Priors bias perceptual decisions in autism, but are less flexibly adjusted to the context

Running title: Inflexible prior weight in autism

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LAY SUMMARY

Based on our experience, we have expectations about our environment. Theories suggest that the symptoms encountered in autism could be due to atypical expectations, leading to an impression of an unpredictable world. Using a visual discrimination task, we showed that adults with and without autism are biased by their expectations. Yet, the extent to which expectations biased perception did not depend on the context in autism. This higher inflexibility found in autism may explain symptoms such as resistance to change.

ABSTRACT

According to the predictive coding framework, percepts emerge from combinations of sensory input and prior knowledge, whose relative contributions depend on their reliability. Recent predictive coding theories suggest that Autism Spectrum Disorder (ASD) could be characterized by an atypical weighting of priors. Here, we assessed whether individuals with ASD can flexibly adjust the weight (precision) of the prior to the context. Thirty-one neurotypical adults (NT) and 26 adults with ASD participated in a visual discrimination task designed to elicit a time-order effect (TOE). The TOE reflects the integration of priors with sensory estimates. We used two experimental contexts: a narrow stimulus range (*Narrow* condition) and a broader range (*Broad* condition) in order to induce a prior with a higher and lower precision, respectively. Both groups learned a prior that biased their perception, as shown with the TOE. As expected, the NT group had a larger TOE in the *Narrow* condition than in the *Broad* condition, revealing a contextual adjustment of the prior precision. In contrast, ASD participants were more inflexible: the extent of the TOE was not modulated by the context. In addition, the accuracy increased when the stimulus range decreased in both group, which may be interpreted as a contextual adjustment of the sensory precision. To conclude, adults with and without ASD implicitly learned a prior mean, but ASD participants failed to flexibly adjust the prior precision to the context. This increased inflexibility in ASD could account for many symptoms, such as their intolerance of uncertainty.

Keywords: Autism, Contraction Bias, Inflexibility, Learning, Predictive coding, Prior, Time-order effect

INTRODUCTION

Our expectations shape our perception, so that we tend to see what we expect to see (i.e., the most likely percept). These expectations rely on our prior knowledge, accumulated through our past experience, as we implicitly learn the underlying statistics of the environment. Rather than being veridical, perception can be seen as a knowledge-driven inference (Clark, 2013). The general tendency to perceive sensory inputs as being closer to our expectations than they really are, is called a contraction bias. This well-known phenomenon was first described by Fechner (1860), who highlighted that the temporal presentation order of stimuli influenced judgments. This tendency to judge stimuli as resembling the average stimulus was further developed by Hollingworth (1910). In his description of the Central Tendency of Judgment, he wrote that *"Judgments of time, weight, […], have all shown the same tendency to gravitate toward a mean magnitude, the result being that stimuli above that point in the objective scale were underestimated and stimuli below overestimated".* In laboratory conditions, measuring a contraction bias can provide insights about the way priors are learned and how they influence perception. More globally, it can shed light on the predictive mechanisms of the brain, which have been formalized in the Bayesian framework.

In this framework, sensory input (*likelihood*) and expectation (*prior*) are combined to generate a percept (*posterior*). Having optimal priors requires being able to extract the statistical regularities of the environment (mean and variance of a stimulus feature), and to flexibly adjust the relative precisions (i.e., inverse variance) of the prior and sensory information in a context-dependent way. Informative priors, associated with a high precision (i.e., low variance), will influence perception to a larger extent than noisy priors (i.e., high variance, low precision). The flexible adjustment of the sensory and prior precision balance plays a central role in perception, as it allows getting the best estimate of the environment. Having an accurate internal model of the world helps coping with the environmental noise and minimizing mismatches between expectations and sensory inputs (i.e., prediction errors).

In contrast, having a suboptimal internal model or sensory/prior precision imbalance could alter perception, or even lead to disorders. Autism Spectrum Disorder (ASD) was recently presented as a disorder of perceptual inference (Haker, Schneebeli, & Stephan, 2016). Several theories propose that the symptoms encountered in ASD could be due to an atypical functioning of the predictive brain (Brock, 2012; Palmer, Lawson, & Hohwy, 2017; Pellicano & Burr, 2012; Sinha et al., 2014; Van de Cruys et al., 2014). The first theories suggested that perception would be very realistic in ASD, either because prior precision would be systematically low (Pellicano & Burr, 2012) or because sensory precision would be high (Brock, 2012). Other theories focused on the ratio of prior and sensory precisions to account for ASD (Lawson, Rees, & Friston, 2014; Palmer et al., 2017; Van de Cruys et al., 2014). In particular, Van de Cruys and colleagues developed the hypothesis of a high and inflexible precision of the prediction error in autism (HIPPEA) (Van de Cruys et al., 2014). Note that the precision of the prediction error is a function of the ratio of sensory and prior precisions. The HIPPEA theory therefore suggests that in ASD, this precision ratio would remain high and would not be flexibly adjusted to the context.

If the predictive mechanisms are suboptimal in ASD, the world would seem quite unpredictable to them. It could explain that the social domain is particularly impaired, as it is a complex and dynamic environment, where predictions need to be adapted to the context and updated frequently. In these situations, one also needs to decide if the environmental fluctuations are learnable and thus useful to update priors or are completely noisy interferences that can better be ignored. As people with ASD have difficulties dealing with uncertainty (Jenkinson, Milne, & Thompson, 2020; Joyce, Honey, Leekam, Barrett, & Rodgers, 2017), having a more rigid behavior or stereotyped movements could be a way to restore some predictability (Van de Cruys et al., 2014). This Bayesian perspective of ASD intends to account for the two core symptoms of ASD: persistent deficits in social interaction and communication (which often need to be adapted to variable contexts), and restricted, repetitive behaviors, interests or activities (which help to reduce the overload resulting from excessive variability) (DSM-5, American Association, 2013).

These Bayesian theories of ASD were formulated based on post-hoc interpretations of studies, but more recently, some empirical studies were designed to directly assess prior influence on perception in ASD. Behavioral studies showed that individuals with ASD were able to make perceptual averaging and were influenced by prior knowledge, suggesting intact priors in ASD (Corbett, Venuti, & Melcher, 2016; Croydon, Karaminis, Neil, Burr, & Pellicano, 2017; Ego et al., 2016; Van de Cruys, Vanmarcke, Van de Put, & Wagemans, 2017). In contrast, some studies concluded on a decreased use of prior knowledge in children and young adults with ASD (Karaminis et al., 2016; Król & Król, 2019). In ASD, prior learning was found to be typical (Manning, Kilner, Neil, Karaminis, & Pellicano, 2016) or atypical (Lawson, Mathys, & Rees, 2017) in volatile environments, while a recent study revealed a slower prior learning in ASD (Lieder et al., 2019). Previous behavioral experiments assessing contraction biases in adults with ASD suggested that the inflexibility of prior learning could play a central role in ASD (Sapey-Triomphe, 2017), consistently with the HIPPEA hypothesis.

