Preserved low-level visual gain control in autistic adults [version 1; peer review: 2 approved with reservations]

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Abstract

Background: No sensory stimulus is an island entire of itself, the processing of visual inputs is highly influenced by surrounding spatial context. Some accounts of Autism Spectrum Disorder have suggested that the sensory difficulties reported in the condition could arise from differences in contextual modulation of sensory stimuli, specifically problems with gain control mechanisms that regulate incoming sensory information as a function of sensory context.

Methods: Here we examined the spatial modulation of visual processing in autistic and neurotypical adults by assessing surround suppression for two low-level visual features: orientation and luminance. We used an established psychophysical task with known neurocomputational correlates and interrogated group differences in suppression magnitude.

Results: We found that the magnitude of surround suppression for both visual features was equivalent in autistic adults and matched neurotypical controls. Additionally, there was no relationship between suppression magnitude and autism symptom severity.

Conclusion: These results suggest that for low level visual features, the spatial gain control mechanisms regulating sensory input are preserved. These findings have important theoretical implications for establishing the types of gain control mechanisms that are compromised in autism, and the extent to which there are differences in contextual processing.

Keywords

Autism, Gain Control, Divisive Normalisation, Surround Suppression, Precision
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Introduction

Autism spectrum disorder (ASD) is a pervasive neurodevelopmental condition that can result in difficulties with social interaction, communication and sensory processing. Altered perception is well documented in autistic people, with hypo and hyper sensitivities reported across various sensory modalities (Robertson & Baron-Cohen, 2017; Simmons et al., 2009). However, the biological mechanisms that give rise to the sensory processing difficulties in autism remain poorly understood.

Autistic people demonstrate superior performance on visual search tasks (Blaser et al., 2014; O’Riordan et al., 2001; O’riordan, 2004), and there are reports of reduced susceptibility to some visual illusions (Chouinard et al., 2018; Happé, 1996; Mitchell et al., 2010), though the findings are mixed (Manning et al., 2017; Van der Hallen et al., 2015). Interpretations of these differences in autistic perception have focussed on either enhanced “bottom-up” perceptual functioning (Mottron et al., 2006) or weaker “top-down” central coherence (Happé & Frith, 2006). The latter suggests that autism is characterised by a neurocognitive processing style in which there is greater focus on the smaller and potentially irrelevant aspects of a visual scene, owing to a reduced sense of the wider context. Indeed, problems contextualising sensory inputs may be crucial to understanding the pathogenesis of autism (Lawson et al., 2015b). Newer neurocomputational theories of autism highlight a key role for differences in cortical gain control - mechanisms for contextualising neural responses (Friston et al., 2013; Lawson et al., 2014; Palmer et al., 2017; Pellicano & Burr, 2012; Rosenberg et al., 2015; Van de Cruys et al., 2014). Empirically, a great deal of research has focussed on how temporal context (i.e. the recent sensory past) impacts on perception in autism (Ewing et al., 2013; Lawson et al., 2015a; Lawson et al., 2017; Lawson et al., 2018; Pellicano et al., 2007; Pellicano et al., 2013; Turi et al., 2015), but the impacts of spatial context on autistic perception are less well understood.

One classic example of how spatial context impacts on visual processing is through surround suppression, manifest in perceptual biases such as the tilt illusion (Clifford, 2014; Gibson & Radner, 1937; Schwartz et al., 2007). In this illusion, the perceived orientation of a central grating can be influenced by the orientation of the context in which it is embedded. There is convergent evidence across electrophysiological (Blakemore et al., 1970), psychophysical (Solomon et al., 1993; Solomon & Morgan, 2006), computational (Schwartz et al., 2007; Schwartz et al., 2009), and human functional imaging (McDonald et al., 2010; Song et al., 2013a) studies to support the view that surround suppression is driven by the inhibition of the neural responses to a stimulus by the pooled neural activity of cells in the surrounding cortex. Mathematically, this inhibition has been described as divisive normalisation (Schwartz et al., 2007), a canonical computation that reduces redundancy in the visual system by increasing signal-to-noise ratio (Carandini & Heeger, 2011). Surround suppression, then, serves as a form of local gain control in which the driving neural responses to a stimulus are scaled according to neighbouring variance, i.e. precision (Lawson et al., 2015b).

