Original Article



Perceptual inference and autistic traits

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Abstract

Autistic people are better at perceiving details. Major theories explain this in terms of bottom-up sensory mechanisms or in terms of top-down cognitive biases. Recently, it has become possible to link these theories within a common framework. This framework assumes that perception is implicit neural inference, combining sensory evidence with prior perceptual knowledge. Within this framework, perceptual differences may occur because of enhanced precision in how sensory evidence is represented or because sensory evidence is weighted much higher than prior perceptual knowledge. In this preliminary study, we compared these models using groups with high and low autistic trait scores (Autism-Spectrum Quotient). We found evidence supporting the cognitive bias model and no evidence for the enhanced sensory precision model.

Keywords

autism spectrum disorder, perceptual enhancements, perceptual inference, signal detection theory, weak priors

Introduction

People with autism spectrum disorder (ASD) are better at perceiving details, while also having difficulties interpreting contextual meaning. For instance, people with ASD are better at discriminating pitch (Bonnel et al., 2003; Heaton et al., 2008), but have trouble using pitch to interpret speech prosody (McCann and Peppe, 2003). Most explanations of these phenomena have focused on differences in sensory function, such as enhanced sensory discrimination (Mottron et al., 2006), or on differences in cognitive style, such as a bias for detail over contextual information (i.e. "weak coherence") (Frith, 2003; Happé and Frith, 2006). As such, there is a long-standing debate between proponents of models of perception in ASD that treat differences as primarily the product of bottom-up or stimulus-driven processes and proponents of models that treat those same differences as products of top-down or cognitively driven processes.

Recently, these alternative explanations have been recontextualized within a new framework (Pellicano and Burr, 2012), which hints at how sensory and cognitive processes might work together to shape perception differently in ASD. Applied to perception more generally, this framework treats perception as implicit inference (Friston, 2005; Gregory, 1980). Imagine a radiologist who must discriminate whether a shadow on a brain scan is a tumor. The goal is to infer a *cause* (tumor or cyst), given the *evidence* (shadow). This inference is inherently uncertain. The best

the radiologist can do is to make an informed hypothesis, given *prior knowledge* (training). Analogously, to say that perception is implicit inference is to say that such a process occurs whenever we perceive and that the work is done by the perceptual system without awareness. But instead of tumors, scans, and training, the *causes* to be inferred are objects in the world; the *evidence* is the features that the sense organs transmit; and the *prior knowledge* comes from learning about the world by interacting with it. The theory, then, is that perception is implicit inference about the causal structure of the world, which balances sensory evidence against driving perceptual expectations (Friston, 2005).

Within this framework, perceptual differences in autism can be explained as differences in the ways that implicit perceptual inferences are made (for details and examples, see Pellicano and Burr, 2012; for commentaries, see Brock, 2012; Friston et al., 2012; Teufel et al., 2013; Van Boxtel and Lu, 2012). One possibility, which has recently been

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put forward by Pellicano and Burr (2012), is that in ASD, the balance is tipped in favor of sensory evidence, with prior knowledge given less weight (Mitchell and Ropar, 2004). In other words, autistic people might have generally weaker prior expectations, a kind of top-down perceptual/ cognitive bias for sensory evidence (cf. Frith, 2003; Happé and Frith, 2006; Mitchell and Ropar, 2004). From this perspective, autistic people might be like radiologists who trust little in their training, relying heavily on their scans. The other possibility, suggested by Brock (2012), is that in autism, the perceptual system might have better evidence to work with, if, for instance, early sensory representations are less noisy or more precise. This would be a form of bottom-up sensory enhancement (cf. Mottron et al., 2006). The purpose of this study is to make a first attempt at disentangling these broad hypotheses and thus to provide a first empirical investigation into the new framework in which they are embedded.

