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# Association between autistic traits and emotion adaptation to partially occluded faces

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ABSTRACT

Prolonged exposure to a happy face makes subsequently presented faces appear sadder: the facial emotion aftereffect (FEA). People with autism spectrum disorders and their relatives have diminished holistic perception of faces. Levels of autism can be measured continuously in the general population by autistic traits using the autism-quotient (AQ). Prior work has not found any association between AQ and FEA in adults, possibly due to non-holistic processing strategies employed by those at the higher end of the spectrum. In the present study, we tested whether AQ was associated with FEA to partially occluded faces. We hypothesized that inferring emotion from such faces would require participants to process their viewable parts as a gestalt percept, thus we anticipated this ability would diminish as autistic traits increased. In Experiment 1, we partially occluded the adapting faces with aligned or misaligned opaque bars. Both conditions produced significant FEAs, with aftereffects and AQ negatively correlated. In Experiment 2, we adapted participants to obscured faces flickering in luminance, and manipulated the facilitation of holistic perception by varying the synchronization of this flickering. We found significant FEAs in all conditions, but abolished its association with AQ. In Experiment 3, we showed that the association between AQ and FEA in the occluded conditions in Experiment 1 was not due to the recognizability or perceived emotional intensity of our adaptors; although the overall FEAs were linked to emotional intensity. We propose that increasing autistic traits are associated with diminishing abilities in perceiving emotional faces as a gestalt percept.

## 1. Introduction

Humans have an incredible ability to perceive and recognize facial emotions in others, with emotion perception thought to be driven mainly by two types of information conveyed by an emotional face: featural (e.g., the curve of a smiling mouth; Martin, Slessor, Allen, Phillips, & Darling, 2012; Tanaka et al., 2012) and holistic (i.e., the percept of the face as a single, coherent whole; Calder & Jansen, 2005; Calder, Young, Keane, & Dean, 2000). One group of people thought to suffer from deficits in the holistic perception of faces are those with Autism Spectrum Disorders (ASD). ASD is typically characterized by a wide range of social and communication impairments, including deficits in facial expression perception (Behrmann, Thomas, & Humphreys, 2006). However, the existence of emotion perception impairment in ASD is still a topic of heated debate (Bird & Cook, 2013; Harms, Martin, & Wallace, 2010), with some authors speculating that they might not even exist at all (Bird & Cook, 2013). Autistic traits have been widely accepted as a continuous construct with ASD at one extreme, and from there extend continuously into the neurotypical population (Baron-Cohen, 1997; Frith, 1991). These traits can be measured using a self-administered questionnaire called the Autism-spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). This tool has been used to examine possible associations between autistic traits and particular cognitive processes, including those of face processing (Ewbank et al., 2014; Rhodes, Jeffery, Taylor, & Ewing, 2013), with increasing levels of autistic traits linked to reduced processing of facial identity and selectively poorer face recognition in men, but not women (Rhodes et al., 2013).

Emotion adaptation paradigms have been used to examine emotion processing abilities in those with ASD. Viewing a happy face for several seconds leads to subsequently presented faces appearing sadder, with such shifts in perception known as facial expression aftereffects (FEA; Webster, Kaping, Mizokami, & Duhamel, 2004). Adaptation paradigms are particularly useful as

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they can reveal differences in emotion perception even when recognition performance alone has failed (Liu, Montaser-Kouhsari, & Xu, 2014). One adaptation study found emotional faces generated similar FEA to happy faces in people with ASD and neurotypical controls (NT), but the ASD group exhibited smaller FEA to sad faces (Rutherford, Troubridge, & Walsh, 2012). Interestingly, adapting to negative emotions (e.g. fear, anger and disgust) was more likely to evoke a negative afterimage in people with ASD, in contrast to NT who perceived positive aftereffects, suggesting abnormal processing of emotions in ASD. However, it has been argued that these aberrant aftereffects in ASD may have been due to such cases having difficulties in using emotional labels, rather than impaired processing of emotion *per se* (Cook, Brewer, Shah, & Bird, 2014). Cook et al. (2014) demonstrated comparable FEA between adults with autism and NT controls when such labeling issues were removed. It may therefore seem that levels of autism are not associated with any differences in the perception of emotion as indexed by FEA.

It has been hypothesized that those with ASD may only exhibit seemingly intact emotion adaptation aftereffects due to atypical processing of faces (Cook et al., 2014). Those with ASD could have developed the use of compensatory face processing strategies to counter any experienced difficulties: for example, non-holistic, whereby they extract facial information from individual facial features rather than processing the face as a coherent whole (Joseph & Tanaka, 2003; Klin, Jones, Schultz, Volkmar, & Cohen, 2002). Support for this suggestion comes from evidence that the mouth appears to abnormally drive emotion perception in those with ASD (Neumann, Spezio, Piven, & Adolphs, 2006; Spezio, Adolphs, Hurley, & Piven, 2007) and their subclinical relatives (Adolphs, Spezio, Parlier, & Piven, 2008). In these cases, seemingly neurotypical face adaptation aftereffects might be due to them perceiving faces from the mouth region. Indeed, this is certainly a possibility as previous work has shown that a mere curved line, mimicking a happy mouth's curve, can still produce FEA in the absence of any face (Xu, Dayan, Lipkin, & Qian, 2008). It should be stressed, though, that it is far from clear whether those with ASD (and their subclinical relatives) actually perceive facial emotion in a similar way as subclinical individuals merely high in autistic traits. The possibility that there is a diminishing ability to perceive emotion in a holistic fashion as autistic traits increase in the neurotypical population is certainly, however, of interest. Such a finding would infer that those with ASD are not abnormal in their emotion perception behavior *per se*, but merely utilizing a neurotypical face processing strategy that is similar to those that are subclinically high in autistic traits.