In the present study, we aimed to investigate whether ASD is characterized by inflexible priors. More specifically, we compared the extent to which priors biased perception in a context designed to elicit a strong versus a weak prior (i.e., a prior with a high vs. a low precision). For this purpose, we used a two-alternative forced choice task in the visual modality to quantify the time-order effect (TOE) in individuals with and without ASD. The TOE is a specific case of contraction bias in a task consisting of a sequential presentation of stimuli. Across trials, subjects can implicitly learn a prior from the mean and variance of the stimulus distribution (e.g., mean size and variance of a series of discs displayed on a screen). According to the Central Tendency of Judgment (Hollingworth, 1910), all percepts are driven toward the prior (i.e., the mean size of the discs). So, the magnitudes of the stimuli that are below the mean are overestimated, while the magnitudes of the stimuli that are above the mean are underestimated. In particular, the first stimulus is even more biased toward the mean, probably because its representation gets more noisier while it is kept in memory for longer (during the retention interval between stimulus presentation and response). This delay would decrease the sensory precision, and therefore relatively increase the weight of the prior on the posterior of the first stimulus. With this mechanism, the first stimulus is perceived as being closer to the mean. In pairs of stimuli where the first stimulus is the closest to the mean, the magnitude difference between percepts seems to be enhanced, and thus the comparison is facilitated. In contrast, in pairs of stimuli where the first stimulus is the furthest away from the mean, the magnitude difference between percepts seems to be smaller, and thus the comparison is harder. Hence, the accuracy level can be modulated by the order of presentation of the two stimuli (larger stimulus presented first or second), yielding a TOE. The TOE is a robust effect that was observed across multiple sensory modalities (Ashourian & Loewenstein, 2011; Harris, Arabzadeh, Fairhall, Benito, &

Diamond, 2006; Hellström, 1985; Hellström & Rammsayer, 2015; Karim, Harris, Langdon, & Breakspear, 2013; Preuschhof, Schubert, Villringer, & Heekeren, 2010; Raviv, Ahissar, & Loewenstein, 2012; Sinclair & Burton, 1996; van den Berg, Lindskog, Poom, & Winman, 2017).

In our study, adults with and without ASD participated in a two-alternative forced choice task designed to elicit a TOE. They had to compare the size of two discs presented successively in blocks where stimuli were drawn from a narrow range of disc diameters (161 to 248 pixels, variance of 24 pixels) or a broader range of disc diameters (139 to 287 pixels, variance of 44 pixels). Importantly, the ratio between the two discs displayed was constant, only the variance of the distribution was modulated. As the prior distribution should reflect the underlying statistics of the environment, the smaller the variance of the sensory inputs is, the higher the prior precision should be. This means that when the stimulus range becomes narrower, the TOE should get stronger. Within the neurotypical group, we expected the TOE to be stronger in blocks with a narrow range of stimuli than in the blocks with a broader range. Such a difference between conditions would reveal a flexible adjustment of the prior precision depending on the context. In addition, we expected the mean accuracy to be higher in the narrow condition than in the broad condition, as recent studies showed that the just noticeable difference is smaller when the stimulus range is narrower (Namdar, Algom, & Ganel, 2018; Namdar, Ganel, & Algom, 2016). Furthermore, with this design, we could also make specific predictions about the results of the individuals with ASD, deducted from the Bayesian theories of ASD. The hypo-prior account of ASD (Pellicano & Burr, 2012) would predict a decreased TOE. The high sensory sensitivity theory (Brock, 2012) would also predict a decreased TOE, but with a higher accuracy. The HIPPEA hypothesis (Van de Cruys et al., 2014) would predict an inflexible weighting of the prior precision, and so, no difference in the strength of the TOE depending on the context (i.e., same TOE in the narrow and broad conditions).

MATERIALS AND METHODS

1. Participants

Thirty-one neurotypical (NT) participants and 26 participants with ASD participated in this behavioral study. The demographic characteristics of the two groups are given in Table 1. The two groups were matched in gender ratio and age. In addition to these participants, two ASD subjects and four NT subjects participated in the study but were discarded from the analyses as they were outliers compared to the other participants: they clicked on the same buttons for more than 70% of the trials throughout the entire task (between 70% and 86% of similar responses, depending on the subjects).

Inclusion criteria were being between 18 and 50 years old and having normal or corrected-to-normal vision. Exclusion criteria for neurotypical participants were having a known diagnosis of neurological or psychiatric disorder, being under current neuropsychiatric medication, and scoring above 32 at the Autism-Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). Eleven participants with ASD reported being under current medication, and seven participants with ASD reported having one or more comorbidities (anxiety disorder (2), depression (3), PTSD (1), ADHD (3), OCD (1), agoraphobia (1) and dyslexia (1)).

Individuals with ASD received their diagnoses from a multidisciplinary Expertise Center for Autism (University Hospitals of KU Leuven) in a standardized way according to the criteria of the Diagnostic and Statistical Manual of mental disorders 5 (DSM-5, American Association, 2013). All ASD participants had an Intelligence Quotient (Wechsler Adult Intelligence Scale - WAIS) above 75.

This study was approved by the medical Research Ethical Committee UZ / KU Leuven. Written informed consent was received from all participants before starting the experiment.

Please, insert Table 1 around here

2. Stimuli

Stimuli were dark grey discs (luminance of 5.0 cd/m²) displayed at the center of a light grey background (luminance of 61.4 cd/m²) on a Dell Monitor U2410 (spatial resolution 1920 x 1200). Participants were seated at a viewing distance of about 60 cm to the screen in a darkened and quiet room.

The diameters of the stimuli used in the *Narrow* and *Broad* blocks are given in Table 2. The diameters of the first disc (D1) followed a logarithmic distribution. The diameters of the second disc (D2) were calculated so that the ratio between the two discs remained the same in every stimulus pair (ratio: 0.93). The mean size of the discs was centered around 200 pixels (D1 in the stimulus pair S4), meaning that participants should implicitly learn a prior around 200 pixels. As stimuli were distributed along a logarithmic scale, the average size of discs displayed in the two conditions slightly differ (*Narrow*: 201 ± 24 pixels, *Broad*: 204 ± 44 pixels), but the logarithms of the averages are the same in each condition (*Narrow*: 2.30 ± 0.05 pixels, *Broad*: 2.30 ± 0.09 pixels). Stimuli were presented using the Psychtoolbox in MATLAB (R2018a version).