Physiologically, there is evidence from both molecular and genetic studies to suggest an increased excitation-inhibition (E-I) balance in autism (Rubenstein & Merzenich, 2003; Yizhar et al., 2011), and this is also suggested by the high incidence of seizures in people diagnosed with autism (Tuchman & Rapin, 2002). Computationally, reduced cortical inhibition would be realised via reduced divisive normalisation, and computational accounts of autism have proposed that weaker normalisation might explain the cognitive processing differences in autism across a range of domains (Rosenberg et al., 2015). However, empirical evidence for the reduced normalisation account of autism is limited. Two recent studies, one testing normalisation for low-level visual features (Van de Cruys et al., 2018) and another for high-level social cues (Palmer et al., 2018), indicate that normalisation is preserved in autism. Further studies are needed to inform this attractive model and better understand the impact of spatial context on sensory processing in autism.

Here we administered psychophysical measures of surround suppression to autistic and neurotypical adults as behavioural assay of the integrity of gain control in low-level vision. We employed an established paradigm to assess individual differences in the magnitude of surround suppression, which is known to correlate with visual cortex size, GABA concentration and also peripheral-central primary visual connectivity (Song et al., 2013a; Song et al., 2013b; Song et al., 2017). This ensures that the relationship between these specific behavioural metrics of context and inhibitory cortical processes are well established. We assessed two low level visual features, orientation and luminance, and predicted that if compromised gain control is pervasive in autism, then we would see reduced surround suppression for both of these features relative to neurotypical participants.

Methods

Participants

Volunteers were recruited via email and telephone call from the Developmental and Executive Functions database held at the UCL Institute of Cognitive Neuroscience (ICN). A total of 27 adults (19 male) with a diagnosis of ASD were recruited, and 20 age-matched neurotypical (NT) participants with no psychiatric or neurological conditions (13 male) served as controls. The groups were matched on age (Welch’s t = 0.0574, p = 0.955; mean age ASD = 38.148 ± 1.927, NT = 37.950 ± 2.866). The Wechsler Adult Intelligence Scale (WAIS 3rd edition) was administered to quantify IQ (ASD FSIQ = 114.037 ± 2.730, NT FSIQ = 120 ± 2.602). We were unable to obtain IQ data for one participant with ASD, otherwise both groups were matched (Student t = -1.581, p = 0.121). As expected, autistic participants had a higher Autism Quotient score (AQ; Baron-Cohen et al., 2001) than the neurotypical participants (Welch t = 5.736, p<.001).

Although we abide by the terminology of the DSM IV, and refer to “Autism Spectrum Disorder”, we acknowledge that many people on the spectrum prefer identity-first language and so we also use “ autistic person” throughout (Kenny et al., 2015).
Autistic participants were diagnosed by independent clinicians according to the DSM-IV criteria (American Psychiatric Association, 2000). Of the autistic group, 19 had a diagnosis of Asperger’s, one of high functioning autism, one of Asperger’s and attention deficit hyperactivity disorder (ADHD), one of ASD and learning difficulties, and three of ASD. This classification information was not available for two participants at the time of testing, but one scored above the AQ clinical cut-off of 32. Participants with ASD were also assessed on the Autism Diagnostic Observation Scale (Lord et al., 2000; ADOS, mean score = 9.15) by a member of the research team trained to the level of researcher reliability.

All participants had corrected-to-normal or normal vision. Ethical approval was provided by the UCL Ethics Committee (0929/001). Written informed consent to take part in the study and for the publication of anonymised data were obtained from the participants. Participants were compensated for their time.

Apparatus
The computer-based tasks were implemented using MATLAB 7.7.0.471 (R2008b, MathWorks, Inc.), and Cogent 2000 in a quiet and darkened room. Tasks were conducted on a Dell Precision M4500 Computer PC, with a Samsung SyncMaster monitor (screen size: 480 × 300 mm; screen resolution: 1680 × 1050; refresh rate: 120 Hz). Head position was fixed with a chin rest 800 mm from the computer screen. This ensured a constant direct viewing distance for all participants, that the stimuli subtended a consistent visual angle.

