic phenotypic variability are added. At the individual level, higher-order control over perception is not mandatory in autism when it interferes with performance of tasks that can be more economically processed locally or using a low-level processing mode, whereas the involvement of higher-order control is mandatory in non-autistics even when it is detrimental to performance. At a subgroup level, the extreme amplitude of positive and negative expertise effects appear to be influential in the autistic pattern of perceptual performance, with productive training for the processing of certain materials ranging from quasi-null (speech for some autistics) to extreme (material-specific domains of special interest). We propose to attribute both the choice of domain of special ability and some aspects of the phenotypic variability characterizing autistic subtypes to a brain-behavior cycle rooted in perceptual expertise effects.

The mapping of autistic perceptual characteristics on anatomical and functional organization of the visual cortex is now less speculative than in the previous version of EPF. The revised EPF takes into account both functional-anatomical mapping of low-level autistic visual perception resulting from Bertone *et al.*'s (2005) findings, the most recent views on the organization of the visual perceptual cortex (Grill-spector & Malach, 2004), and the consistent pattern of atypical posterior involvement observed in numerous brain imaging studies. We contend that this model has an explanatory value for the autistic pattern of performance in large number of visual-perceptual tasks. The revised EPF is supported by a possibly equivalent over-involvement of primary

auditory cortex, devoted to "simple" perceptual operations in auditory tasks and auditory related autistic behaviors (Samson *et al.*, this issue).

The use of "high" vs. "low" level information processing to qualify autistic performance may be misleading. Accordingly, the superior involvement of perceptual regions in so called "high-level" tasks may be associated with a significant superiority of the autistic group. A successful, problem-solving use of perceptual areas leads to a reconsideration of the definitions of "perception" and "perceptual areas" as well as of the relation between perception and general intelligence in autistic individuals.

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