

The Use of Prior Knowledge for Perceptual Inference Is Preserved in ASD



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Clinical Psychological Science
1–12

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DOI: 10.1177/2167702617740955

www.psychologicalscience.org/CPS



Abstract

An amorphous collection of black and white patches (so-called Mooney images) can be perceived dramatically differently before versus after exposure to the natural source image. Prior experience causes the patches to (re)organize and fit together in a meaningful whole. Given recent hypotheses on a weaker role of priors in perception in individuals with autism spectrum disorders (ASD), we looked at improvements in recognition accuracy for Mooney images, before and after exposure to their source image, in typically developing (TD) individuals varying in ASD-like traits, and in a clinical group of adolescents with ASD (versus matched TD sample). We found typical prior-based performance improvements irrespective of ASD-like traits or ASD diagnosis, suggesting that the fast formation and application of specific priors is preserved in ASD. Together with earlier studies reporting intact use of other types of perceptual priors, these findings narrow down the candidate Bayesian accounts that are plausible for ASD.

Keywords

autism spectrum disorder, perceptual inference, Mooney images, two-tone images, Bayesian perception, perceptual priors, top-down, open data, open materials

Received 2/22/17; Revision accepted 10/10/17

Perception is sometimes described as “controlled hallucination” (e.g., Horn, 1980) to emphasize the constructive, generative contribution of the perceptual brain, not just passively receiving inputs but proactively synthesizing what may have caused those sensory inputs. This idea is often formalized with a Bayesian account of perception (Lee & Mumford, 2003), in which priors or predictions are combined with inputs, to infer their hidden causes. In experimental paradigms, the brain’s active contribution is often masked because of stimulus randomization, which reduces expectations, or because stimuli are used that are readily identified seemingly without the need for top-down processes. The strategy that researchers apply to expose this contribution often comes down to giving the visual system a hard time, by using ambiguous, noisy, or distorted stimuli. Mooney or two-tone images (Mooney, 1957), made by low-pass filtering and thresholding grayscale photographs, are one such type of stimulus that has been repeatedly used to investigate top-down influences in perception (Fig. 1). For such a stimulus it is immediately

clear that it helps greatly if we have a specific model of the source image on the basis of which it is generated. Those models are often (implicitly) learned, in some cases through very little experience, as is evidenced by the Mooney images. As soon as we have seen the “template” (grayscale solution image) once, we automatically disambiguate the two-tone version, often with a radical shift in experience from fragmented patches to coherent percept. In the most compelling cases, we will have great difficulties to return to the naïve, disorganized percept. Several studies have measured the neural correlates of the influence that top-down prior knowledge has on the encoding of (resolved) Mooney images (Dolan et al., 1997; Gorlin et al., 2012; Grutzner et al., 2010; Hsieh, Vul, & Kanwisher, 2010), and have shown that such effects occur from very early on in the visual

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Fig. 1. Mooney or two-tone image (left) and its grayscale source image or “template” (right).

processing stream (Aru, Rutiku, Wibral, Singer, & Melloni, 2016; Mayer, Schwiedrzik, Wibral, Singer, & Melloni, 2016; Samaha, Boutonnet, & Lupyan, 2016). Recently there has been an increased interest in the individual differences in the ability to resolve these images (Teufel et al., 2015; Verhallen et al., 2014), suggesting individual variation in top-down strength in perception.

Autism spectrum conditions or disorders (ASD) refers to a cluster of early-onset neurodevelopmental conditions characterized by social-communicative deficits and restricted, repetitive behavior, and interests (American Psychiatric Association, 2013). Given the widespread atypicalities in cognition and perception, in addition to social problems, in these individuals, several researchers have proposed that general information processing alterations could be at the basis of ASD. At the core of many of these proposals is an imbalance between bottom-up and top-down information processing. Given the interplay between priors and likelihoods, Bayesian inference is a natural way to articulate those views. However, their precursors are older and can be found in the weak central coherence (WCC; Happé & Frith, 2006) and the enhanced perceptual functioning (EPF; Mottron, Dawson, Soulières, Hubert, & Burack, 2006) accounts. The WCC assumes a weaker role for gestalts, gist, or meaning in perception and cognition in ASD, suggesting that the perceiver’s contribution in abstracting regularities from inputs is reduced, or at least is not applied spontaneously. In perception, this is usually tested by measuring a local versus global bias in processing a given stimulus (e.g., hierarchical Navon stimuli), but without an explicit top-down component. EPF, on the other hand, primarily argues for stronger local, low-level perceptual processing in ASD, but also suggests that “higher-order processing is optional in autism and mandatory in non-autistics” (Mottron et al., 2006, p. 34). Evidence for this primarily comes from categorization (Soulières, Mottron, Giguère, & Larochelle, 2011; Soulières, Mottron, Saumier, & Larochelle, 2007)

and global perception tasks (Van der Hallen, Evers, Brewaeys, Van den Noortgate, & Wagemans, 2015), where it is clear that individuals with ASD are very well able to do the tasks, but do them slower or with more effort.