Psychophysical paradigm
The task procedures are as reported previously in (Song et al., 2013b; Wright et al., 2018).

Discrimination thresholds. First, we determined individual discrimination thresholds for a given feature value (luminance or orientation) for each participant (Figure 1). Each stimulus was presented for 300 ms, with a 200-ms interstimulus interval, and the trial ended with a randomly sampled dynamic coloured mask to eliminate afterimages.

To measure orientation discrimination thresholds, participants were presented with two successive sinusoidal gratings (spatial frequency: 1.5 cycles per visual degree; grating size: 1.5° visual angle) and asked to indicate whether the second stimulus was tilted more to the left (left key press) or the right (right key press)
relative to the first stimulus. One stimulus has a fixed orientation of 0° and the other was adapted according to a 2-up, 1-down staircase. This means that two correct responses led to a decrease in the difference in feature value on the next trial, and one incorrect response led to an increase in this difference. The staircasing procedure stopped after 19 reversals, and the orientation discrimination threshold was calculated by averaging feature value across the last 13 reversals, when participants were correct 70.71% of the time (Wright et al., 2018). Stimuli had constant uniform grey background, with luminance at 50% of the monitor maximum. The staircase step size was 0.1°.

The procedure for measuring luminance discrimination thresholds was the same except that luminance stimuli were composed of uniform grey circles (same size as the grating stimuli above, 1.5° visual angle), with a constant uniform grey background. Monitor luminance was set to 20% of the monitor maximum. The staircase step size was 0.78% of the maximum monitor luminance and participants were asked to indicate whether the second stimulus was darker (up arrow key press) or lighter (down arrow key press) relative to the first stimulus.

**Orientation surround suppression.** In a first adjustment phase, participants performed four trials to initially gauge their point of subjective equality. In these trials they were presented with two gratings on screen, one of which had a central orientation of 0° and a surround of 20°. Participants were asked to rotate the orientation of the grating without a surround (left or right button press) to match the orientation of the central grating with a surround.

Next participants entered the main experimental phase to measure the magnitude of surround suppression (Figure 2). Two central circular stimuli (one with a surround and one without) were presented one after the other. Orientation stimuli were composed of a sinusoidal grating (spatial frequency: 1.5 cycles per visual degree; central grating size: 1.5° visual angle; surround grating size: 6° visual angle. Each stimulus appeared for 300 ms with a 200-ms interstimulus interval and the trial ended with a randomly sampled coloured dynamic mask to eliminate afterimages. Participants responded to indicate whether the central circle of the second stimulus, relative to the first, was rotated more to the left (left key press) or more to the right (right key press).

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**Figure 2.** Example trial sequence for measuring the magnitude of surround suppression for luminance (top) and orientation (bottom). In each case, participants were presented with two consecutive stimuli and had to respond whether the central stimulus presented second, relative to the central stimulus presented first, was tilted more to the right/left (for orientation), or brighter/darker (for luminance). The stimulus with the dark surround (for luminance) and with the 20° surround (for orientation) were held constant throughout though their appearance first or second was counterbalanced. The other central stimulus varied from trial to trial according to one of seven predetermined stimulus values. After making a response a randomly sampled dynamic coloured mask appeared to eliminate any afterimages across trials.
The interval (first or second) containing the surround grating was counterbalanced across trials. In every trial one stimulus was fixed (central grating 0°, surround grating 20°) whilst the other grating without a surround varied around seven possible orientations. These were determined according to the formula:

\[ s1 s2 s3 s4 s5 s6 s7 = \text{starting value} + [a \ldots a] + 1.5t \{[-3° -2° -1° 0° 1° 2° 3°]\]  

in which a is the participants point of perceptual equality determined in the adjustment section (see above) and t is the participants discrimination threshold. The starting value in the orientation task was 0°, and the luminance task 50% of the maximum monitor luminance. Each of the seven orientations was presented 18 times in a random order for a total of 126 trials.