Please, insert Table 2 around here

3. Experimental paradigm

The task was a two-alternative forced choice task where participants saw two discs successively and had to compare their sizes. The paradigm is shown in Figure 1. At each trial, a first disc D1 was displayed for 600 ms, followed by an inter-stimulus interval of 1000 ms and by a second disc D2 displayed for 600 ms. Then, an answer screen with a plus and a minus sign was displayed for 1200 ms. Participants had to click on the side of the plus or minus signs if they estimated that the second disc was larger or smaller than the first one, respectively. Participants had to answer using the left and right arrow keys of the keyboard, using their dominant hand. The sides of the plus and minus signs were counterbalanced between participants. The inter-trial interval was jittered between 1300 ms and 1700 ms (uniform distribution, 1500 ms on average) to reduce predictability.

Participants performed a short training consisting of four trials (including feedback) and four blocks (two *Narrow* blocks and two *Broad* blocks, without feedback). Each block consisted of 110 trials and lasted for about 7 minutes. Within each block, ten different pairs of discs (five with D2>D1 and five with D2<D1) were presented 11 times each (see Table 2).

There was a *Narrow* and a *Broad* condition, where the distributions of the diameters of the discs (Table 2) were either narrow or broad, respectively. Note that the ratio of diameters between D1 and D2 remained constant throughout the task and was the same in the *Narrow* and *Broad* conditions. Only the variance of the stimulus distributions differed between conditions (i.e., 44 pixels vs. 24 pixels), all the other parameters remained the same. A *Narrow* block refers to a block where the stimuli displayed have a diameter belonging to a narrow range (161 to 248 pixels) and presenting the stimulus pairs S2, S3, S4, S5 and S6 (Table 2) for D2 larger or smaller than D1 (i.e., total of 10 pairs). A *Broad* block refers to a block where the stimuli displayed have a diameter belonging to a broader range (139 to 287 pixels) and presenting the stimulus pairs S1, S2, S4, S6 and S7 (Table 2) for D2 larger or smaller than D1.

We expected the *Narrow* condition to elicit a prior with a high precision (as the stimulus distribution had a low variance) and the *Broad* condition to elicit a prior with a lower precision (as the stimulus distribution as a higher variance). Participants performed two *Narrow* blocks and two *Broad* blocks successively. The order of the sequence of blocks (*Narrow* first or *Broad* first) was counterbalanced between participants. Between the second and the third block (i.e., between the change of condition), there was a break of 10 minutes, during which the participants filled in the Autism-Spectrum Quotient questionnaire (Baron-Cohen et al., 2001).

Please, insert Figure 1 around here

4. Statistical analyses

The demographic data were compared between groups using Student t tests. The mean accuracy was compared to chance level (50%) using one-sample t-test. We assessed the effect of conditions (*Narrow* and *Broad*) and group (NT and ASD) on the mean accuracy and response time using an ANOVA with *group* as a between-participant factor and *condition* as a within factor. We used post-hoc t-tests to compare the mean accuracy (i.e., percentage of correct answers) and response time (i.e., time spent between the appearance of the response screen and the response) between groups, and paired t-tests for within group comparisons.

When significant effects were found, we report the effect size as Cohen's *d*. Note that $d = 0.01$ is considered as a very small effect size, $d = 0.20$ as a small effect size, $d = 0.50$ as a medium effect size, $d = 0.80$ as a large effect size and $d = 1.20$ as a very large effect size (Cohen, 1988; Sawilowsky, 2009).

Correlations with the AQ were assessed using Pearson correlation tests. A Pearson's *r* of 0.10 is considered as a small effect, 0.30 as a medium effect and 0.50 as a large effect.

In order to determine if there was a time-order effect, we compared the accuracy for a given D1 in the trials where D2 was larger or smaller than D1. For each of the five D1 values displayed, we used paired t-tests to compare the mean accuracy in trials with D1<D2 and D1>D2, and we applied Bonferroni correction to the p-values resulting from the five t-tests. For a given D1, if trials with D1<D2 and D1>D2 do not differ, then it means that there is no time-order effect, whereas a significant difference in accuracy means that there is a time-order effect leading to a positive or negative bias toward the mean.

To quantify the time-order effect, we plotted the mean accuracy as a function of five types of stimulus pairs (Table 2), defined as follows. The contraction bias toward the mean disc size (200 pixels) should lead to an easier (*positive bias*) or harder (*negative bias*) comparison depending on whether D2 is larger or smaller than D1, and whether D1 lies below or above the mean (i.e., time-order effect) (e.g., Ashourian & Loewenstein, 2011; Preuschhof et al., 2010). The further the disc size is from the mean, the stronger the time-order effect is. We therefore, a priori, defined pairs of stimuli (each time, one with D1<D2 and one with D1>D2) that should be associated with a large negative bias (P1), a small negative bias (P2), no bias (P3), a small positive bias (P4) or a large positive bias (P5) (see Table 2). For these pairs of stimuli, we refer to “small” or “large” biases, as the absolute difference between the logarithms of the prior and D1 sizes is 0.06 for P1 and P5, 0.03 for P2 and P4, and 0 for P3. Unless there is a general response bias toward one type of answer, the curves D1>D2 and D1<D2 should be symmetrical. We therefore flipped the D1>D2 curve and averaged the D1>D2 and D1<D2 curves, which allows removing a response bias of non-interest (e.g., general tendency to answer “+” in all trials). Then, we applied a second-order polynomial fit on the curves presenting the accuracy as a function of the five types of stimulus pairs.

The coefficients of the polynomial fit were used as estimates of the amplitude of the time-order effect. Coefficients close to zero mean that the accuracy was not modulated by the stimulus order (D2 larger or smaller than D1) or by the position of the stimuli on the stimulus range (below or above the mean). In contrast, high coefficients reflect such a modulation, and so, a time-order effect. We can therefore predict that low coefficients (i.e., flat curve) reflect a weak bias toward the prior (Figure 3A.1), whereas high coefficients (i.e., steep curve) reflect a strong bias toward the prior (Figure 3A.2). In addition, if the fit coefficients do not differ between the *Narrow* and *Broad* blocks (i.e., no slope difference between conditions), it means that the prior inflexibly modulate perception (Figure 3A.3). In contrast, if the coefficients are higher in the *Narrow* than *Broad* condition, it reveals a context-dependent modulation of the prior weight on perceptual decisions (Figure 3A.4). Note that the second-degree coefficient indicates the steepness of the curvature and which way the curve is bending (values are positive if the parabola is concave and negative if it is convex). We performed an ANOVA on the fit coefficients with group (NT or ASD) as a between-participant factor and condition (*Narrow* or *Broad*) as a within factor, and used post-hoc t-tests. Our hypothesis was that the time-order effect would be stronger in the *Narrow* than *Broad* condition in the NT group, and that the difference between conditions would be smaller in the ASD group if the prior weight is less adjusted to the context in ASD.