In Bayesian terms the principles of EPF and WCC could be described as “weak” or uninformative priors, leading to perceptual inference that is much more determined by the inputs (e.g., more “veridical” or more detailed, i.e., “enhanced”) instead of by prior knowledge or internal constraints (Pellicano & Burr, 2012). The assumption is either that people with ASD do not learn proper (informative) priors or that something goes awry when they need to apply these priors to particular sensory inputs. In any case, it is formalized by positing broader prior distributions (i.e., higher uncertainty about prior expectations), which will bias percepts to a lesser extent. Although the true value of a Bayesian approach (over EPF or WCC) will become clear only with studies that explicitly model perceptual inference under uncertainty, connecting the broader Bayesian literature with perception in ASD is already affording new paradigms and interesting distinctions for the study of ASD. As one example, one can roughly distinguish two types of priors: structural priors and contextual priors (Seriès & Seitz, 2013). Common examples of structural priors include the expectation that light comes from above or that convex shapes are likely to be foreground objects (instead of background). Such priors are either innate or implicitly learned through early and ample experience with the statistics of the natural environment. They are therefore also very widely applicable to any (even novel) visual input and are most likely encoded in early perceptual cortices. Most illusions also rely on structural priors, and show that such priors are often not very malleable. Despite findings of reduced susceptibility to (some) illusions (Mitchell, Mottron, Soulières, & Ropar, 2010), several recent studies suggest that structural priors are actually

intact in ASD (Croydon, Karaminis, Neil, Burr, & Pellicano, 2017; Manning, Neil, Karaminis, & Pellicano, 2015; Spanò, Peterson, Nadel, Rhoads, & Edgin, 2015).

The second type of priors, contextual ones, are more changeable based on shorter-term implicit or explicit learning (Serriès & Seitz, 2013). Those expectations are bound to a specific spatiotemporal context or set of cues, so they are usually much more limited in application. A typical example is the contextual cueing effect in visual search, where implicitly learned distractor configurations help to reduce target search times. Mooney images can also be put in this category because the acquired prior information will not bias perception of other inputs, even in encounters with similar objects. Here, too, evidence on intact contextual cueing in ASD does not support the weak priors account (Barnes et al., 2008; Brown, Aczel, Jiménez, Kaufman, & Grant, 2010). Other tasks based on learned top-down influences yielded more conflicting findings. For example, Molesworth, Chevallier, Happé, and Hampton (2015) found reduced contextual influences in categorization, but Mottron, Burack, Iarocci, Belleville, and Enns (2003) and Loth, Gómez, and Happé (2010) found intact performance in a silhouette identification task and a Mooney task, respectively. However, the latter two studies had very small sample sizes in both the number of participants and the number of trials/stimuli. Hence, we wanted to verify and extend our knowledge here, with a larger study that really tries to hone in on the top-down contribution in perception.

As an antipode to the weak priors case for ASD, schizophrenia is sometimes characterized as a matter of stronger top-down priors, hence an overconfidence in or overreliance on top-down constructs, at the cost of actual sensory inputs (Fletcher & Frith, 2009; Schmack et al., 2013; Teufel et al., 2015), possibly explaining the persistent delusions or hallucinations in these patients. In a recent study, Teufel et al. (2015) presented participants with two-tone images twice, once before exposure to the full color images (“templates”) they were derived from, and once afterward. Participants had to indicate whether or not the Mooney images contained people, which was the case for half of the images. The difference in discrimination sensitivity before versus after exposure to the templates can be taken as a measure of the capacity to use top-down information to disambiguate perceptual inputs. In their first experiment, Teufel et al. showed that patients in early stage psychosis benefited more from the prior information compared with matched healthy participants. In addition, a second experiment confirmed that, in typically developing (TD) participants, too, psychosis-proneness (measured with a questionnaire) correlates positively with the improvement based on top-down information.