**Luminance surround suppression.** The procedure for measuring luminance surround suppression was largely the same as for orientation in terms of trial numbers, stimulus sizes and timing, with the following exceptions:

Central luminance stimuli were composed of uniform grey circles. In the adjustment phase both left and right stimuli appeared in the presence of a surround, one black and one white (position counterbalanced). Participants were instructed to adjust the luminance of the central circle with the white surround so that it was equal in luminance to the circle with the black surround, using the up and down arrow keys. The luminance of the central circle on the black surround stimulus was fixed at 50% throughout.

In the main experimental phase participants were again presented sequentially with concentric circles of which the surround was either white or black (Figure 2). Participants were instructed to indicate whether the central circle in the second interval, was lighter or darker than the central circle in the first interval. The luminance of the central circle on the black surround stimulus was fixed at 50% throughout, and the luminance of the central circle in the white surround varied from trial to trial. These values were set according to the participants predetermined discrimination threshold and gauged point of subjective equality, in a manner identical to the orientation experiment.

**Psychometric curve fitting**

The spatial suppression magnitude (corresponding to a psychophysical bias, or the threshold/midpoint of a sigmoidal curve) was estimated using the Palamedes MATLAB Toolbox (Version 1.10.3, Prins & Kingdom, 2018; this software is also functional in the open-source Octave). The proportion correct responses (lapses), and correct responses independent of stimulus equality, in a manner identical to the orientation experiment.

The resulting estimates were bootstrapped with 400 simulations to obtain a standard deviation for the estimates. We performed goodness of fit analyses on each fit compared to a standard model. Preliminary model comparisons using the likelihood ratio test (Prins & Kingdom, 2018) indicated that the assumptions of fixed guess and lapse rate were valid.

**Statistical analysis, power and exclusions**

Statistical analysis was conducted in MATLAB 2019b, and JASP 0.11.1 (JASP Team, 2019). Wherever assumptions of normality or equal variances between the groups were violated (as assessed by Shapiro-Wilk and Levene’s tests) we compared the autistic and neurotypical groups on their discrimination thresholds and spatial suppression magnitudes using non-parametric statistics (Mann Whitney U tests) and in the interests of completeness also conducted parametric statistics (Student’s or Welch’s t tests) on transformed data wherever possible. In addition to frequentist null hypothesis significance testing, we also assessed all group differences using estimation statistics and present these results as estimation plots which visualise the effect size for the group difference (Ho et al., 2019). Estimation statistics highlight the magnitude of an effect size and its precision, estimated using bias corrected and accelerated bootstrapping, without making any assumptions about the normality of the data (Ho et al., 2019). The relationship between ASD symptoms (as assessed by the ADOS) and discrimination thresholds/suppression magnitudes were assessed with Pearson’s r correlations.

Initially, participants were excluded if the staircase procedure failed when estimating discrimination thresholds or if performance indicated an issue with calibration (i.e. performance at the lowest stimulus level was above chance, or at the highest level was below chance). Following parameter estimation, exclusions were made if the model was unable to converge on a maximum likelihood estimate, if more than 90% of the simulations for the goodness of fit test failed, or finally if the confidence interval of the estimated bias parameter fell outside of the stimulus levels for each participant (Wright et al., 2018). Following these criteria, the number of participants in each group, and confirmation that these exclusions had no effect on age or IQ is reported in Table 1.

We initially powered the study to detect an overall main effect of task (i.e. suppression magnitude greater than zero) based on the large effect size (d=1.62) reported previously (Wright et al., 2018). Power analysis was conducted using G Power 9.1.9.2 (Faul et al., 2007) and indicated that we required a
Figure 3. Example logistic fits for individual participants. The surround suppression magnitude for each participant for luminance (top) and orientation (bottom) was taken as threshold (bias/midpoint) of the psychometric curve, shown as the dotted line on each plot. Blue plots show ASD participants and orange shows NT. Logistic functions were fit to proportion correct responses for each individual participant and then the bias was compared statistically across the groups.