ASD is diagnosed as a spectrum condition (American Psychiatric Association (APA), 2013), and self-report methods have revealed autistic traits among individuals in the general population who have not received an ASD diagnosis (Baron-Cohen et al., 2001; Hurst et al., 2007; Lau et al., 2013). Autistic traits are known to correlate with the sensory and perceptual differences found in ASD (Robertson and Simmons, 2013), and in direct comparisons, individuals with higher overall trait scores have been shown to exhibit perceptual styles commonly associated with ASD to a larger degree than individuals with lower scores (Grinter et al., 2009). The debate over how to explain these differences within ASD also extends to explanations of perceptual differences due to autistic traits, and thus, the new framework for contextualizing this debate in terms of perceptual inference should also apply here (cf. Palmer et al. (2013) for related research on movement). In this study, we attempt to disentangle the weak prior and enhanced precision hypotheses that emerge within this framework, by comparing individuals higher and lower in autistic traits, with a view to extending our findings to the ASD population in future research.

The first difficulty encountered is how to represent these alternatives so that they can be distinguished behaviorally (Brock, 2012; Pellicano and Burr, 2012). Our initial approach to this problem is to re-frame the alternatives in the context of signal detection theory (SDT), a general framework for quantifying the capacity of a system to discriminate signal and noise inputs (Figure 1). SDT is useful here because it makes a conceptual distinction between sensory evidence and perceptual judgment over that evidence, treating perception as the outcome of a judgment made on the grounds of noisy internal sensory representations (for the textbook presentation, see Macmillan and Creelman, 2005). Our justification for choosing SDT as a framework is that this core distinction provides a relatively principled way to experimentally separate the influence of sensory precision on the one hand from the influence of prior expectations in the making of perceptual judgments on the other. Such a strategy is not without its limitations, as we shall discuss. Nevertheless, we contend that it offers a useful heuristic for delineating the weak prior and enhanced precision hypotheses.

Within SDT, perceptual judgment is dependent on two parameters. One is the discriminability index d', which represents the difference between sensory noise and sensory "signal + noise" distributions (Figure 1). This index is sensitive to two factors: the difference or separation between signal and noise, which is to say how much the signal "stands out" from background noise along the stimulus dimension, and more interestingly the variance in these distributions or how spread out they are. This second factor—which is also an estimate of how precisely the signal is represented in the sensory system—captures the notion of "precision" intended by the enhanced sensory precision hypothesis as indicated by Brock (2012).

Another signal detection parameter is the response criterion c, which represents the cutoff point on the stimulus dimension above which a stimulus will be categorized as signal. A more negative criterion is more liberal or inclusive, and a more positive criterion is more conservative (Figure 1). This index is also sensitive to two factors—the relative subjective utility or value of categorization hits and misses and prior expectations about relative base rates (BRs) of signal and noise stimuli. In encoding prior knowledge and making it available to perceptual decisions about the environmental causes of sensation, this second factor is indicative of the kinds of model expectations discussed by Pellicano and Burr (2012) and relevant to their weak prior hypothesis.

Our experiment is an SDT design, in which we manipulated sensory noise by manipulating the variance of signal and noise distributions (signal-to-noise ratio (SNR) manipulation) and in which we manipulate prior expectations by manipulating relative BRs of signal and noise trials (BR manipulation). We used the Autism-Spectrum Quotient (AQ) questionnaire to measure self-reported autistic traits (Baron-Cohen et al., 2001) and to define a group of neurotypical participants into low AQ and high AQ subgroups. We protected ourselves against false positives by not selecting subgroups with extreme scores and by using an unselected group of 29 student volunteers with a median split to divide them into low and high scorers. If the enhanced sensory precision model applies to autistic traits, then d' in the high AQ group will be less influenced by the SNR manipulation. If Pellicano and Burr's (2012) weak prior model applies to autistic traits, then c in the high AQ group will be less influenced by the BR manipulation.