Our own study largely mirrors that by Teufel et al. (2015) in schizophrenia, in that we also tested a clinical group, in this case individuals with ASD, in addition to a (larger) group of typical participants varying on a subclinical trait, in this case the Autism-Spectrum Quotient (AQ) questionnaire, which measures autism-like traits. Indeed, there is evidence to suggest that autistic traits represent a continuum across the general population with individuals with an ASD diagnosis being situated at the extreme end of this distribution (e.g., Constantino & Todd, 2003). This continuum idea is also partly being incorporated in recent evolutions regarding the *Diagnostic and Statistical Manual of Mental Disorders* (5th ed.; *DSM-5*; American Psychiatric Association, 2013). The AQ has been introduced as a valuable instrument to rapidly screen where an individual is situated on the hypothetical autism-spectrum continuum, ranging from “typicality” to ASD, and has been widely used in research practice (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). Moreover, those autistic traits appear to be highly stable in the general population, regardless of the degree of autistic-like behaviors (Robinson et al., 2011).

Consistent with the WCC account and the weak priors account of ASD, we expect a reduced effect of prior knowledge, as measured with our Mooney task, reflected in a reduced performance improvement in adolescents with ASD compared with TD adolescents (Study 2). Similarly, in our typical population we expect that the performance improvement goes down with increasing autism-like behaviors (Study 1).

Study 1

Method

Participants. After exclusions (see the Supplemental Material available online), complete data from 282 participants (40 males, $M_{\text{age}} = 18.6$, $SD_{\text{age}} = 1.91$, age range 17–39) remained for further analyses. Participants completed the online task and questionnaire from home, as an obligatory part of their course program.

Stimuli and materials

AQ questionnaire. We used a Dutch translation of the AQ questionnaire (Baron-Cohen et al., 2001; Ponnet, Roeyers, & Buysse, 2001). The chosen answers on each of the 50 items of the AQ questionnaire were coded into their corresponding binary score, and total AQ and subscale scores were calculated by summation of all scores over the (relevant) items (as described in Baron-Cohen et al., 2001), resulting in six AQ (sub)scores per participant. A higher AQ (sub)score reflects the presence of more ASD-related traits.

Mooney task. We used 100 Mooney images selected from the stimuli created by Imamoglu, Kahnt, Koch, and Haynes (2012) by smoothing and thresholding a large number of grayscale images selected from an online database using concrete search words and criteria. As a consequence, the grayscale images from which the Mooney images were derived included a single, recognizable foreground object (animate or inanimate). In addition, we created 20 new Mooney images using similar procedures as Imamoglu et al. All images were 400×400 pixels large. The resulting set consisted of 120 Mooney images and corresponding grayscale images.

Procedure. The structure of our Mooney task was inspired by the experimental design in Teufel et al. (2015). The Mooney task consisted of six experimental blocks. For each participant, a random set of 6×10 images was chosen from 120 possible Mooney images (with their corresponding grayscale image). Each experimental block consisted of three phases of 10 trials (10 different images). In the first phase (“pre phase”) participants were asked to identify the object in the image by typing one word into a response box. We urged participants to guess as much as possible, if they were not sure they could recognize the image, but they were free to just press enter if they had no clue at all. After these 10 trials, a template exposure phase followed. Participants were shown the 10 grayscale images that corresponded to the Mooney images they had seen in the previous phase. Each grayscale image was shown once, in random order. This phase provided participants with prior knowledge about image content necessary to perceive a coherent percept of the objects displayed in the Mooney images. To diminish purely bottom-up priming effects, Mooney and grayscale images were presented in blocks of 10 and never back-to-back. Finally, in the after-exposure phase (“post phase”), participants were presented with the same 10 Mooney images they had seen in the first phase of the block and were again asked to name the image in one word. Image presentation was again randomized. Participants had to press the enter key to start each new block or phase.

Mooney images were always displayed for 1 s in the pre and post phases; templates were shown for 2 s in the exposure phase. Interstimulus intervals were always 750 ms. No measurements were made during the template exposure phase in which participants passively viewed the grayscale images. During the recognition phases (pre- and postexposure phases), there was no time limit for naming the image. Each participant did the Mooney task before filling out the AQ questionnaire.

Our experimental design deviates from that by Teufel et al. (2015) in a few important ways. First, we did not use Mooney control images without identifiable objects.

We used open responses, which, contrary to their yes/no face detection task, did not require such control images. The reason for this is that identifying the specific content of the image is less likely to be possible based only on local features, but requires making a global match with the template. In addition, we wanted to stay away from face detection, which might be a special kind of stimulus for individuals with ASD, given their social problems. Second, we did not start the experiment with a practice run but immediately started with the first experimental block. Third, we ran 6 instead of 12 experimental blocks. Fourth, we used grayscale instead of color images to provide participants with top-down knowledge. Fifth, these grayscale templates were presented only once instead of three times during the exposure phase. Finally, Mooney images were shown for 1 s instead of 400 ms, with identical template exposure durations and intertrial intervals.