Table 1. Following exclusions (see main text above) participants were still matched on age and IQ for each of the reported analyses.

| Post exclusion experimental sample                          | N (ASD) | N (NT) | Absolute value of Welch t statistic | p value |
|-------------------------------------------------------------|---------|--------|------------------------------------|---------|
| Age - luminance discrimination threshold                    | 25      | 20     | .228                               | .821    |
| IQ - luminance discrimination threshold                     | 25      | 20     | 1.40                               | .169    |
| Age - orientation discrimination threshold                   | 25      | 18     | 0.187                              | .853    |
| IQ - orientation discrimination threshold                    | 25      | 18     | 1.427                              | .161    |
| Age - luminance surround suppression                        | 17      | 14     | 1.422                              | .170    |
| IQ - luminance surround suppression                         | 17      | 14     | .810                               | .425    |
| Age - orientation surround suppression                      | 22      | 17     | 0.082                              | .935    |
| IQ - orientation surround suppression                       | 22      | 17     | 1.05                               | .301    |

Results

Discrimination thresholds
As the assumption of equal variances between the groups (Levene’s Test $F(1)= 6.806, p = 0.012$) was violated, a Welch’s $t$ test was used to assess group differences in luminance discrimination thresholds. Luminance discrimination thresholds were not significantly raised in the ASD group ($t(38.378) = 1.708, p = 0.096$); however, a borderline difference in group means was suggested by non-parametric bootstrapping shown on the estimation plot in which the CI for the effect size of the difference only very slightly overlaps with zero (mean difference, -4.24, 95% CI, [-9.4,0.158]; Figure 4A).

For the orientation discrimination thresholds, the assumption of normality (NT group, Shapiro-Wilk $W = .920, p = 0.051$, NT group, Shapiro-Wilk $W = .857, p = 0.001$) was violated, despite
approximately equal variances between the two groups. Both parametric and non-parametric tests revealed borderline but not significant differences in the mean orientation discrimination threshold ($t(41) = 1.774$, $p = 0.083$; $U = 301.5$, $p = 0.061$). Upon log transformation, both groups were approximately normally distributed and equal variances could be assumed. Parametric statistical tests revealed a marginally significant difference between the two groups ($t(41) = 2.060$, $p = 0.046$). This borderline difference in group means was confirmed with non-parametric bootstrapping on the raw data shown on the estimation plot in Figure 4B (mean difference, -0.179, 95% CI, [-0.351, 0.0254]).

Taken together these analyses indicate some suggestion of marginally, but not definitively, raised discrimination thresholds for both luminance and orientation in ASD.

Surround suppression magnitude
In both the luminance and orientation task, the ASD and NT groups were confirmed to have suppression magnitudes greater than zero (one-sample $t$ tests, all $p < 0.001$), indicating that overall both tasks capture the expected perceptual shifts as a result of spatial context.

Statistical comparisons indicated equivalent luminance surround suppression in both the ASD and NT groups. The assumptions of normality and homoscedasticity were met for both groups, a $t$-test revealed no significant difference in the group means ($t(29) = 0.357$, $p = 0.723$), indicating preserved surround suppression in ASD. Non-parametric bootstrapping as shown on the estimation plot indicated that this was a robust null effect (mean difference, -0.296, 95% CI, [-20.4, 12.5]; Figure 5A).

Group comparisons of suppression magnitude for the orientation task also indicated equivalent contextual biases. Suppression magnitude for the ASD group was non normally distributed (Shapiro-Wilks $W = 0.813$, $p < 0.001$) whereas the NT group did not violate this assumption. Both parametric and nonparametric tests revealed no significant group difference in suppression magnitude ($t(37) = -0.263$, $p = 0.794$; $U = 188$, $p = 0.989$). Negative log transformed values met the assumptions for a $t$-test which confirmed the null result ($t(36) = -0.099$, $p = 0.922$; note that one participant with a slightly positive suppression magnitude could not be transformed and was excluded from this analysis. In the full sample, without data transformation, non-parametric bootstrapping seen in the estimation plot confirms a robust null effect of the group difference in orientation suppression magnitude (mean difference, 0.073, 95% CI, [-0.428, 0.622]; Figure 4B).