It has been suggested that amodal completion, the ability to infer a stimulus's full form when it is partially obscured (Kasai & Murohashi, 2013; Michotte, Thines, & Crabbe, 1964), is related to processing in the Lateral Occipital Complex (Hegdé, Fang, Murray, & Kersten, 2008; Lerner, Hendler, & Malach, 2002), a region shown to exhibit abnormal neural responses (Hubl et al., 2003) and volumetric differences (Ecker et al., 2012; Nickl-Jockschat et al., 2012) in ASD. By inducing amodal completion during emotion adaptation, for example by applying opaque bars over the adapting face, we can test our participants' abilities to utilize holistic information during emotion perception (Nakayama, Shimojo, & Silverman, 1989; Yokoyama, Noguchi, Tachibana, Mukaida, & Kita, 2014). As mentioned above, those with ASD and their relatives may use non-holistic strategies to process facial emotion. By partially obscuring the face, our participants will be required to perceive emotion through amodal completion of the viewable face parts into a gestalt percept. We anticipate that such a paradigm will reveal an association between emotion adaptation and autistic traits that has previously been unobserved. By contrast, if no association between AQ and FEA to obscured faces were to be found, then it would imply that holistic perception of facial emotion does not diminish in the form of FEA across increasing levels of autistic traits.

In the current study, we sought to answer two questions: 1) Does the FEA to partially obscured faces reveal a previously unidentified association with autistic traits in adults? 2) Can partially obscured adapting faces be amodally completed to generate FEA in NT adult participants? We designed the following experiments to test these possibilities. In the first experiment, we tested whether partially obscuring our adapting faces would reveal a previously unidentified relationship between FEA and AQ. Under such circumstances, participants will have to amodally complete the partially viewable adaptor face into a single holistic percept to process its emotion and produce FEA.

## 2. Experiment 1

In our first experiment, we adapted our participants to happy faces that were partially occluded by using aligned or misaligned opaque bars (Fig. 1). Our use of opaque bars has a number of benefits over commonly employed paradigms that are typically reported to test holistic processing. These tasks include: face inversion paradigms (Yin, 1969), where holistic processing is thought to be disrupted by faces being viewed upside down, or face composite tasks (Young, Hellawell, & Hay, 1987), where holistic processing is disrupted by misaligning two face halves. First, we are testing participants with face configurations that are still kept within their canonical formation (i.e., the T-shaped inner zone of the face's features), instead of disrupting this template through inversion or misalignment of the adapting face. Thus, any processing of our occluded faces' emotions must be due to our participants' typically employed abilities to perceive an upright face as a whole percept. Further to this, it is still unclear whether inversion merely disrupts holistic processing in a quantitative (Sekuler, Gaspar, Gold, & Bennett, 2004) or qualitative (Rossion, 2008) fashion. Similarly, there have been recent concerns as to what aspects of face processing the composite face task actually indexes (Murphy, Gray, & Cook, 2016). The fact that those with ASD have been shown to exhibit neurotypical face inversion effects but atypical composite effects (Teunisse & de Gelder, 2003) would seem to suggest that the two tasks might measure qualitatively different aspects of face processing. These debates suggest a simpler paradigm whereby faces' configural information is kept relatively intact, but partially occluded, might reveal the extent to which participants' can typically process facial emotion in a holistic fashion as indexed by FEA.

Here we present aligned or misaligned bars over an adapting face. We anticipate that the aligned bars should facilitate a coherent perception of the adapting face due to its fairly natural display. If participants are able to fill-in the missing facial parts in high-level cortical areas, and form a global representation of the faces, then the FEA should consist of the viewable local (i.e., viewable featural information, such as the eyes) and global (i.e., ability to infer emotion by grouping viewable parts together into a whole percept) components of the aftereffect. Those high in autistic traits have been associated with diminished abilities in global perception (Brosnan, Scott, Fox, & Pye, 2004; Kasai & Murohashi, 2013). We therefore anticipate that the holistic component in our FEA will diminish as autistic traits increase due to diminishing abilities in amodal completion of the viewable parts coherently. In our misaligned condition, however, we anticipate that the unnatural positioning of the bars will disrupt holistic perception of the adapting face for all participants; prior work has shown such unnatural items are more difficult to process than those that are occluded in a natural way (Johnson & Olshausen, 2005). We therefore expect no association to be found between autistic traits and FEA in this condition.

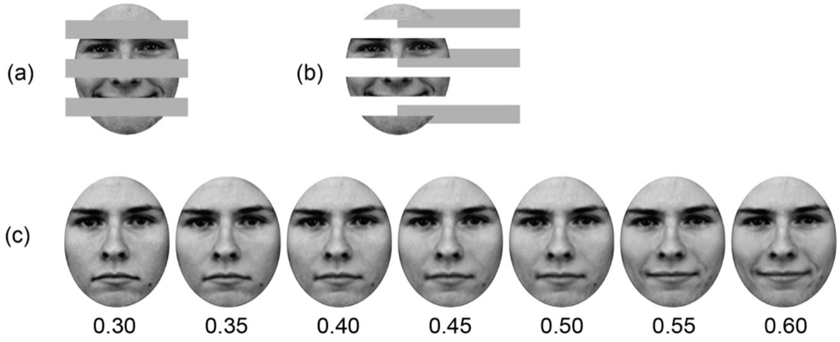


**Fig. 1.** Facial stimuli used in Experiment 1. (a) Static aligned occluder face, AO; (b) Static misaligned occluder face, MO; (c) Test faces, proportion of happiness ranged from 0.3 to 0.6.

### *2.1. Methods*

#### *2.1.1. Participants*

Thirty participants (14 males, mean age: 26.5 ± 2.5 years) from Nanyang Technological University consented to participate in both experiments presented here. All participants had normal or corrected-to-normal vision. The study was approved by the Institutional Review Board at Nanyang Technological University, Singapore and carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

#### *2.1.2. Apparatus and stimuli*

Visual stimuli were presented on a 17-inch Philips CRT monitor controlled by iMac Intel Core i3 computer, with a refresh rate of 85 Hz and resolution of $1024 \times 768$ pixels. A chin rest was fixed at a distance of 75 cm from the monitor, thus each pixel subtended a visual angle of 0.024°. The luminance values below were measured with a Minolta LS-110 photometer. Experiments were conducted in Psychophysics Toolbox extensions in Matlab R2010a (Brainard, 1997). During the experiment, eye movements were recorded by Mobile Eye-XG (Applied Science Laboratories, Massachusetts, USA) with a sampling rate of 30 HZ.