Methods

Participants and AQ grouping

In all, 29 students at Aarhus University (20 females, mean age = 24.3 years, standard deviation (SD) age = 2.98 years)

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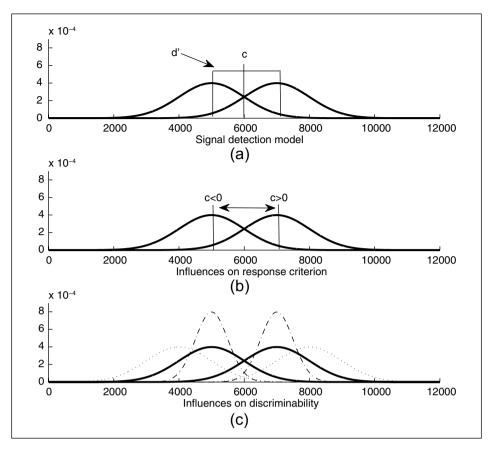


Figure 1. Graphical representation of signal detection theory. (a) The separation between the two distributions represents the ability to discriminate sensory signal and noise (d'). The response criterion, c, indicates bias and represents the cutoff point above which the observer will categorize a stimulus as signal. (b) A more negative c indicates a more liberal (i.e. inclusive) response criterion, and a more positive c indicates a more conservative criterion. (c) Representation of how discriminability (d') can be influenced by either the distance between signal and signal + noise distributions (dotted line) or their variance (dot-dash line). For structural similarities between signal detection theory and Bayesian explanations of perception in autism, compare to Figure 1 in Brock (2012).

participated in the study for a small base reimbursement fee (150 Danish Crowns (DKK)) with a small task-dependent additional incentive (0–80 DKK). All participants reported normal or corrected-to-normal vision and reported that they had no neurological or psychiatric diagnoses. No participants were diagnosed with ASD. All provided written informed consent, and the experiment was conducted within local ethical guidelines.

All participants completed the AQ questionnaire, which had been translated into Danish for the sample. Questionnaires were completed prior to arrival, but were not scored until all data were collected. Following the completion of the study, a total AQ score was calculated for each participant as the number of items endorsed on the questionnaire. On the basis of their responses, ad hoc low AQ (n = 14) and high AQ (n = 15) groups were defined using a median split on total AQ score (median AQ = 14).

The low AQ group consisted of six males and eight females. Mean total AQ score for the low AQ group was 9.1 (SD = 2.27; range = 5-12). The high AQ group consisted of 3 males and 12 females. Mean total AQ score for

the high AQ group was 19.27 (SD = 5.43; range = 13-31).

Stimuli and apparatus

Stimuli were displayed on a 22" light-emitting diode (LED) display with a resolution of 1920 × 1080 pixels. Participants viewed the stimuli at a comfortable distance of about 500 mm, and responses were made using the arrow keys on a standard keyboard. Stimuli were presented using Presentation (Neurobehavioral Systems) and generated online using the VisGen visual stimulus generation package.

Participants were presented with Gabor patches composed of sine-wave gratings with a regular spatial frequency of 0.63 cycles/mm, wrapped in a Gaussian envelope of mean 0.5 mm and SD 2.12 mm. Similar stimuli have previously been used to investigate perception in ASD (Bertone et al., 2005) and ASD-like traits (Brock et al., 2011). Gabor patches were pre-masked and post-masked in time by identical plaids consisting of two Gabor

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patches oriented orthogonally at 45° and 315°. All stimuli were presented at the center of the display.

Each trial began with presentation of the pre-mask for 400 ms, which also drew participants' fixation. This was followed immediately by the Gabor stimulus, which was presented for 32 ms. After this, a blank screen was presented for a regular interstimulus interval (ISI) of 196 ms, and then, the post-mask was presented for 400 ms. The orientation of the Gabor stimuli varied by trial, and the orientation was used as the cue by which participants were asked to classify the stimuli in the signal detection task.

Procedure and design

The signal detection task was presented as the "microchip game." In the game, participants were asked to imagine that they were quality control inspectors working at a microchip factory. Participants were told that their screen displayed the output of a microscope, which presented a sequence of microchips. They were told that for each chip shown, they would have to decide whether it was functional and thus suitable for sale or defective and thus suitable for scrap.