Correlations with symptoms
To assess the relationship between autistic symptoms and our measures of sensory processing we conducted correlations. There was no significant correlation between ADOS scores and either luminance discrimination threshold (Pearson’s $r = -0.093$, $p = 0.658$) or orientation discrimination threshold (Pearson’s $r = -0.05$, $p = 0.801$) or luminance spatial suppression magnitude (Pearson’s $r = -0.114$, $p = 0.676$) or orientation spatial suppression magnitude (Pearson’s $r = -0.274$, $p = 0.222$). Raw data are available at Open Science Framework (see Underlying data) (Sandhu, 2019).

Discussion
In this study we investigated the magnitude of surround suppression for two low level visual features in autism, using
established psychophysical tasks that are optimised to detect individual differences and have known physiological correlates (Song et al., 2013a; Song et al., 2013b; Song et al., 2017). We found robust evidence for equivalent surround suppression for both visual features in both groups and no evidence for diminished surround suppression in ASD (Figure 4). This suggests that local gain control mechanisms for low level visual stimuli are preserved in autism.

It is often reported that autistic people perform differently on tasks that require processing visual information embedded in broader context. This includes the superior abilities in finding ‘embedded figures’ within a larger scene (Shah & Frith, 1983), more veridical perception in visual illusions that rely on global image properties (Happé, 1996), and better identification of the smaller constituent parts of a stimulus which make up larger global wholes (Plaisted et al., 1999). However, there are often inconsistent findings across each of these domains (Van der Hallen et al., 2015; White & Saldaña, 2011). This reflects not only heterogeneity in autistic cognition but also the fact that we need more precise definitions and measurements of context. A promising approach is to start from known mechanisms involved in the contextualisation of neural responses and then administer behavioural assays of those processes in autistic and neurotypical participants. Here we took this approach with two tasks that assess surround suppression in early visual cortex.

Surround suppression occurs when neurons are inhibited by a stimulus outside their classical receptive field, i.e. the ‘surround’, which produces profound biases in perception for the central stimulus. The surround provides context for the driving neural responses to the central stimulus, often scaling or controlling the gain on their output (Schwartz et al., 2007). While the precise neural circuitry governing surround suppression is still debated, the measure of surround suppression that we employed here is known to correlate with visual cortex size, via the scaling of intracortical connections (Song et al., 2013b). Song et al. (2013b) found a trade-off between discrimination sensitivity and contextual modulations that is associated with variation in visual cortical surface area. Individuals with larger V1 surface area had lower orientation discrimination thresholds and, conversely, were less susceptible to orientation surround suppression. However, in this paper we demonstrate that orientation surround suppression and discrimination thresholds are similar in ASD and neurotypical participants (Figure 3B, Figure 4B), which is consistent with population receptive field mapping studies showing equivalent V1 cortical surface area in autism (Schwarzkopf et al., 2014). Taken together, this would suggest that at least for primary visual processing, there is no difference in the balance between discrimination sensitivity and context sensitivity.

It is notable that in Song et al. (2013b), the relationship between cortical surface area and discrimination thresholds/surround suppression, did not hold for luminance. For luminance, surround suppression dynamics are believed to arise from the very earliest stages of visual processing, specifically in the retina (Shapley & Enroth-Cugell, 1984). Recently there has been renewed interest in retinal processing across neuropsychiatric conditions as a readily accessible part of the central nervous system that may exhibit pathology relevant changes (Schwitzer et al., 2017). While there are reports of retinal alterations in ASD (Creel et al., 1989; García-Medina et al., 2017), our finding of preserved luminance suppression would indicate...
that contextual gain control mechanisms operating at the level of the retina are preserved, though that is not to say that other retinal functions are not compromised.