A black fixation cross (1.04 cd/$m^2$) was presented at the center of a white screen (51.25 cd/$m^2$) throughout the experiment, subtending a vertical and a horizontal angle of 0.34° and 0.048°, respectively. We selected three facial images with happy, neutral and sad expressions of the same person (AM14) from the Karolinska Directed Emotional Faces database (Lundqvist, Flykt, & Öhman, 1998). All stimuli used in the experiments were derived from these three pictures and of the same size ($3° \times 3.53°$). The stimuli were shown on the right side of the fixation with a center to center distance 3.85° horizontally and 0° vertically.

*2.1.2.1. Test stimuli.* A set of intermediate face images with emotions ranging from happy to sad were generated by morphing the happy face with the neutral face, and the neutral with the sad face, using MorphMan 4.0 (STOIK Imaging, Moscow, Russia). All images were grayscaled and ovally cropped with a size of $3° \times 3.53°$ to remove external features. A total of 21 images were created in incremental steps of 0.05, with 0 representing the saddest face and 1 the happiest face. Images with proportions equal to 0.3, 0.35, 0.40, 0.45, 0.50, 0.55 and 0.60 were used as test faces (Fig. 1c) in both experiments (29.22 cd/$m^2$).

*2.1.2.2. Adapting stimuli.* We adapted participants to two types of partially obscured faces: the 'aligned occluder' (AO) and 'misaligned occluder' (MO). The 'aligned occluder' (AO) adaptor (Fig. 1a) was generated by applying three gray bars (24.32 cd/$m^2$) on top of the happy face (20.07 cd/$m^2$) that was used to create our test faces. The three bars were placed over the mouth, on the forehead, and between the eye and mouth region with equal distances between the parallel bars. The 'misaligned occluder' (MO) face was created in a similar way to the AO face, except that the three bars were moved aside in an unnatural position to disrupt coherent perception (Fig. 1b). For both stimuli, the mouth region is partially obscured, thus making facial expression perception a bit harder (but still possible) as happy facial expressions rely on being perceived largely from the mouth region (Chen & Chen, 2010; Gosselin & Schyns, 2001).

*2.1.2.3. Autism-spectrum quotient (AQ).* The AQ is a self-administered tool with 50 items measuring autistic traits on a continuous basis (Baron-Cohen et al., 2001). Participants rated statements on five subscales (social skill, attention switching, attention to detail, communication, and imagination) using a four-point Likert scale from definitely agree, slightly agree, slightly disagree and definitely disagree. These rated responses were then coded in the AQ scoring system. The total AQ score ranges from 0 to 50, with higher values indicating greater autistic tendencies. As autistic traits are continuously distributed in the general population (Baron-Cohen et al., 2001; Hoekstra, Bartels, Cath, & Boomsma, 2008; Rhodes et al., 2013; Wakabayashi, Baron-Cohen, Wheelwright, & Tojo, 2006), we therefore used it as a measure of the autistic phenotype in the present study.

#### *2.1.3. Procedure*

We used a two-alternative forced choice paradigm in all experiments. This experiment measured the effect of face occlusion on FEA. The adapting faces were either aligned or misaligned occluded faces, while the test faces were fully viewable. Throughout the experiment, participants were required to maintain their fixation on the central cross. We used an eye tracker to ensure eye fixation throughout the whole experiment. There were three conditions in total presented in a randomized block design: 1) a baseline condition with no adaptor (baseline); 2) adapting to the Aligned Occluder face (AO); and 3) adapting to the Misaligned Occluder face (MO). The three conditions were run in separate blocks with two blocks per condition. Different random orders of the total 6 blocks were used for different participants. Over the 2 blocks for each condition, each test face was repeated 20 times giving 140 trials per adaptor condition. In total, each participant completed 420 trials across the whole experiment. Two consecutive blocks were separated by a 5-min break to avoid any carryover effects from the previous adaptor into the next block.

At the beginning of each block, the eye-tracker was calibrated and validated with a 9-point calibration system with an accuracy of 1°. Participants started each block of trials by fixating on the cross and then pressing the space bar (Fig. 2). After an initial