Participants were shown example trials. They were told that the plaids (pre-masks and post-masks) represented the chips. They were told that when a current was passed through the chips, oriented lines would appear very briefly, with this phase of the trial represented as the Gabor stimuli. Participants were informed that the orientation of the lines shown during this time was the only property which indicated whether a chip was functional or defective. Specifically, they were told that, all else being equal, a higher orientation indicated a higher probability that the chip was functional, but that this indicator was also unreliable. At the end of each trial, participants used the arrow keys to indicate whether they thought the chip was functional (up arrow) or not (down arrow). After giving their response, participants were informed of whether or not they had categorized the chip correctly. The task was thus a ves-no forced choice orientation discrimination task with feedback.

Across the experiment, orientation was treated as a noisy stimulus parameter. "Defective" chips were sampled from a set of orientations, whose angle was Gaussian distributed with a mean orientation of 20°, and "functional" chips were sampled from a set of orientations, whose angle was Gaussian distributed with a mean orientation of 28°.

Trials were divided into four blocks, which differed factorially from one another in two ways. Blocks could have a high or low SNR manipulation. This was a difference in the SD of the distributions of orientations from which the stimuli (i.e. "chips") were sampled. Blocks could also have a high or a low target BR manipulation. This was a difference in the ratio of functional and defective chips presented. In the low SNR/low BR block,

orientation distributions had an SD of 8°, and the ratio of functional to defective chips was 25:75. In the low SNR/high BR block, orientation distributions had an SD of 8°, and the ratio of functional to defective chips was 75:25. In the high SNR/low BR block, orientation distributions had an SD of 4°, and the ratio of functional to defective chips was 25:75. In the high SNR/high BR block, orientation distributions had an SD of 4°, and the ratio of functional to defective chips was 75:25.

Each block consisted of 40 training trials and 200 test trials (total = 960 trials). The entire experiment took around 45–60 min to complete. At the end of each test trial, participants were awarded 0.1 DKK for a correct categorization (Hits and Correct Rejections), which was added to their base reimbursement. Training trials were included to establish prior expectations about the frequency of the occurrence of functional chips prior to the test block and thus to strengthen the BR manipulation. Although no reward was provided in training trials, participants were still given feedback on the correctness of their classification, in order to learn about the distributions from which the stimuli were being sampled.

Discriminability and response bias parameters were estimated separately for each block. The discriminability parameter d' was estimated within subjects as the difference between the Z-transformed hit rate (i.e. rate at which functional chips were categorized correctly) and the Z-transformed false alarm rate (i.e. rate at which defective chips were categorized as functional) (Macmillan and Creelman, 2005). The response bias was estimated as the response criterion parameter c, which was calculated as the sum of the Z-transformed hit rate and the Z-transformed false alarm rate, divided by -2 (Macmillan and Creelman, 2005). The experiment was thus a 2 (AQ group) \times 2 (BR manipulation) \times 2 (SNR manipulation) mixed factorial design with d' and c as dependent measures.

Results

A three-way analysis of variance (ANOVA) on d' revealed a main effect of SNR manipulation (i.e. SD of distributions of orientations from which the Gabor patches or "chips" were sampled) ($F(1, 27) = 123.75, p < .001, \eta_p^2 = .82$). As SDT would predict, Figure 2 indicates a higher SNR corresponded to a higher d'. The most relevant effect for the enhanced sensory precision hypothesis, that AQ grouping would interact with SNR manipulation, was not significant ($F(1, 27) < .01, p = .952, \eta_p^2 = 0$). No other effects approached significance.

A three-way ANOVA on c revealed a main effect of BR manipulation (i.e. relative frequency of functional and defective chips) (F(1, 27) = 168.14, p < .001, $\eta_p^2 = .86$). As SDT would predict, Figure 3 indicates that a higher BR of functional chips corresponded to a more negative (i.e. a more liberal or inclusive) criterion. The most relevant

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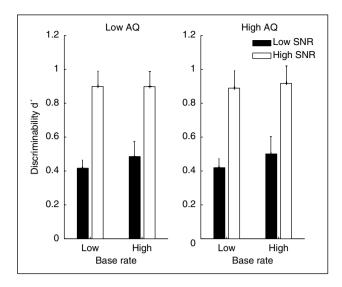


Figure 2. Mean discriminability (*d'*) for each combination of AQ group, BR manipulation, and SNR manipulation. AQ: Autism-Spectrum Quotient; BR: base rate; SNR: signal-to-noise ratio.

effect for the weak priors hypothesis, that AQ group would interact with BR manipulation, was significant (F(1, 27) = 4.79, p = .03, $\eta_p^2 = .15$). Figure 3 suggests that across levels of the SNR manipulation, response criterion was less affected by the BR manipulation in the high AQ group.