All t-tests were two-tailed. The statistical significance threshold was set at $p < .05$. Data were analyzed using Matlab (version R2019a), and the statistical analyses were performed using R (version 3.6.3).

RESULTS

1. Mean accuracy and response times

1.1. Overall results

On average, over the four blocks, the percentage of correct answers was 83.2% (±6.1) in the NT group and 86.1% (±9.2) in the ASD group. The average response time for correct answers (RTc) was 311 ms (±162) in the NT group and 349 ms (±178) in the ASD group. All participants got less than 2% of unanswered trials. The mean accuracy and RTc did not significantly differ between groups. The Autism-Spectrum Quotient was not significantly correlated with the mean accuracy ($r = 0.20$, $p = .13$).

1.2. Condition effect

When considering all trials, the mean accuracy level was 86.1% (±6.6) in the *Narrow* blocks and 80.3% (±6.5) in the *Broad* blocks in the NT group. In the ASD group, the mean accuracy level was 88.9% (±8.9) in the *Narrow* blocks and 83.4% (±10.3) in the *Broad* blocks (Figure 2A). We performed an ANOVA on accuracy with the factors group (ASD and NT) and condition (*Narrow* or *Broad*). There was a strong main effect of condition (*F*(1,55) = 66.2, *p* < .0001) with the *Narrow* blocks being easier than the *Broad* blocks (*t*(56) = 8.2, *p* < .0001, *d* = 1.09). There was no group effect (*F*(1,55) = 2.1, *p* = .16) nor interaction between group and condition (*F*(1,55) = 0.1, *p* = .82).

When considering all trials, the mean RTc in the NT and ASD groups were, respectively, 298 ms (±153) and 327 ms (±184) in the *Narrow* blocks, and 323 ms (±191) and 371 ms (±187) in the *Broad* blocks in NT (Figure 2B). The ANOVA on RTc with the factors group and condition revealed a condition effect (*F*(1,55) = 5.0, *p* < .05), with faster RTc to answer in the *Narrow* than *Broad* blocks (*t*(56) = 2.2, *p* < .05, *d* = 0.30). There was no group effect and no interaction.

When considering only the trials involving the six stimulus pairs presented in both conditions (see Table 2), the mean accuracy levels in the *Narrow* and *Broad* blocks were 85.2% (±6.9) and 82.6% (±5.2) in the NT group, and 88.5% (±9.2) and 85.1% (±10.2) in the ASD group, respectively. The ANOVA on these accuracy and RTc measures also showed a condition effect (accuracy: *F*(1,55) = 18.7, *p* < .0001, *d* = 0.57; RTc: *F*(1,55) = 4.7, *p* < .05, *d* = 0.29), no group effect and no interaction.

Finally, there was no effect of the block order (*Narrow* first or *Broad* first) on the accuracy or RTc in neither group.

Please, insert Figure 2 around here

2. Time-order effect

2.1. Presence of a time-order effect (raw data)

In order to visualize whether there was a time-order effect, the accuracy was plotted as a function of the D1 diameters for trials where D2 was larger or smaller than D1 (Figure 3B-F). A time-order effect was observed in both groups, as there was either a positive bias (increased accuracy) or a negative bias (decreased accuracy) depending on whether D2 was larger or smaller than D1. An absence of time-order effect would have been characterized by no difference between the D1<D2 and D1>D2 curves. For each of the five D1 values, we compared the pairs of stimuli where D2 was smaller or larger than D1 using paired t-tests. Note that the *p*-values given in the following section are corrected for five comparisons using Bonferroni correction (i.e., *p*-values multiplied by 5).

In the NT group, the accuracy differed between trials with D1<D2 or D1>D2, for four D1 values in the *Narrow* condition (corrected p-values ranging from .04 to < .0001, d ranging from 0.50 to 1.58, Figure 3B) and in the *Broad* condition (all corrected p-values < .0001, d ranging from 0.93 to 1.94, Figure 3C). In the ASD group, the accuracy differed between stimulus pairs for the two highest D1 values in the *Narrow* condition (corrected p-values ranging from < .001 to < .0001, d ranging from 0.86 to 1.19, Figure 3E), and for the three highest D1 values in the *Broad* condition (corrected p-values ranging from < .005 to < .0001, d ranging from 0.75 to 1.69, Figure 3F). The effect sizes reported here are between medium to very large.

Please, insert Figure 3 around here

2.2. Curve-fitting of the time-order effect

To quantify the time-order effect, the data points of the curves D1<D2 and D2>D1 were averaged for the pairs corresponding to the five levels of facilitation (see Methods). Then, we estimated a second-order fit of this curve in the *Narrow* and *Broad* conditions in order to compare the slopes between conditions (Figures 3D and 3G). Note that the individual fitted curves of the NT and ASD participants are shown as Supplementary Information (Figure SI.1).

In the NT group, the fits were $y = -6.03*10^{-3} x^2 + 2.79 x – 229$ ($R^2 = 1$) in the *Narrow* condition and $y = -1.16*10^{-3} x^2 + 0.75 x – 21$ ($R^2 = 1$) in the *Broad* condition. In the ASD group, the fits were $y = -1.48*10^{-3} x^2 + 0.86 x – 24$ ($R^2 = 1$) in the *Narrow* condition and $y = -0.68*10^{-3} x^2 + 0.49 x + 14$ ($R^2 = 1$) in the *Broad* condition.

Please, insert Figure 4 around here

2.3. Contextual modulation of the time-order effect

We used an ANOVA to assess the effect of group (NT vs. ASD) and condition (*Narrow* vs. *Broad*) on the fit coefficients of second ($\boldsymbol{x^2}$) and first ($\boldsymbol{x}$) degrees. The coefficients assess the extent of the time-order effect (see Methods) and are plotted in Figure 4. There was a main effect of condition on the fit coefficients ($\boldsymbol{x^2}$: $F(1,55) = 5.0$, $p < .05$; $\boldsymbol{x}$: $F(1,55) = 5.3$, $p < .05$), a tendency toward a group effect ($\boldsymbol{x^2}$: $F(1,55) = 3.4$, $p = .07$; $\boldsymbol{x}$: $F(1,55) = 3.7$, $p = .06$), and a tendency toward an interaction between group and condition ($\boldsymbol{x^2}$: $F(1,55) = 2.3$, $p = .13$; $\boldsymbol{x}$: $F(1,55) = 2.2$, $p = .14$). On average, the coefficients were higher in the *Narrow* than *Broad* condition ($\boldsymbol{x^2}$: $t(56) = 2.2$, $p < .05$, $d = 0.29$; $\boldsymbol{x}$: $t(56) = 2.3$, $p < .05$, $d = 0.30$), and there was a tendency toward higher coefficients in NT than ASD ($\boldsymbol{x^2}$: $t(112) = 1.8$, $p = .07$, $d = 0.34$; $\boldsymbol{x}$: $t(112) = 1.9$, $p = .06$, $d = 0.35$).