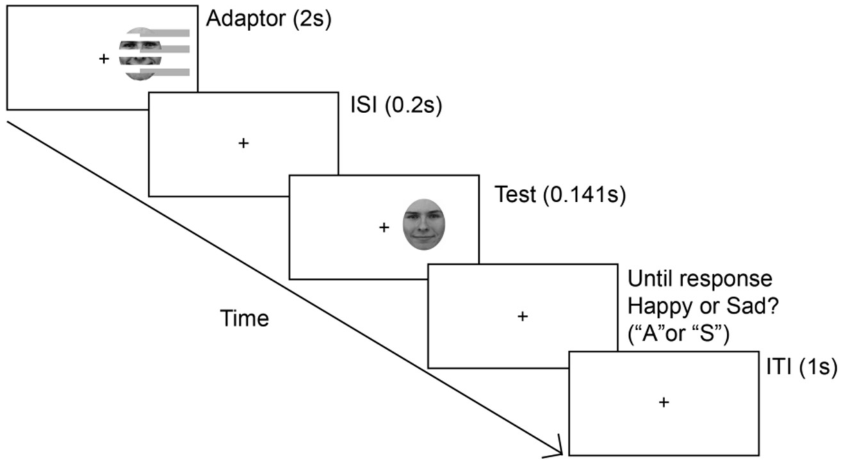


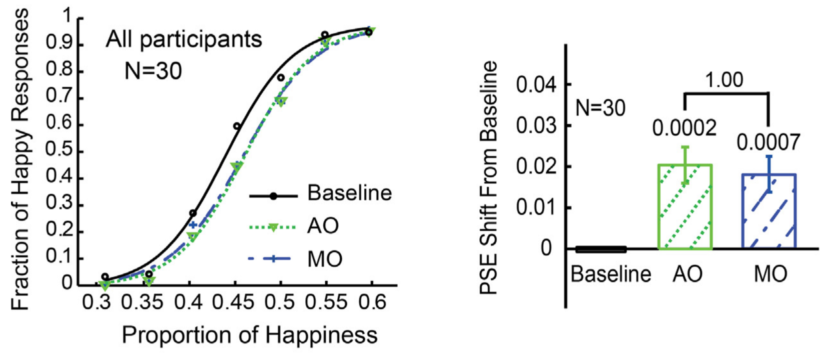
**Fig. 2.** Trial sequence for the misaligned occluder (MO) condition. The adapting face first appeared for 2 s, followed by a 200 ms inter-stimulus-interval (ISI), a test face then appeared for 141 ms. A beep played immediately afterwards to prompt a response. Participants had to press either the "A" or "S" key to indicate their perception of a happy or sad expression. After a 1-s inter-trial interval (ITI), the next trial began. Experimental parameters for all conditions and experiments are detailed in the Methods.

506 ms, the adaptor appeared for 2 s, followed by a 200 ms inter-stimulus-interval (ISI). The test face was then presented for 141 ms. Participants judged the emotion of the test face happy or sad via a key press. This response ended the trial and commenced the next one after a 1 s inter-trial interval (ITI), with the adaptor immediately re-appearing indicating the start of a new trial. Participants received no feedback on their performances at any time.

### *2.1.4. Data analysis*

To measure FEA, we first calculated the proportions of happy responses to the individual test faces in each of the adaptation conditions. The proportions of happy responses were then plotted against the proportions of happiness in the morphed test face. These results were then fitted with a sigmoidal function for each condition in the form of $f(x) = 1/[1 + e^{-a(x-b)}]$, where $b$ equals to

(a) PSE shift from all participants. (b) Summary of all participants.



(c) PSE shift of a subject with low AQ. (d) PSE shift of a subject with high AQ.

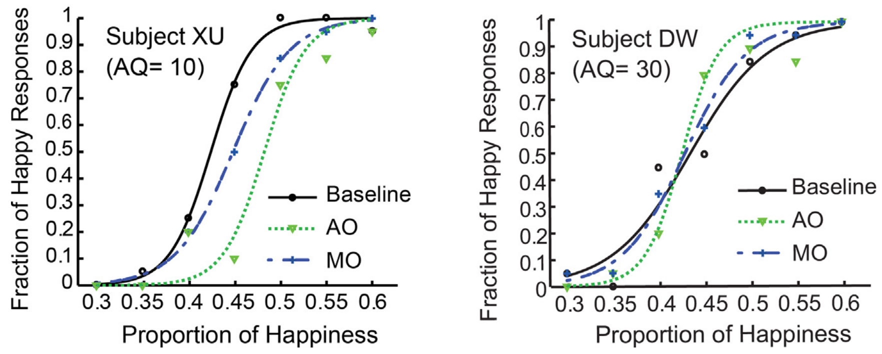


**Fig. 3.** Results of occluded face adaptation. (a) Psychometric curve of data averaged from all 30 participants. Baseline, no adaptation baseline (black circle solid line); AO, aligned occluder adaptor (green triangle dotted line); MO, misaligned occluder adaptor (blue cross dash-dotted line). (b) Summary of PSE shifts from all 30 participants. Error bars indicate SEMs with $p$-values obtained by pairwise comparison (Bonferroni corrected). (c) Psychometric curves from a naïve subject with low AQ score (AQ = 10). (d) Psychometric curves from a naïve subject with high AQ score (AQ = 30). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

50% point of the psychometric function [the point of subjective equity (PSE)] indicating chance performance, and $a/4$ determines the slope and indicates the response sensitivity. The magnitude of the aftereffect was calculated by subtracting the PSE of the baseline (no adaptation) from the adaptation condition(s) of interest. We conducted repeated measures Analysis of Variance (ANOVA) to compare PSEs among different conditions, and then used two-tailed paired samples *t*-tests (with Bonferroni correction) to compare the PSEs between particular comparisons of conditions. The relationship between aftereffects, autistic traits (AQ) and other factors were quantified by Pearson correlations and multiple linear regressions. All analyses were performed in Matlab (Mathworks, Massachusetts, USA) and SPSS (IBM, NY, USA).

The eye tracking data were analyzed in the following steps. We calculated the proportion of time when participants broke fixation during the experiment. By using the in-built algorithm from the software ASL Results, we measured the total amount of time when participants' gaze fell out 1° from the fixation point for each condition (corrected for head motion). The duration of breaking fixation was then divided by the total amount of time of that particular condition, by which we get the proportion of breaking fixation (PBF). In order to examine breaking of fixation in each adaptation condition in a similar way as we do with our aftereffect magnitudes, we subtracted the PBF of the baseline condition from the condition of interest.

## 2.2. Results and discussion

### 2.2.1. Descriptive statistics of AQ

The AQ score ranges from 8 to 30 (Mean = 19.00, SD = 6.01) among the recruited participants. Skewness and Kurtosis of the AQ were 0.43 and 0.83 respectively, both within acceptable range of parametric analysis (George & Mallery, 2010). There were no significant gender differences in the AQ score ($t(28) = -0.73$, $p = 0.47$, Cohen's $d = 0.27$).

### 2.2.2. Emotion aftereffects and AQ

We were initially interested in whether or not our participants as a group could exhibit emotion adaptation aftereffects to the occluded faces. We had anticipated that when the bars were aligned, it would be easier to infer the whole face due to amodal completion. By contrast, when the bars were misaligned, we expected that inferring the whole face may become more difficult, thus amodal completion would be disrupted. It has been suggested that participants high in autistic traits might have difficulties in integrating face parts into a coherent whole. We therefore compared the effects of amodal completion in the aligned and misaligned faces on facial expression adaptation in Experiment 1, and its relation to autistic traits.