Statistical analysis. Accuracy (0/1) per trial was determined based on a comparison of a participant’s answer with a list of possible answers for each image as determined beforehand. The list contained the exact basic level category of the foreground object in the Mooney image (e.g., *snake* but not *animal* or *reptile*), as well as synonyms and similar labels at the subordinate level (e.g., *puma* and *leopard*). Apart from the ground truth of the content, the response options were gathered by inspecting the data from a pilot test on 20 participants and from another 20 participants included in Study 1 for possible correct options. The algorithmic correction was done by applying a fuzzy string matching algorithm using the Levenshtein distance (Levenshtein, 1966). Accuracy was coded as 1 when a sufficiently high degree of similarity between the typed answer and a possible answer was identified and coded as 0 when this similarity was lacking. Contrary to Study 1, autocorrected responses of Study 2 were manually validated to confirm that the algorithm correctly accepted typographical errors, diminutives, and plurals without creating any false positives.

Three Mooney images were generally not recognized even when previously exposed to the solution (specifically, less than 0.20% proportion correct in the post phase). Those were eliminated from further analyses, even though including them did not qualitatively change our findings.

We applied a generalized (logistic) linear mixed models (GLMM) on the binary accuracy data. AQ scores were standardized to ensure convergence of all model fits. The models were fitted with lme4 in R (Bates, Mächler, & Bolker, 2012). Complete source code, materials, data, and (extra) statistical analyses are available on the project page on the Open Science Framework (<https://osf.io/4e7hr/>).

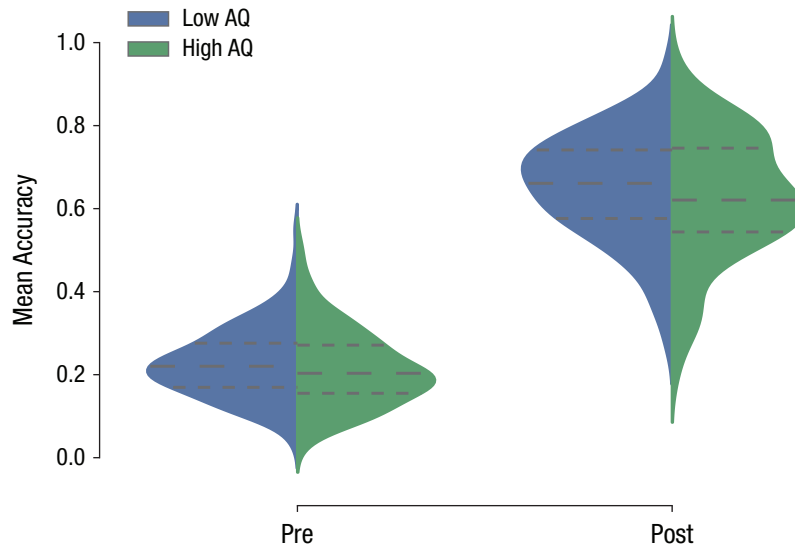


Fig. 2. A violin plot of the mean accuracies before and after exposure to the grayscale images separately for individuals with lower Autism Quotient (AQ) score (below median, in blue) and individuals with high AQ score (above median, in green). Dashed lines are median accuracies, dotted lines indicate quartiles (25th and 75th percentile). Envelopes are the kernel density estimation of the distribution of accuracies.

Results

The average AQ score ($M_{AQ} = 17.73$), range of scores (3–43), and standard deviation ($SD_{AQ} = 6.61$) are comparable with other studies using much larger and more diverse samples (Baron-Cohen et al., 2001; Palmer, Paton, Enticott, & Hohwy, 2015; Ruzich, Allison, & Smith, 2015), despite the lower proportion of males in our sample and the fact that we used only psychology students. Seven participants even scored 32 or higher, which is in the range of scores of individuals with an ASD diagnosis (Baron-Cohen et al., 2001). This means that there should be a sufficient range to find a relation with task performance, should one exist.