There is some evidence that processing in the magnocellular, but not parvocellular, retinal pathway is different in ASD (Greenaway et al., 2013; Laycock et al., 2007; Sutherland & Crewther, 2010). Interestingly, evidence for this comes from a study showing raised luminance thresholds in autistic children using a paradigm optimised to isolate light/dark contrast detection driven by M-cells (Greenaway et al., 2013). Here we also show a trend towards raised luminance discrimination thresholds in ASD compared to NT participants (Figure 3A), although this is not specific to magnocellular processing since this trend also exists for orientation thresholds (Figure 3B). We interpret these data with caution since there isn’t strong evidence for a significant difference in discrimination thresholds in either case. However, it is interesting that the direction of these trend differences contradict accounts of autism that focus on enhanced perceptual processing (Mottron et al., 2006), since raised discrimination thresholds indicate that a larger objective difference in stimulus attributes might be required for ASD participants to maintain the same level of accuracy as neurotypical participants. More work is needed to understand at what level of visual processing the detail-focussed perceptual style thought characteristic of autism actually emerges.

Computationally, surround suppression is mediated by divisive normalisation, a canonical neural model that allows for the contextualisation of single, or pooled, neural firing (Carandini & Heeger, 2011). In divisive normalisation, local variance from the surround divides or scales the driving neural responses of the central stimulus. There are countless studies demonstrating that the perceptual biases reported in surround suppression arise from this form of gain control (Carandini & Heeger, 2011; Clifford, 2014; Schwartz et al., 2007; Schwartz et al., 2009). Recently there have been a number of computational accounts of autism that highlight the possibility of altered gain control in the condition (Lawson et al., 2014; Palmer et al., 2017; Rosenberg et al., 2015; Van de Cruys et al., 2014), and one in particular that proposed divisive normalisation is reduced in autism (Rosenberg et al., 2015). However, here the absence of group differences in orientation or luminance suppression would suggest that normalisation is preserved in ASD, at least for the very earliest levels of visual processing, i.e. the retina and V1. This is consistent with recent studies examining cross-orientation suppression in ASD (Van de Cruys et al., 2018) and another that quantified normalisation explicitly in the context of neuronal channels representing eye gaze direction (Palmer et al., 2018), both of which found evidence for intact normalisation. Future studies should investigate normalisation in the context of mid-level visual processing, especially as it is in these extrastriate visual areas that larger cortical surface areas are reported in autism (Schwarzkopf et al., 2014).

To summarise, here we show that surround suppression for two low-level visual features - orientation and luminance - is equivalent in autistic and neurotypical participants. These results help us to establish the scope of theories proposing context insensitivity (Vermeulen, 2012) or reduced normalisation (Rosenberg et al., 2015) and suggest that we need to take a more precise look at the idea of “context” in autism (Lawson et al., 2015).

Data availability
Open Science Framework: Preserved Low Level Visual Gain Control in Autistic Adults. https://doi.org/10.17605/OSF.IO/YE7S6 (Sandhu, 2019).

This project contains the following underlying data:
- Demographics_public: demographics information on the anonymised participants, including age, gender, group, Weschler IQ, Autism Quotient (AQ), Autism Diagnostic Observation Schedule (ADOS) score.
- Summary.csv: a folder containing example output from the analysis of the suppression magnitudes (from curve fitting analysis) and discrimination threshold for each participant in csv format, ready for analysis in either JASP or estimation plots (labelled appropriately).
- Summary.mat: a folder containing three .mat files, one summarising the luminance dataset, one summarising the orientation data set, and one with demographic information.
- Raw_data: a folder containing 4 sub folders (one for each experiment), which each contain the data from all participants.
- READ_ME: Information document explaining each (sub) folder in each folder above.

Data are available under the terms of the Creative Commons Zero “No rights reserved” data waiver (CC0 1.0 Public domain dedication).

Software availability
The code for the analysis of the task can be found at: https://github.com/timothysandhu/GainControlASD.

Archived code at time of publication: https://doi.org/10.17605/OSF.IO/YE7S6 (Sandhu, 2019).

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Open Peer Review

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The authors set out to test the hypothesis of decreased divisive normalization in ASD, using a well-established surround suppression paradigm. Contrary to the hypothesis, they find equivalent surround suppression in ASD.