The facial expression aftereffect (FEA) was calculated by subtracting the PSE (50% happy responses) of the baseline from the adaptation conditions for each participant. The mean values for all participants are illustrated in Fig. 3a. The summary of FEAs of all 30 subjects is shown in Fig. 3b. Adapting to the aligned (AO) or misaligned occluded faces (MO) both generated significant FEAs relative to the no adaptation baseline condition (both $ps < 0.001$). Although the magnitude of FEA in MO seems slightly smaller than AO, there was no significant difference between the two adaptation conditions ($t(29) = -0.67$, $p = 1.00$, Cohen's $d = 0.02$). These results suggest that as a group, our participants could produce emotion adaptation aftereffects to the obscured faces, despite the mouth's curvature being obscured: this area is typically the most informative area for judging happy emotions (Chen & Chen, 2010; Schyns, Petro, & Smith, 2007). The happy emotion conveyed by our faces must therefore be inferred from the adaptors' remaining viewable face parts during adaptation.

Inspection of the psychometric curves produced by individual subjects revealed that there were substantial variations in their FEAs. Subjects with relatively low AQ showed FEA after adapting to the aligned occluded face, but a diminished effect for the misaligned face: an example of a single naïve participant's results are shown in Fig. 3c. In contrast, others with relatively high AQ did not show any FEA after adapting to either adaptor (example in Fig. 3d). We therefore further divided the participants into low and high AQ groups by its median (AQ = 19). By doing this, we have 14 participants in each group, and two participants with an AQ of 19 who were not included in the following analysis. A mixed model two-way ANOVA with AQ level (high vs. low) as a between-subject factor and adaptation condition (AO vs. MO) as a within-subject factor was performed to examine any differences between the groups' FEA magnitudes. A significant main effect was found for AQ ($F(1, 26) = 5.13$, $p = 0.032$, $\eta^2 = 0.17$) due to the higher AQ group exhibiting larger FEAs than the low AQ group. However, there was no significant effect for adaptation condition ($F(1, 26) = 0.55$, $p = 0.46$, $\eta^2 = 0.02$), nor any significant interaction ($F(1, 26) = 0.002$, $p = 0.96$, $\eta^2 = 0.00$).

We then examined whether there was an association between FEA and autistic traits as measured by AQ scores, and found significant correlations between the two in both the aligned ($r(30) = -0.55$, $p = 0.002$, Fig. 4a) and misaligned ($r(30) = -0.38$, $p = 0.039$, Fig. 4a) conditions. These negative correlations indicate that as autistic traits increase, then so too does FEA amplitude become smaller to partially obscured faces. As the total AQ score can be split up into five subscales assessing different areas, we

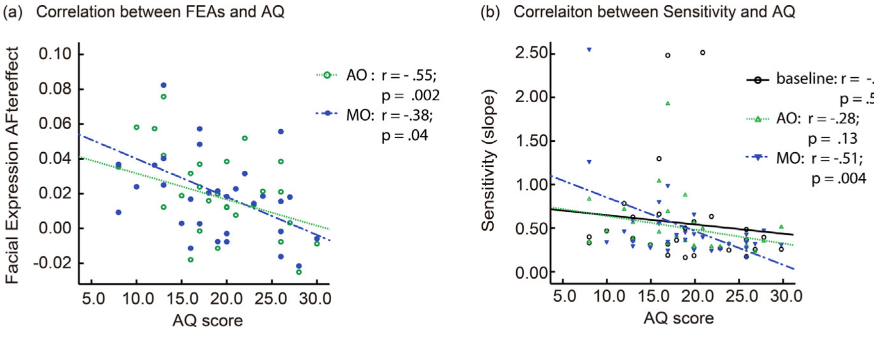


**Fig. 4.** Correlations between facial emotion aftereffect, AQ, and sensitivity. (a) Relationship between AQ and FEAs after adapting to occluded static faces. AO, aligned occluder adaptor (green circle dotted line); and MO, misaligned occluder adaptor (blue dot dash-dotted line). In this figure, FEAs were plotted as a function of individual AQ. The correlations were significant for both groups. (b) Relationship between AQ and sensitivity in judging the emotion of test faces in the baseline (black circle solid line), AO (green triangle dotted line) and MO (blue triangle dash-dotted line) conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
Correlation coefficient between AQ and FEA to static obscured faces.

| | AO | MO |
|---|---|---|
| AQ score | −0.547 (0.002)$^*$ | −0.379 (0.039)$^*$ |
| Subscale 1: Social skill | −0.36 (0.05) | −0.23 (0.22) |
| Subscale 2: Attention switching | −0.42 (0.02)$^*$ | −0.32 (0.09) |
| Subscale 3: Attention to detail | −0.31 (0.09) | −0.07 (0.73) |
| Subscale 4: Communication | −0.36 (0.06) | −0.34 (0.07) |
| Subscale 5: Imagination | −0.13 (0.50) | −0.20 (0.29) |

AO: aligned occlude adaptor; MO: misaligned occlude adaptor; $^*p < 0.05$.

tested whether any particular sub-score was driving these effects (Table 1). Results indicated that the attention switching subscale and social skills were negatively correlated with FEA in the aligned occluded condition (AO) ($r = -0.42$, $p = -0.02$; and $r = -0.36$, $p = 0.05$, respectively).

As mentioned in the Section 1, Rhodes et al. (2013) found qualitatively different relationships between face identity adaptation and AQ for male and female participants. To examine whether any such gender specific relationships existed for emotion adaptation, we ran the correlations again, but this time separately for males and females. Females exhibited a negative correlation between FEA and AQ in the aligned condition ($r(16) = -0.57$, $p = 0.02$), with the same trend in males, albeit non-significant (males: $r(14) = -0.50$, $p = 0.07$). In the misaligned condition, neither the males ($r(14) = -0.49$, $p = 0.08$) nor females ($r(16) = -0.021$, $p = 0.33$) exhibited a significant association between AQ and FEA.