Within the NT group, the coefficients were higher in the *Narrow* than *Broad* condition ($\boldsymbol{x^2}$: $t(30) = 2.4$, $p < .05$, $d = 0.42$; $\boldsymbol{x}$: $t(30) = 2.4$, $p < .05$, $d = 0.43$), whereas there were no significant differences within the ASD group ($\boldsymbol{x^2}$: $t(25) = 0.5$, $p = .62$, $d = 0.10$; $\boldsymbol{x}$: $t(25) = 0.6$, $p = .58$, $d = 0.11$).

Between groups, the coefficients were higher in the *Narrow* condition in the NT than ASD group ($\boldsymbol{x^2}$: $t(55) = 2.5$, $p < .05$, $d = 0.64$; $\boldsymbol{x}$: $t(55) = 2.6$, $p < .05$, $d = 0.65$). There were no between group differences in the *Broad* condition ($\boldsymbol{x^2}$: $t(55) = 0.2$, $p = .82$, $d = 0.06$; $\boldsymbol{x}$: $t(55) = 0.3$, $p = .76$, $d = 0.08$). The effect sizes measuring the group differences were medium to large in the *Narrow* condition, and very small in the *Broad* condition.

2.4. Correlation between the time-order effect and the Autism-spectrum Quotient

We assessed whether the flexible adjustment of the prior weight on perception (difference in time-order effect between the *Narrow* and *Broad* conditions) was related to the number of autistic traits assessed by the Autism-Spectrum Quotient (AQ). The difference in fit coefficients between the *Narrow* and *Broad* conditions was correlated with the AQ ($\boldsymbol{x^2}$: $r = 0.30$, $p < .05$; $\boldsymbol{x}$: $r = -0.30$, $p < .05$). Within groups, the correlations were not significant (NT group: $\boldsymbol{x^2}$: $r = 0.29$, $p = .12$, $\boldsymbol{x}$: $r = -0.28$, $p = .13$; ASD group: $\boldsymbol{x^2}$: $r = 0.18$, $p = .37$, $\boldsymbol{x}$: $r = -0.18$, $p = .37$).

DISCUSSION

We conducted a behavioral study designed to elicit an implicit prior learning and aiming at assessing whether individuals with ASD can flexibly adjust the weight of their prior depending on the context. First, we showed that adults with and without ASD can implicitly learn a prior about the mean magnitude of the stimuli, and have their perception biased toward this prior. NT participants adjusted the weight of their prior to the context, so that a small stimulus range led to the formation of a strong prior (i.e., high precision), whereas a broader stimulus range was associated with a weaker prior (i.e., lower precision). In contrast, the precision of the prior was not adjusted to the context in the ASD group.

In terms of discrimination abilities, the two groups did not differ in their accuracy levels and were both influenced by the context. Indeed, the stimulus resolution was affected by the stimulus range: a smaller range was associated with a higher accuracy level and faster responses in both groups.

Implicit learning of the prior mean in NT and ASD adults

According to the Bayesian brain theories, individuals constantly learn the underlying statistical regularities of their environment to build up or adjust their prior knowledge. Here, we observed that throughout the discrimination task, adults with and without ASD built up a prior about the mean size of the stimuli. Note that this learning was implicit, as they were not asked to compute any average, and that learning the average did not provide any advantage to complete the task successfully. Both the NT and ASD groups showed a strong time-order effect, a robust effect already described in NT participants for a variety of stimulus features (Ashourian & Loewenstein, 2011; Harris et al., 2006; Hellström, 1985; Hellström & Rammsayer, 2015; Karim et al., 2013; Preuschhof et al., 2010; Raviv et al., 2012; Sinclair & Burton, 1996; van den Berg et al., 2017).

The presence of a time-order effect in the ASD group demonstrates that adults with ASD can implicitly infer the mean of the stimuli, and have their perception biased by this prior knowledge. This result is consistent with other studies involving children or adults with ASD and showing that their perception is indeed influenced by prior knowledge (Corbett et al., 2016; Croydon et al., 2017; Manning, Tibber, Charman, Dakin, & Pellicano, 2015; Sapey-Triomphe, 2017; Van de Cruys et al., 2017). As priors were found to modulate the perceptual experience of adults with ASD, it does not support the theory suggesting that ASD is characterized by weak priors (Pellicano & Burr, 2012).

Implicit learning of the prior precision: a more inflexible adjustment in ASD

The core aspect of our experiment was that we manipulated the variance of the distribution of the sensory inputs to modulate the precision of the prior distribution. We had hypothesized that a narrow range of stimuli would lead to a precise prior, whereas a broader range of stimuli would lead to a less precise prior. In the NT group, we confirmed this hypothesis: the smaller the stimulus range was, the stronger the prior bias was. This result shows that NT individuals can implicitly learn the variance of a distribution, and that they can flexibly adjust the precision of their priors depending on the context.

In contrast, in the ASD group, the strength of the time-order effect did not differ between the *Narrow* and *Broad* conditions. This result suggests that the prior precision was not flexibly modulated by the context in ASD. Similarly, a study assessing ensemble perception in ASD revealed that performance differed less across the different stimulus distributions in children with ASD than in typically developing children (Van der Hallen et al., 2017). This inflexibility is in line with the hypothesis of a high and inflexible precision of the prediction error in autism (Van de Cruys et al., 2017), as the prediction error precision is function of the sensory and prior precisions. Note that we do not have evidence for a higher precision ratio, but only for a more inflexible prior precision in ASD. In the first descriptions of children with ASD, Kanner had already noticed an intolerance for change, suggesting an inflexibility to adjust internal representations: "*Their world must seem to them to be made of elements that, once they have been experienced in a certain setting or sequence, cannot be tolerated without all the original ingredients in the identical spatial or chronological order*" (Kanner, 1943). This result also echoes the increased perceptual inflexibility found in other studies in ASD (e.g., D'Cruz et al., 2013; Robertson, Kravitz, Freyberg, Baron-Cohen, & Baker, 2013).