To interpret this interaction, post hoc t-tests were used to compare the low and high AQ groups within each level of the BR manipulation, with criterion estimates averaged across levels of SNR. These tests revealed a significant group difference when there was a higher BR of functional chips (t(27) = 2.5, p = .019), and this difference survived Bonferroni corrections for multiple comparisons (adjusted accepted significance level = .025). When the BR was low, groups were not revealed to be significantly different, although there was a nonsignificant trend (t(27) = 1.74, p = .094).

Tangentially, there was also a BR × SNR interaction $(F(1, 27) = 4.92, p = .03, \eta_p^2 = .15)$ that was not qualified by AQ group. Figure 3 suggests that overall, participants' response criteria were less affected by differences in BR information, when the SNR was higher.

Discussion

A recently presented model of perceptual differences in ASD proposes that they are caused by weak prior expectations and a corresponding enhanced reliance on sensory evidence when making implicit perceptual inference (Pellicano and Burr, 2012). Such a mechanism is, however, difficult to disentangle from an alternative explanation that is also consistent with a framework that treats perception as implicit inference—which is that for autistic people, sensory information is more precise or less noisy

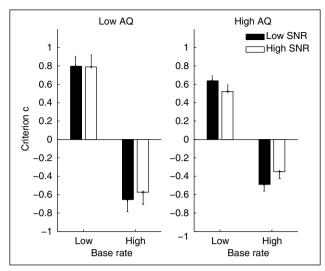


Figure 3. Mean response criterion (*c*) for each combination of AQ group, BR manipulation, and SNR manipulation. AQ: Autism-Spectrum Quotient; BR: base rate; SNR: signal-to-noise ratio

and therefore a better source of data (Brock, 2012). We used a signal detection theoretic approach to disentangle these two hypotheses in the context of a study on autistic traits in an unselected sample of neurotypical volunteers.

We reasoned that if perceptual differences are due to enhanced sensory precision, then a high AQ group would show more resistant discriminability to variations in sensory noise (i.e. increased variance in the angle of functional and defective chips). We also reasoned that if perceptual differences are caused by weak prior expectations, then a high AQ group would show more resistant response criteria to variations in signal BR (i.e. more or less defective chips in the block). We found no evidence for enhanced sensory precision. We did, however, find that in the high trait group, BR exerted a decreased influence on response bias. Specifically, we found that the high AQ group was less influenced by a high signal BR, and we found a similar nonsignificant trend when BR was low. We take this to be the first evidence of weak perceptual priors as a mechanism for the perceptual differences typically associated with ASD.

The main controversy in understanding these differences is between bottom-up theories focused mainly on enhancements in sensory function (e.g. Mottron et al., 2006) and top-down theories focused mainly on differences in cognitive preferences (e.g. weak coherence—Happé and Frith, 2006). Until now, this controversy has proven difficult to resolve because bottom-up and top-down explanations tend to operate in their own frameworks, to entail different kinds of experimental questions and designs, and to thus produce divergent sources of data that have proven problematic to integrate (Dakin and Frith, 2005). A model of perception as implicit neural inference

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offers a context for relating these explanations more directly to one another. Within this framework, enhanced perceptual functioning (Mottron et al., 2006) can be recast as enhanced precision of sensory evidence (i.e. Brock, 2012), while perceptual biases for certain aspects of stimuli (Happé and Frith, 2006) can be recast (more generally) in terms of how prior perceptual expectations are built up and employed in perceptual inference (i.e. Pellicano and Burr, 2012; see also Mitchell and Ropar, 2004). In this context, the present experiment provides preliminary support for an explanation in terms of top-down mechanisms.