We had hypothesized that apparently neurotypical levels of emotion adaptation aftereffects in ASD were likely due to non-holistic processes. We therefore wondered whether diminishing holistic perception of emotional faces might express itself as autistic traits increased in a neurotypical population, as shown by FEA to partially obscured faces. The negative correlations between AQ and FEA (Fig. 4a) for both AO and MO suggests that our participants scoring high in AQ may be less efficient in grouping emotional information from the viewable face parts of the adaptors, and thus produced diminished or nonexistent FEA. This finding is consistent with the 'weak central coherence' theory which posits a diminished ability for global integration in people with high AQ (Happé & Frith, 2006). Those high in autistic traits perform better on tasks involving local processing, but worse on tasks that rely upon holistic processing (Brosnan et al., 2004; Happé & Frith, 2006). Our results suggest that seemingly neurotypical emotion adaptation aftereffects in ASD are likely due to non-holistic processing of facial emotion; those high in AQ were probably unable to produce FEA in the present experiment due to the occluded bars disrupting the view of the mouth's curve in our adaptors. Instead, any aftereffects being produced by our participants may be due to their ability to amodally infer emotion holistically from the partially viewable face parts: an ability that seems to diminish as levels of autism increase (Happé & Frith, 2006; Sucksmith, Roth, & Hoekstra, 2011).

### *2.2.3. Emotion sensitivity and AQ*

In addition to emotion adaptation aftereffects, we examined our participants' abilities to discriminate the test faces' emotions. As earlier mentioned, there is still some debate as to whether or not emotion recognition abilities are related to autistic traits. To test this, we calculated participants' sensitivity at judging emotion by extracting the slope of the psychometric curve (a/4, details in Section 2.1.4); steeper slopes indicate increasingly superior abilities in categorizing test faces' emotions. Results from a repeated-measures ANOVA showed no significant difference in the sensitivity after adapting to the three conditions ($F(1.5,43.88) = 0.18$, $p = 0.78$, $\eta^2 = 0.00$). We then correlated these values indexing emotion recognition with AQ and found no significant association in the baseline ($r(30) = -0.11$, $p = 0.57$, Fig. 4b), nor AO ($r(30) = -0.28$, $p = 0.13$) conditions. Curiously, the correlation between sensitivity in MO and AQ was significant ($r(30) = -0.51$, $p = 0.004$), with increasing levels of AQ associated with diminishing sensitivity at judging the emotion of test faces. Adapting to an unnatural setting (misaligned occluded face) may disrupt subsequent sensitivity to emotion recognition in those high in AQ. Why this might be the case seems at present unclear, but the corner of the misaligned bar would be over the mouth of the subsequently presented test face. Our high AQ participants may have been more susceptible to low level adaptation of this feature which then disrupted their attempts at discerning emotion from the test faces' mouth region. By contrast, our low AQ participants were likely judging emotion in a holistic fashion and so were not affected by adaptation to the misaligned bar.

As in the case of FEA, we were interested to see whether there were any effects of gender in the associations between emotion sensitivity and AQ. We therefore conducted correlational analyses of emotion sensitivity with AQ by gender. Results showed that while there was no correlation in the baseline and AO conditions for both genders (all $ps > 0.20$), the sensitivity in the MO condition was significantly correlated with AQ for females ($r(16) = -0.58$, $p = 0.02$) but not males ($r(14) = -0.49$, $p = 0.07$). This indicates that females with increasing levels of autistic traits found categorizing the emotion of the test faces increasingly harder after adapting to the misaligned obscured face.

It was unclear from prior research whether levels of autism can modulate emotion processing. Low functioning autistic children have difficulties in identifying emotional faces' expressions (Gross, 2004; Tantam, Monaghan, Nicholson, & Stirling, 1989; Weeks & Hobson, 1987). Other studies, however, have found no evidence of such an impairment in basic emotion recognition of static (Adolphs, Sears, & Piven, 2001; Baron-Cohen, Spitz, & Cross, 1993; Grossman, Klin, Carter, & Volkmar, 2000; Volkmar, Sparrow, Rende, & Cohen, 1989), or dynamic facial expressions (Gepner, Deruelle, & Grynfeltt, 2001) in autism. A recent meta-analysis on 16 studies found that ASD individuals had difficulties in the recognition of five basic emotions (sad, anger, surprise, fear and disgust) but did not have difficulties in recognizing happiness (Uljarevic & Hamilton, 2013). Remarkably, even in a neurotypical sample, we have found that levels of autism can modulate happy emotion perception, as shown through emotion adaptation aftereffects. In contrast, autistic traits were associated with the ability to explicitly categorize the emotions of the test faces in the misaligned condition, but not in the baseline and aligned conditions. Thus, it suggests that adaptation to the misaligned occluders increasingly disrupts sensitivity to facial emotion as AQ increases.

### *2.2.4. Eye movement and attention*

We found that participants with higher AQ scores tended to have smaller FEA. Previous research in neurotypical participants has shown that increased attention can boost face identity or face figural (distortion) aftereffects (Rhodes et al., 2011), with reduced attention decreasing FEA (Liu & Xu, 2014). As people with ASD appear to have diminished interest in viewing socially relevant stimuli such as faces (Riby & Hancock, 2008), the relationship between AQ and FEA in Experiment 1 might have purely been due to reduced attention of the adaptor image as AQ increased. While our paradigm makes it hard to interpret how much attention our participants were directing towards the adapting faces, as we requested them to view a fixation cross, it may be that our high AQ participants break fixation less frequently and reduce their attention towards the adapting face, thus leading to smaller FEA. We therefore examined the eye tracking data to see whether attention by breaking fixation was correlated with FEA and AQ. Detailed calculations of how we calculated the proportion of time that participants broke fixation during the experiment (PBF, proportion of breaking fixation) can be found in the Data Analysis Section 2.1.4.