In Figure 2 we plotted all accuracy data (pre phase: $M = 0.22$, $SD = 0.09$; post phase: $M = 0.64$, $SD = 0.14$) separately for lower and higher AQ, based on a median split of the AQ scores. In our GLMM analysis however, we added AQ as continuous variable instead of as a categorical level. Apart from AQ, the model included gender, block, and phase (pre vs. post exposure). There is a clear effect of exposure to the grayscale solutions ($z = -36.17$, $p < .001$) as can be seen from the difference in accuracy in the pre versus post phase (Fig. 1). The overall effect of block was significant ($z = 2.36$, $p = .02$), caused by the improvement in performance going from Block 1 to Block 2 (Fig. S2 in the Supplemental Material). We also obtained a significant interaction effect of Block \times Phase ($z = 4.48$, $p > .001$), indicating that people learned to make use of prior

information across blocks. Gender does not affect performance ($z = 0.37$, $p = .71$), nor does AQ ($z = -1.67$, $p = .09$). Crucially, the interaction effect of interest, between phase and AQ, was also not significant ($z = 1.18$, $p = .24$), suggesting that the recognition benefit that people show after exposure with the template does not vary with ASD-related traits.

Likelihood ratio tests of the model with and without the interaction effect confirms that there is no evidence for the complexer model ($\chi^2 = 1.39$, $p = .24$), nor for the model including only a main effect of AQ compared with a model without AQ ($\chi^2 = 1.43$, $p = .23$).

Despite the lack of main effect of AQ, we examined the role of AQ in a more fine-grained way by testing the correlations of all five subscales of the AQ with the difference scores per individual. Those were computed by subtracting pre phase recognition accuracy from post phase accuracy, as a measure of the use of prior knowledge in perceptual recognition in our task. The only correlation that survives the more conservative (Bonferroni-corrected) .01 significance level, is with the Imagination subscale (see Fig. S1B). However, this correlation is small (Pearson $r = .17$, $p = .005$) and is already present for the pre phase accuracy (Fig. S1C), suggesting that the spontaneous capacity to disambiguate the Mooney image, rather than the use of prior knowledge per se, varies with the participant's score on the Imagination subscale. Note that a higher score on the Imagination subscale means more autism-like here, meaning an *impoverished* capacity to imagine.

Table 1. Overview of the Average Group-Level Scores on Descriptive Measures

Variable	TD participants, <i>M</i> (<i>SD</i>)	ASD participants, <i>M</i> (<i>SD</i>)	TD vs. ASD	Group-level difference?
Age ^a	14.38 (1.28)	14.04 (1.49)	$t_{45} = -0.82, p = .42$	No
Full-scale IQ ^a	105.96 (8.69)	104.33 (8.74)	$t_{45} = -0.64, p = .52$	No
Verbal IQ ^a	105.83 (7.60)	102.87 (15.39)	$t_{45} = -0.84, p = .40$	No
Performance IQ ^a	106.00 (12.29)	108.09 (14.40)	$t_{45} = 0.54, p = .60$	No
SRS (overall) ^b	49.46 (9.11)	80.26 (11.45)	$t_{45} = 10.23, p < .001$	ASD > TD

Note: ASD = autism spectrum disorder; SRS = Social Responsiveness Scale; TD = typically developing. All tests are two-sample two-tailed *t* tests (comparison ASD group and matched TD group).

^aNo group differences on age or IQ, given that groups (ASD and TD) were matched on these variables.

^bWe found an expected significant main effect of group on overall SRS score and subscale scores, with higher scores in the ASD group compared with the TD group.

Study 2

Method

Participants. After exclusions (see the Supplemental Material), data for 23 adolescents with ASD (19 males, $M_{\text{age}} = 14.04$, $SD_{\text{age}} = 1.49$) and 24 TD adolescents (20 males, $M_{\text{age}} = 14.38$, $SD_{\text{age}} = 1.28$), matched on age, gender, and IQ, were available for analysis. IQ was estimated based on four subtests of the Wechsler Intelligence Scale for Children (Wechsler, 1991). The subtests used included Block Design, Picture Arrangement, Vocabulary, and Similarities. Participants completed our Mooney task as part of a larger test battery consisting of different experimental tasks. Additional descriptive information about the presence of autistic traits was collected using the Dutch Social Responsiveness Scale (SRS; Constantino & Gruber, 2007; Noens, De la Marche, & Scholte, 2012), and a trained clinical psychologist administered the Dutch version of the Autism Diagnostic Observation Schedule 2 (ADOS-2) module 3 (Dutch version: de Bildt et al., 2009; Gotham, Risi, Pickles, & Lord, 2007) from all participants with a clinical diagnosis. ASD diagnoses were reconfirmed in 22 of the 23 adolescents, with the new ADOS Algorithm for *DSM-IV/ICD-10* (ADOS-2). Because the analyses did not differ depending on whether we included or excluded the participant scoring below the ADOS-2 cutoff score, we followed the clinical diagnosis of the participants and reported the results of the full ASD group. An overview of the descriptive information of both groups can be found in Table 1. All adolescents had normal or corrected-to-normal vision and were Dutch-speaking. Recruitment of ASD participants was set up via the patient database of the Autism Expertise Centre of the University Hospital in Leuven. The study was approved by the Medical Ethics Commission of UPC-KU Leuven and participants provided written informed consent before the start of the experiment.