We say preliminary because the study is focused on self-reported autistic traits as measured using the AQ and not ASD per se. To the extent that autistic traits in the neurotypical population are interesting in their own right, our results contribute to a better understanding of some of the visual processing mechanisms that might be associated with those traits. In the context of perception in ASD, to the extent that individuals with ASD typically score higher on the AQ (Baron-Cohen et al., 2001; Lau et al., 2013), and to the extent that AQ scores are correlated with perceptual differences common to ASD (Robertson and Simmons, 2013), our results also point toward a possible mechanism for explaining those differences. With that said, this inference is indirect. Research on perception and autistic traits is not a substitute for research on perception and ASD, and thus, we emphasize that it remains an open question whether the difference in the effect of BR on response criterion that we find here between low and high AQ groups translates to a difference between neurotypical individuals and individuals with ASD. Likewise, it remains open whether individuals diagnosed with ASD will be more resistant to sensory noise within our paradigm, and thus, it remains possible that the perceptual differences demonstrated by such individuals are also driven by enhanced sensory evidence. Further to this point, we note that although the effects discovered were quite robust, due to the intensity of the psychophysical paradigm, the low (n = 14) and high (n = 15) AQ groups were relatively small. Thus, replication with ASD participants will be of particular interest.

A further limitation in the present design is introduced by our application of SDT to model the effects of signal BR on performance. Recall that the purpose of this manipulation was to determine whether individuals higher in autistic traits were more resistant to changes in BR information and thus more influenced by the sensory evidence provided by the stimulus than by prior knowledge of stimulus context as represented in the BR. Recall also that SDT was used to model this decrease in influence because it is well known that bias as estimated using the criterion c is sensitive to BR information. The problem is that this method is equivocal concerning where this bias occurs in the perceptual decision-making process. In the form applied here, SDT does not make a formal distinction

between perceptual bias—or bias in the tendency to categorize incoming stimuli in one way rather than another—and response bias—or bias in the tendency to respond as if one perceptual category is more appropriate than another. Given the present design and analysis, it is possible that lower and higher AQ individuals perceived the stimuli in the same way, but that higher AQ individuals responded as if their perceptual categorization of the microchips was less affected by BR. Perceptual and response bias cannot be disentangled given the present design and analysis. We maintain, nevertheless, that both kinds of bias are interesting from the perspective of a model of perception as neural inference, and that this issue warrants further investigation.

We also note that for criterion estimates, there was an interaction between BR and SNR manipulations, which appeared to be driven by a decrease in the effects of the BR manipulation when the SNR was higher. In other words, when the two perceptual categories of "Functional Chip" and "Defective Chip" were easier to discriminate, then participants relied less on prior information. In one sense, this is to be expected. Whenever evidence is better, then it is reasonable to rely less on prior information. This also makes sense from the perspective of a theory of perception as implicit inference, which views perceptual expectations and sensory evidence as functionally interwoven (Friston, 2005). At the same time, this is important because this finding reminds us that even in designs that are optimized to disentangle the relative influences of expectations and evidence in perception, we should not expect the distinction between the two to be absolute. This has potential implications for how we use this theoretical framework to reformulate and reinterpret existing top-down and bottomup theories of perceptual differences in ASD.

One of the implications of the present research is that the differences in perceptual judgments associated with autistic traits may be representatives of differences in learning style. Stated very coarsely, a processing preference for evidence of prior context should make individuals better at learning certain kinds of information and worse at learning other kinds. For instance, given a preference for sensory evidence over contextual priors, one might be better at learning which nations participated on each side in World War I (WWI), but worse at learning about the alliance system in place in Europe at the end of the 19th century. We emphasize that this inference is extremely tentative because our present question is specific to perception and perceptual categorizing and not more general processes of assimilation of information about facts and contexts. We emphasize also that in any case such an inference should not be made for learning in individuals with ASD since we only present evidence concerning autistic traits in the neurotypical population. Thus, we do not raise this issue to make any conclusions, but rather to suggest an open avenue for future research on the links between processing

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preferences in perception and learning styles, which are implied by new ways of understanding perception. We cannot say whether these links provide a meaningful way to understand perception and learning in ASD, only that they provide an interesting lead for future investigation.

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