The overall PBF was 2.34%, indicating that participants maintained fixation on the vast bulk of trials. Pearson correlations conducted between PBF and AQ showed that AQ score was not correlated with the PBF ($r(30) = 0.18$, $p = 0.35$), indicating that the presence of autistic traits did not affect fixation behavior. Moreover, PBF was not correlated with FEA induced by the two static occluders either ($r(30) = -0.03$, $p = 0.86$ and $r(30) = -0.10$, $p = 0.59$ for the aligned and misaligned conditions, respectively). Overall, it seems that the association between AQ and FEA was not due to attention. It should be stressed, however, that our measure for attention was rather limited in what it can inform us, and it might be the case that our low AQ participants paid more covert attention, that is attention without moving the eyes from fixation, to the obscured adapting faces. It thus invites further investigation into this question.

## 3. Experiment 2

FEAs generated by static occluded faces were correlated with AQ in Experiment 1, but what about dynamic occluded faces? In Experiment 2 we investigated whether the association between FEA and AQ could be affected by manipulating holistic processing of the viewable face parts in those high in AQ. The "Law of Common Fate" suggests that elements undergoing a synchronous luminance change facilitates binding, and are thus more likely to be considered as a unitary item (Levinthal & Franconeri, 2011). For example, if we were to flicker the adapting faces' viewable parts rapidly and in synchrony between high and low contrast (i.e., 106 ms high contrast followed by 106 ms of low contrast), then this should facilitate the binding of the adapting faces as a single percept across all participants. This increase in perception of the face parts as a greater whole would therefore lead to greater levels of emotion adaptation relative to static face adaptation in the first experiment. Previous studies have reported comparable contrast sensitivity for flickering stimuli between those with ASD and NT controls (Bertone, Mottron, Jelenic, & Faubert, 2005; Pellicano, Gibson, Maybery, Durkin, & Badcock, 2005). If our low AQ participants were already binding the face parts efficiently in Experiment 1, then this manipulation should have little effect on them. By contrast, those higher in AQ might benefit more from synchronized flickering with an increase in emotion adaptation if synchronized flickering facilitates the binding of the face features. Such a manipulation should therefore abolish the association between AQ and FEA.

Of course, this flickering manipulation will also arguably have the effect of increasing our participants' attention towards the adapting face too. To counter any possible attentional effects of flickering, we will need to test our participants using a face where contrast flickering still occurred to attract attention, but binding was instead disrupted. To accomplish this, we asked participants to adapt to an asynchronous flickering condition where only two of the four face parts were luminance flicked. We hypothesized that if those low in AQ were able to holistically process the partially occluded adaptors in Experiment 1, then asynchronous flickering should disrupt this ability. In contrast, those high in AQ were likely unable to holistically process the partially viewable adaptors in Experiment 1 anyway as shown by their non-existent FEA. Thus, this asynchronous flickering manipulation will abolish the association between AQ and FEA, due to all participants finding it difficult to bind the face parts into a single percept to process emotion. The FEA in this condition should therefore be smaller than the FEA produced in the aligned condition in Experiment 1.

Finally, to our knowledge, no prior study has actually examined the association between emotion adaptation to fully viewable faces and autistic traits in a neurotypical population; an oversight we therefore set out to resolve. We anticipated that the correlation between AQ and FEA would be abolished due to those higher in autistic traits being able to produce aftereffects from the mouth region in the fully viewable face. Such a finding would support recent work in ASD populations in suggesting that levels of autism are not associated with emotion adaptation aftereffects when the whole face is in view (Cook et al., 2014). We also included another flickering luminance condition, this time using a fully viewable face. If flickering does not lead to any attention related increases in emotion perception, then there should be no difference in FEA between the fully viewable static and flickering conditions. If, however, luminance contrasts were to result in increased emotion adaptation due to increased attentional processing, then we should see greater emotion adaptation aftereffects in this condition relative to the static face that is fully viewable.

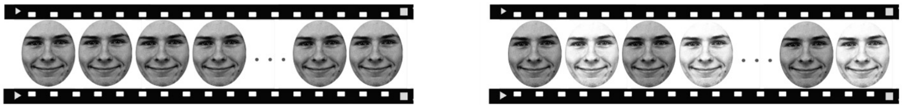
### 3.1. Methods

#### 3.1.1. Subjects

The same 30 participants from Experiment 1 participated in Experiment 2.

#### 3.1.2. Stimuli and procedure

We used exactly the same set of test faces from Experiment 1 in the present experiment. We manipulated the adapting face from Experiment 1 to create four new happy adaptors (Fig. 5). Static full face (Static_F) was merely the intact smiling face image used in


(a) Static happy full face, Static_F

(b) Flickering full face, Flick_F

(c) Synchronized flickering occluded face, SFO

(d) Asynchronous flickering occluded face, AFO

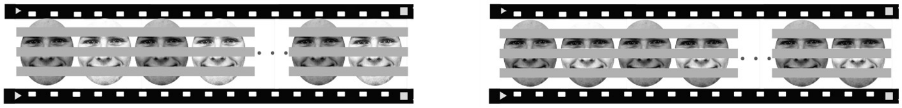


**Fig. 5.** Face adaptors used in Experiment 2. (a) *Static happy full face, Static_F*. The facial image was kept constant with participants perceiving it as a single static happy face during the adaptation period. (b) *Flickering full face, Flick_F*. The face alternated between high- and low-luminance with each luminance frame lasting 106 ms. (c) *Synchronized flickering occluded face, SFO*. This was generated by adding three occluders onto the flickering full face (Flick_F). (d) *Asynchronized flickering occluded face, AFO*. This set was generated in the same way as the synchronized flickering occluded face, except that the eye and chin regions remained at low-luminance throughout while the nostril and forehead flickered between low- and high-luminance in consecutive frames.