Stimuli and procedure. For this study we selected 60 Mooney images from the 120 images used in Study 1.

Mooney images that were either almost always or almost never recognized in Study 1 were gradually removed until 60 images remained. Except for this, the same procedure applies as in Study 1, but given that we only kept 60 images, all participants were presented with the same images in an equal number (6) of experimental blocks (still in a different random order for each participant). Contrary to Study 1, participants completed the task in a dimly lit experimental room (instead of online from home). Also contrary to Study 1, the responses of this study were manually instead of algorithmically corrected.

Results

Statistical analyses were identical to Study 1, except for the fact that we now have the factor Group (ASD vs. TD) instead of a continuous AQ score. The main results are summarized in Figure 3. Note first that the mean accuracies are generally higher than in Study 1 (pre phase: $M = 0.29$, $SD = 0.10$; post phase: $M = 0.77$, $SD = 0.11$), probably because of the elimination of the most difficult images, and because this study was performed in the lab rather than from home. In our GLMM analysis, the main effect of Phase (pre/post) was strongly significant ($z = -17.93$, $p < .001$), indicating that participants used the prior knowledge they received in the exposure phase. Also similar to Study 1, there was significant learning across blocks ($z = 7.73$, $p < .001$), primarily from Block 1 to Block 2 (Fig. S3). However, there was no main effect of Group ($z = 0.64$, $p = .52$), indicating that overall accuracy was the same in both groups. The interaction of Group with Phase, our main focus here, was also not significant ($z = 0.23$, $p = .82$), consistent with what we found in the nonclinical, dimensional setting of Study 1. We also included IQ and overall SRS score as covariates in this GLMM model but only IQ significantly contributed to recognition accuracy ($z = 1.97$, $p = .05$).

Consistent with the above, in likelihood ratio tests, the interaction model (Group \times Phase) did not have

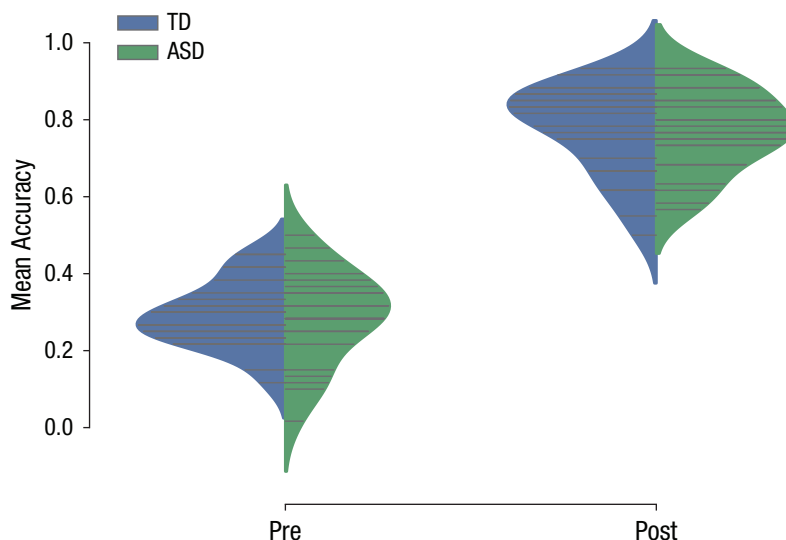


Fig. 3. A violin plot of the mean accuracies before and after exposure to the gray-scale images separately for individuals with ASD (in green) and typically developing (TD) control individuals (in blue). Lines represent individual mean accuracies. Envelopes are the kernel density estimation of the distribution of accuracies.

significantly more evidence than the model with only a main effect of Group ($\chi^2 = .05$, $p = .82$); in fact, the latter model did not even have more evidence than the model without Group effect ($\chi^2 = .61$, $p = .44$).

Discussion

Our analyses consistently did not support a difference in the impact of top-down knowledge in perception of Mooney images, as a function of varying ASD-like trait or a clinical ASD diagnosis. These findings go against the weak priors and the WCC account of ASD, but they are consistent with other reports of intact use of both structural and contextual priors in ASD.