In ASD, the decreased adjustability of the prior precision to the context could be due to a slower learning of the prior precision. Indeed, a recent study showed that individuals with ASD updated their prior more slowly, as they weighted recent stimuli less heavily than NT (Lieder et al., 2019). In other contexts, such as category learning, individuals with ASD were also found to learn more slowly (Soulières, Mottron, Giguère, & Larochelle, 2011). In our study, as the strength of the time-order effect was on average lower in the ASD group than in the NT group, we can hypothesize that the ASD participants may not have had enough time to build up a precise representation of the prior distribution. Lieder and colleagues also found that the contraction bias was, on average, lower in the ASD group than in NT (Lieder et al., 2019). Hence, our results suggest that people with ASD can learn an internal representation but are more inflexible to adjust its precision (either because of an impairment to learn it, or because of a slower dynamic to adjust it).

If the precision of the prior is not adjusted flexibly in ASD, then the precision of the prediction error would also be inflexible if the sensory precision is not modulated. This means that small or large mismatches between the sensory input and the prior would be equally surprising. This idea of an inflexibility of the prediction error in ASD was supported by recent studies showing that the response to expected vs. unexpected stimuli was reduced in ASD (Goris et al., 2018; Lawson et al., 2017). Indeed, Goris and colleagues showed that the amplitude of the mismatch negativity response (reflecting the prediction error) was modulated to smaller extent by the context in ASD. In other words, adults with ASD had more inflexible sensory prediction errors, as they were less modulated by the predictability of the context. If prediction errors are not minimized when they should be, it would interfere with an optimal refinement of the prior distribution and could produce overwhelming sensations of constant surprises in ASD.

More globally, the symptomatology of ASD can be related to the atypical prior learning described above. As social behaviors are highly dependent on the context, a slow and/or impaired adjustment of internal representations could lead to difficulties to properly respond to social interactions. It is consistent with the description of ASD in the DSM-5 pointing out "*difficulties adjusting behavior to suit various social contexts*" (DSM-5, American Association, 2013). This increased inflexibility is coherent with the description of non-social symptoms of ASD, such as "*insistence on sameness, inflexible adherence to routines, or ritualized patterns or verbal nonverbal behavior*" (DSM-5, American Association, 2013), and with their intolerance of uncertainty. Note that intolerance of uncertainty in ASD was associated to other symptoms, such as atypical sensory sensitivity and anxiety (Joyce et al., 2017; Neil, Olsson, & Pellicano, 2016; Rodgers et al., 2016). Consistently, people with more autistic traits show a higher preference for predictability (Goris et al., 2019) and could therefore develop more rigid or repetitive behaviors, as a way to restore some predictability and/or to cope with this inflexibility. Indeed, to minimize the mismatch between predictions and sensory input, one can either update his/her internal model or act on the environment to make it fit its prior (e.g., Friston, 2003, 2012). Individuals with ASD would tend to use active inference to change their environment, rather than adjusting their prior.

A contextual effect on discrimination abilities in NT and ASD

In our task, the discrimination abilities to compare the disc sizes did not differ between groups, consistently with the existing literature (for a review, see Simmons et al., 2009). Interestingly, in both groups, the stimulus range had an effect on the mean accuracy level. Indeed, the average level of correct answers was significantly higher when participants were presented with a narrow range of stimuli than with a broader range. This type of range adaptation effect was recently described as the Range of Standards Effects (RSE) (Namdar et al., 2018, 2016). Namdar and colleagues showed that the just noticeable difference (JND) between two visual stimuli is smaller when the range of standard stimuli is narrower. In other words, a smaller range of stimuli is associated with a better discrimination. In our task, we did not measure the JND, but we observed that the overall accuracy increased when the stimulus range decreased (this effect remained significant, even when we only considered the six pairs of stimuli that were present in both the *Narrow* and *Broad* conditions). Namdar and colleagues made hypotheses about the mechanisms underlying the RSE, and suggested that it could be due to a variance in the criterion used to distinguish two stimuli given the context, and/or due to a variance in the signal representation as stimuli further apart will activate different groups of neurons (Namdar et al., 2016). Even though these mechanisms remain to be identified, importantly, the presence of this effect suggests that the discrimination abilities are influenced by contextual cues. It therefore suggests that perceptual acuity can be dynamically adjusted depending on the context. Casted in the Bayesian framework, we could hypothesize that the RSE reflects a dynamic and contextual adjustment of the sensory precision. Hence, as both the NT group and the ASD group showed an RSE, it may indicate that individuals with ASD adjusted their sensory precision to the context. Following this interpretation, our results would be in favor of a model of ASD characterized by an inflexible prior precision and a flexible sensory precision. Future studies should measure the JND in contexts with small and broad ranges of stimuli in individuals with ASD to tests and characterize the RSE more precisely in ASD.

Limitations

We expected the time-order effect to be centered on the mean of the distribution (around 200 pixels), but we observed a slight shift toward lower magnitudes (around 170 pixels). This shift could reflect a general tendency of the participants to answer more frequently that the second disc was larger than the first one, despite the fact that the sides of the plus and minus signs were counterbalanced between participants. Yet, as this shift was similar in the two groups and in the two conditions, we believe that it did not influence the main results of this study.

The two groups were well matched in terms of demographic characteristics, except for the mean education level that was slightly lower in the ASD group than in the NT group. Note that none of the ASD participants had any intellectual disability or showed difficulties to understand the instructions of the task. Besides, some of the ASD participants had comorbidities, such as ADHD. Yet, it should be highlighted that the presence of this comorbidity did not seem to affect the completion of the task. Indeed, all participants showed a good level of attention when performing the task, as the mean percentage of unanswered trials was very low in the ASD group (mean of 0.2% ranging from 0.0% to 1.4% vs. a mean of 0.1% in the NT group, ranging from 0.0% to 1.8%).

Furthermore, even if the two groups did not differ in accuracy, we noticed that some of the ASD participants had very high levels of accuracy in the *Narrow* condition: seven ASD participants (i.e., 27% of the ASD group) had a percentage of correct answers above 97%, whereas only one NT participant (i.e., 3% of the NT group) scored above 97%. Although noteworthy in itself (suggesting extremely accurate perception in these participants), such high performance level could constitute a ceiling effect encountered in some of the ASD participants.

Finally, the time-order effect may indicate that the prior is biasing perception *per se* and/or the perceptual decision. In this discussion, we considered that the time-order effect reflects the fact that percepts are indeed biased by priors, as many findings suggest that prior knowledge is incorporated in the sensory representation (e.g., Kok, Brouwer, van Gerven, & de Lange, 2013).