The report is exemplary both in terms of soundness of experimental and statistical procedures, as well as in clarity of descriptions and graphs.

I don't see any substantial problems, but have one minor remark. Theoretically, in both the introduction and discussion section, the authors hint at the simple equation of models centered on deficient gain control from a predictive coding background, and models of deficient gain control from a population-coding (divisive normalization) background, which seems overly hasty and requires more explanation (see also Spratling, 2017, on divisive vs subtractive predictive suppression). It seems that the precision mechanism as described in PC accounts is much broader (e.g., not necessarily stemming from the same level/population of processing, cf. ‘neighbouring variance’). I think it would strengthen the discussion if the authors would briefly address this nuance and its implications for future empirical work (e.g. how the current findings do or do not invalidate broader precision-based accounts for autism).

I could catch one typo where you refer to the graphs on p. 8, second column (pdf version): I think "4B" needs to be "5B"

References
1. Spratling MW: A review of predictive coding algorithms. Brain Cogn. 112: 92-97 PubMed Abstract | Publisher Full Text

Is the work clearly and accurately presented and does it cite the current literature?
Yes

Is the study design appropriate and is the work technically sound?
Yes

Are sufficient details of methods and analysis provided to allow replication by others?
Yes

If applicable, is the statistical analysis and its interpretation appropriate?
Yes

Are all the source data underlying the results available to ensure full reproducibility?
Yes

Are the conclusions drawn adequately supported by the results?
Yes

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Predictive coding accounts of autism, Perception in autism.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.
report using an orientation surround stimulus (though different to this one and in the periphery/parafovea) that surround suppression does vary with autistic tendency.

2. Was the difference on IQ between the NT and ASD groups not significant (p.3)?

3. What was the contrast of the orientation grating? Foss-Feig et al. (2013) report that suppression (for motion stimuli) is contrast dependent, so this might be important.

4. How did the phase of the gratings between the two presentations vary (or not)? If there was no change in phase did this create an apparent motion cue (between stimulus 1 and 2)? If so, could it be that some participants used the motion cue rather than orientation cue to perform the task?

5. I wasn’t quite clear about the PSE measurement. Why only use 4 trials? Given that this task will be (particularly) subject to both motor control biases and possible memory problems it would seem that this could introduce a lot of noise. Given that the PSE was calculated to determine the range of orientations (luminances) to test for each individual participant, I was unsure why there were so many participants excluded in the main analysis. For the luminance suppression experiment, 10 out of 27 were excluded which seems quite high. Given that the stimulus range was tailored to the participant I don’t understand why there were so many failures to fit, unless this PSE estimation wasn’t really suitable. This might also be problematic (for this condition only) since you state that you need a sample size of 20 participants (I think this is per group, but this is unclear) to detect a moderate effect size, but after exclusions, the sample sizes drop below 20.

6. For the psychometric curve fitting why did you fix both the lapse rate and the guess rate? Couldn’t you let both vary and then, based on some criterion (e.g. I believe that a lapse rate of 6% is often used) exclude some participants.

7. Was the power calculation done separately for orientation and luminance?

I think that this result is interesting and assuming the issues I raise above don’t affect the outcome I think this is an important finding. It would be good to get a consensus about suppression in ASD.

References
1. Flevaris AV, Murray SO: Orientation-specific surround suppression in the primary visual cortex varies as a function of autistic tendency. Front Hum Neurosci. 2014; 8: 1017 PubMed Abstract I Publisher Full Text
2. Foss-Feig JH, Tadin D, Schauder KB, Cascio CJ: A substantial and unexpected enhancement of motion perception in autism. J Neurosci. 2013; 33 (19): 8243-9 PubMed Abstract I Publisher Full Text

Is the work clearly and accurately presented and does it cite the current literature? 
Partly

Is the study design appropriate and is the work technically sound? 
Yes

Are sufficient details of methods and analysis provided to allow replication by others? 
Partly

If applicable, is the statistical analysis and its interpretation appropriate?
Yes

Are all the source data underlying the results available to ensure full reproducibility?
Yes

Are the conclusions drawn adequately supported by the results?
Partly

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Vision

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.