Our conclusion of a lack of main effect of AQ in Study 1 corroborates a study by Verhallen et al. (2014) that found no correlation between AQ and performance on a task in which participants needed to choose the Mooney image (out of three options) that contained a face. Although their single-phase task did not specifically manipulate top-down information, being a Mooney test it does examine a form of global integration of fragmented contours and/or back-and-white patches belonging to figure versus background. It is often assumed that people scoring high on the AQ questionnaire (or people with clinical ASD) have difficulties in forming global configurations but there is now solid empirical evidence against it (e.g., Almeida, Dickinson, Maybery, Badcock, & Badcock, 2014; Chouinard, Unwin, Landry, & Sperandio, 2016; Mottron, Belleville, & Menard, 1999; Mottron, Burack, Stauder, & Robaey,

1999; Mottron et al., 2003). Our study confirms that AQ does not influence the global integration needed to disambiguate the Mooney images (similar performance in the pre phase) and also shows that the use of priors does not covary with AQ (no interaction effect of AQ \times Phase). The latter is consistent with the intact influence of priors in perceptual illusions in individuals with high AQ (Buckingham, Michelakakis, & Rajendran, 2016; Chouinard et al., 2016).

Our post hoc tests did show that the AQ Imagination subscale does correlate significantly with Mooney performance, but this not only affects the difference score, but rather is already present for the pre phase performance. We should be careful in interpreting this finding, because the correlation is rather small and post hoc (though significant after correction) and given that an AQ subscale is based on only 10 items. Still, it seems that the worse a participant's Imagination score (so the more ASD-related imagination), the less he or she is able to find a good solution for Mooney images (pre or post exposure). This might speak to the top-down, generative element needed for Mooney perception, but likely not the top-down strength per se but rather the flexibility in searching for alternative hypotheses, or in detaching from low-level inputs. Top-down ("search space") flexibility and top-down strength are closely related yet distinct capacities. The finding of a link between Imagination and first pass disambiguation of Mooney images underlines the need for more research into possible shared mechanisms between mental imagery, imagination, and top-down influences in perception, especially in relation

to psychiatric disorders with known altered imaginative capacities (Crespi, Leach, Dinsdale, Mokkonen, & Hurd, 2016).

We predicted that, if the weak priors account is on track, individuals with a high AQ score or who are diagnosed with ASD would benefit less than those with low AQ scores or those who do not have an ASD diagnosis (but matched age and IQ). Both of these predictions were refuted, suggesting that the use of top-down information in Mooney images is very much intact in those groups. One earlier study on the perception of Mooney images in ASD is relevant in the context of our findings. Loth et al. (2010) tested the recognition of Mooney images in 14 young adults with ASD (and a matched control group of 14 participants), before and after passive exposure to sequence of couples of a Mooney image and the corresponding grayscale image. Our study has a few advantages compared with this one. Most notably, the Mooney images and grayscale templates were never presented back-to-back in our study (as in Teufel et al., 2015), whereas this was the case for Loth et al. This means that the latter study might have been measuring the effect of local perceptual features linked to the template solutions, instead of the effect of top-down knowledge on making a global match. In addition, we used a much larger stimulus set (60 Mooney images vs. 20 in Loth et al.) and a larger participant group (23 vs. 14). This is no luxury in this type of research, characterized by large stimulus effects (some Mooney images are really compelling, others much less so), large individual differences (especially in the ASD group), and large interactions between individual and stimulus (one Mooney image may be very compelling or easy to solve for one individual, but not at all for another). Nonetheless, our findings confirm the lack of group differences that Loth et al. report for Mooney perception. The authors do note a selectively reduced postexposure performance for faces (so not for other objects), but given that this is based on even less images (data points), reliability is limited, without replication in an independent (larger) image sample. In any case, our stimulus set has only very few faces/people so we cannot test this possibility with our data.

Our results on intact use of top-down knowledge are also consistent with contextual cueing studies in ASD (e.g., Barnes et al., 2008; Brown et al., 2010), where the use of contextual priors is also intact, but in that case priors are learned during many blocks instead of the single exposure (“one-shot”) learning here. These findings also add to a series of reports of normal formation and/or use of priors in ASD in different settings (Ego et al., 2016; Pell et al., 2016; Spanò et al., 2015). However, other studies do claim to have found evidence for weaker priors in ASD (Skewes, Jegindø, &

Gebauer, 2015; Turi, Karaminis, Pellicano, & Burr, 2016), so scholars performing future studies will have to systematically evaluate the differences in settings and priors concerned. One possibility is that priors can be learned but are not readily applied to as wide a range of stimuli as in typical individuals (Van de Cruys et al., 2014; Van de Cruys, de-Wit, Evers, Boets, & Wagemans, 2013) because predictions are more narrowly tuned to certain features. Generalization is known to be a problem in ASD (Plaisted, 2001), but our prior-based behavioral tasks do not always examine this. Another possibility is that problems in ASD arise only with the learning or use of social priors (Balsters et al., 2017; Chambon et al., 2016), but then of course it would be interesting to discover what sets them apart in terms of the complexity of the generative models or in terms of neurobiological implementation. This may lead us to a view in which selectively the acquisition of priors in more complex environments is affected, for example in settings that are more volatile, that comprise multiple competing cues that all vary (signal and noise variability), or in a combination of both. Under those circumstances, properly learning and updating priors for relevant cues requires meta-learning based on accurate estimates of uncertainties (Lawson, Rees, & Friston, 2014; Van de Cruys et al., 2014; Van de Cruys, Van der Hallen, & Wagemans, 2017).