Conclusion

To sum up, using a low-level discrimination task, we showed that adults with ASD can implicitly learn the mean of a prior distribution. However, we found that they were more inflexible to adjust the precision of this prior distribution to the context. This inflexibility may be due to a slower adjustment of the prior precision in individuals with ASD. Future studies should use computational models to characterize the learning rate and could investigate the adjustment of the prior precision over longer time scales. Finally, we showed a range of standards effect whereby the context modulated the accuracy level, which may indicate a flexible adjustment of sensory precision in ASD. Altogether, these results suggest predictive accounts of ASD should focus on the inflexibility of prior precision.

Acronyms

AQ: Autism-Spectrum Quotient, ASD: Autism Spectrum Disorder, D1/D2 : First/Second disc displayed, DSM: Diagnostic and Statistical Manual for mental disorders, HIPPEA: High and Inflexible Precision of the Prediction Error in Autism, JND: Just noticeable difference, NT: Neurotypical, RSE: Range of standards effect, RTc: Response time for correct answers, TOE: Time-Order Effect.

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Competing interests

All co-authors report that they have no competing interests.

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TABLES

	NT group	**ASD group**	*p*
Number of participants	31	26	-
Male / Female number	16 / 15	13 / 13	*ns*
Age (years)	25.0 (±4.7)	27.0 (±8.6)	*ns*
Left / Right-handed	3 / 28	2 / 24	*ns*
Education level (years)	16.7 (±2.2)	14.2 (±2.2)	*
AQ (score /50)	13.8 (±5.7)	31.9 (±7.3)	*

Table 1: Demographic characteristics of the two groups

The table presents the group means (± standard deviations) of the participants included in the analyses. AQ: Autism-spectrum Quotient. *p*: p-values correspond to the results of the Student t-tests and proportion tests performed between groups. * $p < .05$

Narrow range					
	S2	**S3**	**S4**	**S5**	**S6**
D1	173	186	200	215	231
D2	161 or 186	173 or 200	186 or 215	200 or 231	215 or 248

Broad range					
	S1	**S2**	**S4**	**S6**	**S7**
D1	150	173	200	231	267
D2	139 or 161	161 or 186	186 or 215	215 or 248	248 or 287

Table 2: Diameters of the discs

Diameters (in pixels) of the first disc (D1) and second disc (D2) displayed successively at each trial (e.g., S2 presents a 173-pixel large disc, followed by a 161-pixel large disc if D1>D2 or by a 186-pixel large disc if D1<D2). The values were calculated along a logarithmic scale (*Narrow*: log(D1) = 2.24, 2.27, 2.30, 2.33 and 2.36; *Broad*: log(D1) = 2.18, 2.24, 2.30, 2.36 and 2.43). The ratio between the diameters of D1 and D2 remained the same in each stimulus pair. The time-order effect should facilitate more and more the stimulus comparison for the following pairs of stimuli: P1: S6 (D1>D2) and S2 (D1<D2), P2: S5 (D1>D2) and S3 (D1<D2), P3: S4 (D1>D2 and D1<D2), P4: S3 (D1>D2) and S5 (D1<D2), P5: S2 (D1>D2) and S6 (D1<D2).

FIGURE LEGENDS

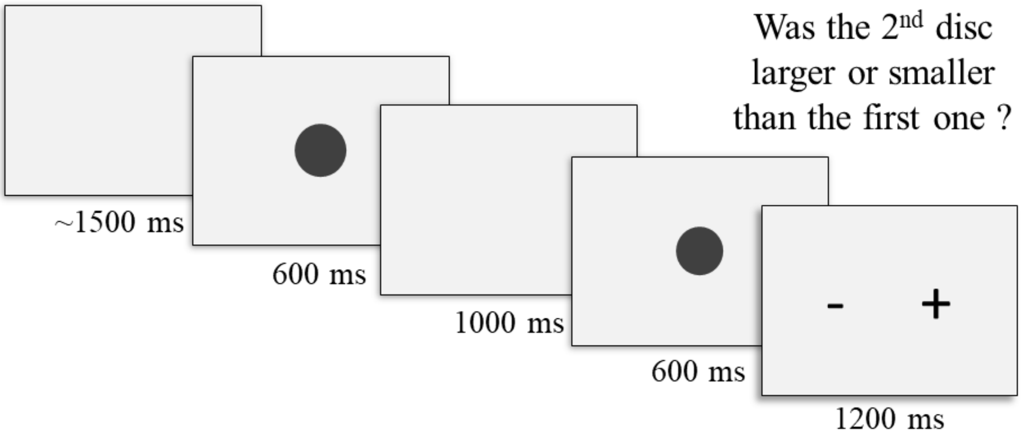

Figure 1: Experimental paradigm

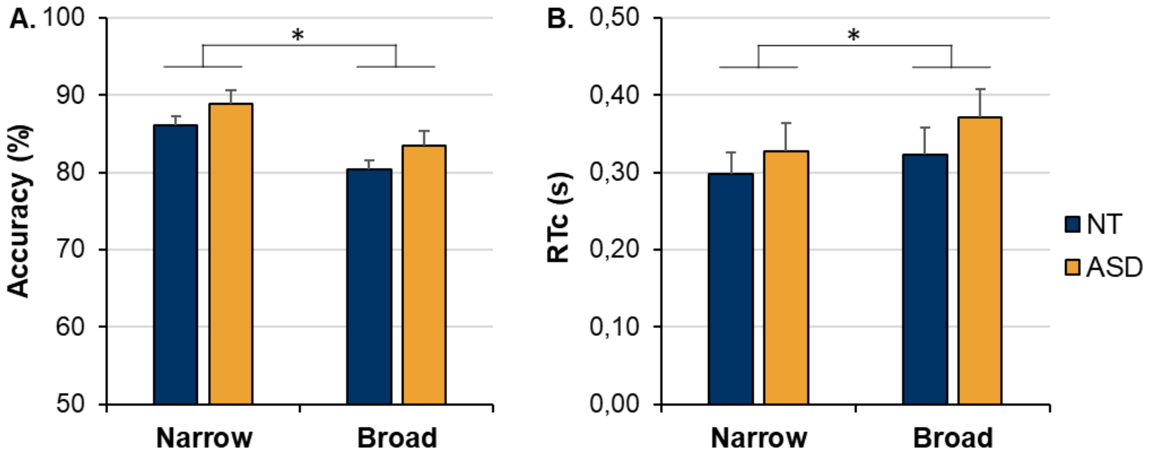

Figure 2: Mean results in the *Narrow* and *Broad* conditions

A. Mean percentage of correct answers. **B.** Mean response time for correct answers (RTc). Error bars correspond to the standard error of the mean. * $p < .05$.