Little is known about the actual format of the prior induced with this kind of Mooney templates. A recent study in TD participants showed that word primes (e.g., “gorilla” if the Mooney contained a gorilla) or image primes of different exemplars of the same category as the object in the Mooney image (Nordhjem, Kurman Petrozzelli, Gravel, Renken, & Cornelissen, 2015) helped recognition as well, suggesting that an activation of a conceptual prior is sometimes sufficient to improve Mooney perception. Indeed, neural changes related to prior information for Mooney images can be found both in higher-level visual and in lower-level retinotopic areas, and those activity patterns are different from the neural correlates of conventional (feature-based) priming (Gorlin et al., 2012; Hsieh et al., 2010).

It might seem surprising that there were no group differences, not even in baseline performance, considering that the basic perceptual processes that this type of recognition relies on may be altered in ASD. For example, in a lot of two-tone images, lighting and shadows causes (after thresholding) the wrong segmentation of objects that makes Mooney images hard to solve. For isolated objects, Becchio, Mari, and Castiello (2010) found that although shadows improve object recognition in TD children, they hamper recognition in children with ASD. Another consequence of thresholding is the loss of figure-ground segregation, a function that

may also be weakened in ASD (Vandenbroucke, Scholte, van Engeland, Lamme, & Kemner, 2009). Mooney transformations also cause the disappearance of (some) informative contours, hence the importance of (amodal) completion of contours based on neighboring surfaces or top-down information. Although the capacity to see illusory contours is intact in ASD (Milne & Scope, 2008), there is some evidence for reduced collinear facilitation and contour integration (Jachim, Warren, McLoughlin, & Gowen, 2015; but see Keita, Mottron, Dawson, & Bertone, 2011).

One could very well criticize the assumption that our (and Teufel et al.'s) difference measure is a pure measurement of strength of top-down priors. Like Teufel et al. (2015), we interpreted the progress from pre to post phase recognition as an effect of the successful application of top-down information (greater progress means greater top-down strength), but as indicated above, our measurement (and hence that of Teufel et al.) may confound the formation of templates in memory with their subsequent use (application). We did not collect data on the memorability of individual template images, but to indirectly probe the effect of memorability on the difference scores we ran our grayscale images through a convolutional neural net (LaMem; Khosla, Raju, Torralba, & Oliva, 2015) that is trained for predicting memorability scores based on a very large image database. This network has been shown to reach near human consistency in predicted memorability (a rank correlation of .64 vs. .68 for humans). There was no correlation ($r = -.019$, $p = .84$) between memorability scores and difference scores, suggesting that memorability of template images is not the most decisive factor in the improvement in performance.

In conclusion, we found that individuals with ASD or with high ASD-related traits performed similarly to TD participants or low-AQ individuals on a task that measured the use of top-down priors in perceptual inference. These findings go against the weak priors or WCC account of ASD, suggesting that these individuals can form and apply contextual priors that help to organize fragmented inputs. Further characterization of the precise conditions in which acquisition or use of priors is compromised in ASD is an important goal for future studies.

Author Contributions

S. Van de Cruys and J. Wagemans designed the study. S. Vanmarcke and I. Van de Put collected the data. S. Van de Cruys analyzed the data. All of the authors interpreted the data. S. Van de Cruys wrote the manuscript, and S. Vanmarcke, I. Van de Put, and J. Wagemans provided revisions. All of the authors approved the final version of the manuscript for publication.

Acknowledgments

Sander Van de Cruys is a postdoctoral and Steven Vanmarcke is a doctoral fellow of the Research Foundation–Flanders (FWO). We particularly want to thank Pieter Moors for valuable discussions on the statistical analyses, and Lore Goetschalckx for help with the memorability net.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

This work was supported in part by the Methusalem program of the Flemish government (METH/14/02), awarded to Johan Wagemans.

Supplemental Material

Additional supporting information may be found at <http://journals.sagepub.com/doi/suppl/10.1177/2167702617740955>

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