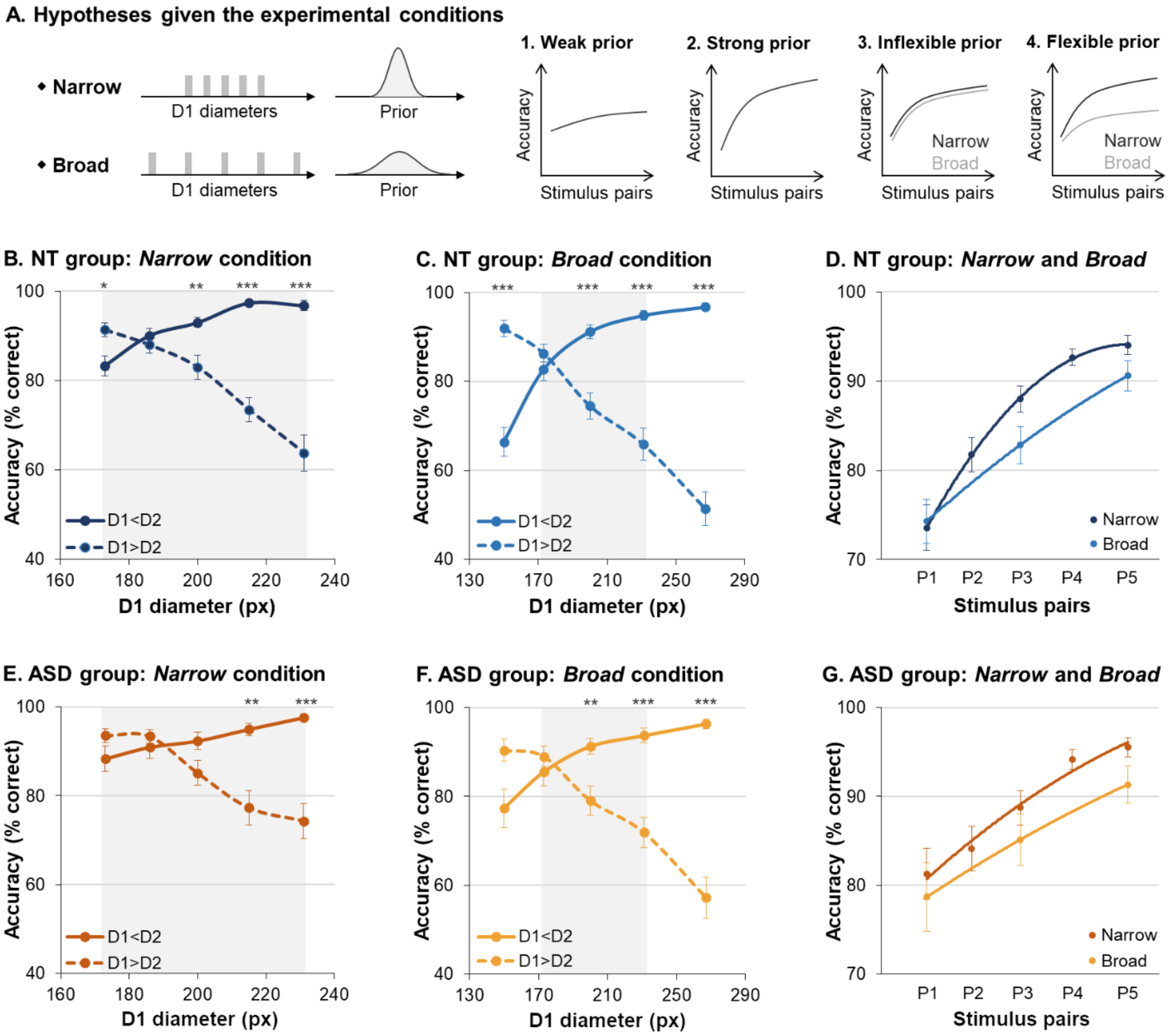

Figure 3: Time-order effect in the Narrow and Broad conditions

A. Presentation of the two experimental conditions (*Narrow* or *Broad* stimulus range) and schematic representation of the expected results under different hypotheses. **B, C, E, F:** Time-order effect observed in the NT (B, C) and ASD (E, F) groups. The grey area indicates the overlapping datapoints between conditions. **D, G:** Second-order polynomial fit of the time-order effect. P1 to P5 correspond to the pairs of discs where the comparison is more and more facilitated by the time-order effect (see Table 2). Error bars indicate the standard error of the mean. * $p < .05$, ** $p < .005$, *** $p < .0005$ after Bonferroni correction for the five comparisons.

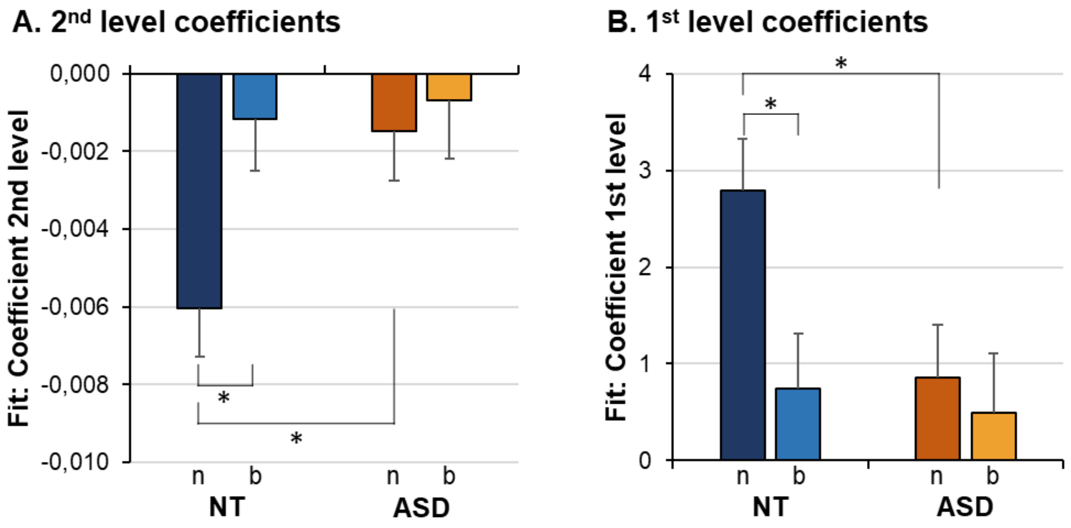

Figure 4: Second-order polynomial fit of the time-order effect

Second (**A**) and first (**B**) level coefficients of the second-order polynomial fit of the time-order effect in the NT (blue) and ASD (orange) groups. The darker colors correspond to the *Narrow* condition (n) and the clearer colors to the *Broad* condition (b). Error bars correspond to the standard error of the mean. * $p < .05$.