Experiment 1, but this time without any occluding bars. Flickering full face (Flicker_F) was generated by alternating a low-luminance happy face (24.37 cd/$m^2$) with an identical but high-luminance face (44.56 cd/$m^2$) in a square wave fashion (Video 1.1), the Michelson contrast between the two faces was 0.29 (Michelson, 1927). Each phase displayed for 106 ms (9.4HZ) with a total duration of 2.12 s. The synchronized flickering occluded face (SFO) was created by applying the three opaque bars over the Flicker_F adaptor so that all face parts flickered congruently (Video 1.2). The asynchronized flickering occluded face (AFO) was the same as the SFO except that the eye and chin regions were always kept at low-luminance between consecutive video frames (Video 1.3). We expected the lack of flickering in the eye and chin regions combined with alternate flickering in the nostril and forehead regions would disrupt amodal completion. In total, we had four sets of face adaptors: flickering full face (Flicker_F); synchronized flickering occluded face (SFO); asynchronized flickering occluded face (AFO), and static full face (Static_F). The experimental procedure was identical to Experiment 1. There were five conditions in total: adapting to (1) Static_F, (2) Flicker_F, (3) SFO, (4) AFO, and (5) no-adaptor (the baseline). All conditions were run in separate and randomized blocks, which were repeated as in Experiment 1.

### *3.2. Results and discussion*

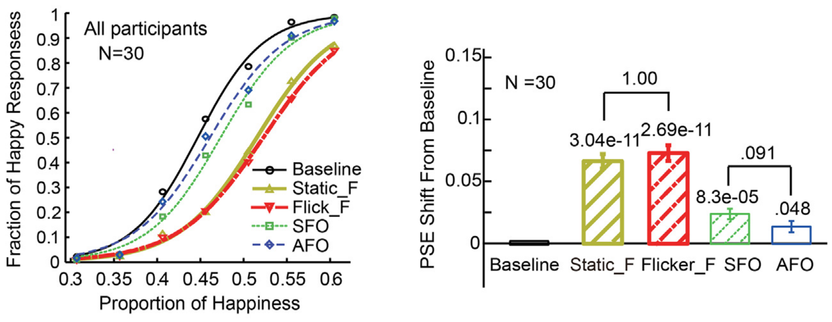
#### *3.2.1. Emotion aftereffects and AQ*

The adaptation aftereffect is calculated by subtracting the point of subjective equality in each adaptation condition from the baseline condition (no adaptation). Bonferroni-corrected pairwise comparisons to the baseline condition in Fig. 6a and b show that all adaptors exhibited significant adaptation aftereffects (FEA): the full static ($t(29) = 11.00$, $p < 0.001$, Cohen's d = 2.24), full flickering ($t(29) = 12.17$, $p < 0.001$, Cohen's d = 2.28), synchronous ($t(29) = 5.75$, $p < 0.001$, Cohen's d = 0.99), and asynchronous ($t(29) = 2.80$, $p = 0.05$, Cohen's d = 0.56) faces. The two fully viewable faces (static and flickering) produced similar FEAs ($t(29) = 1.4$, $p = 1.00$, Cohen's d = 0.26). They generated significantly larger FEAs than the two partial flickering faces (AFO & SFO, $t(29) = 10.27$, $p < 0.001$, Cohen's d = 1.96). Despite Fig. 6b indicating that the SFO produced a larger effect than the AFO condition, this difference was not significant ($t(29) = 3.00$, $p = 0.09$, Cohen's d = 0.51).

Similar to Experiment 1, we grouped the participants into low and high AQ groups, and performed a mixed model ANOVA on FEA, with AQ level (low vs. high) as a between-subject factor, and adaptor type (Flicker_F, Static_F, SFO, and AFO) as a within-subject factor. As Mauchly's test of sphericity was violated ($\chi^2(5) = 16.63$, $p < 0.01$), the results reported here were Greenhouse-Geisser corrected. There was a significant main effect of adaptor type ($F(2.10, 54.69) = 56.78$, $p < 0.001$, $\eta^2 = 0.69$), but not for AQ level ($F(1,26) = 0.32$, $p > 0.57$, $\eta^2 = 0.01$), nor was there any significant interaction ($F(2.10, 54.69) = 0.46$, $p > 0.70$, $\eta^2 = 0.02$). This suggests that there were no differences between the two AQ groups' FEAs.

We were interested in whether there was any clear relationship between the FEA and AQ in each condition in Experiment 2, we performed Pearson correlations between FEA and AQ (Fig. 7). In contrast to Experiment 1, FEA magnitudes did not correlate with individual AQ in any condition (Static_F, $r(30) = 0.10$, $p = 0.59$; Flicker_F, $r(30) = -0.11$, $p = 0.56$; SFO, $r(30) = -0.12$, $p = 0.52$; AFO, $r(30) = 0.07$, $p = 0.70$). Furthermore, correlations between FEA and AQ subscales were not significant (Table 2). These results indicate that the flickering manipulations abolished the relationship between AQ and FEA. Similarly, allowing participants to fully view adapting faces also abolished any relationship between AQ

(a) PSE shift from all participants. (b) Summary of all participants.



(c) PSE shift of a subject with low AQ. (d) PSE shift of a subject with high AQ.

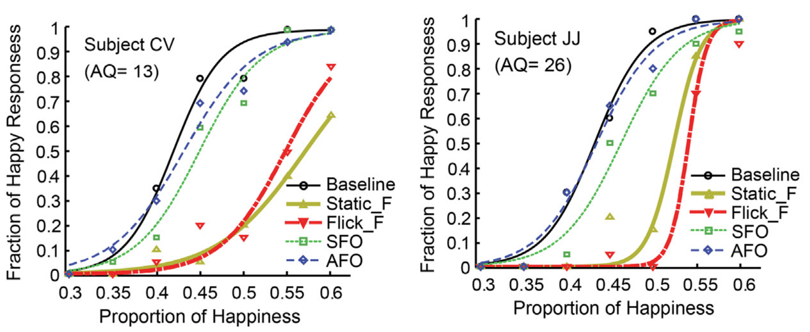


**Fig. 6.** Results of full and occluded flickering faces. (a) Psychometric curve of data averaged from all 30 participants. Baseline, no adaptor (black circle solid line); Static_F, static full face adaptation (yellow triangle thick solid line); Flick_F, flickering full face adaptation (red triangle thick dash-dotted line); SFO, synchronized flickering occluded face adaptation (green square dotted line); AFO, asynchronized flickering occluded face adaptation (blue diamond dashed line). (b) Summary of PSE shifts from all 30 participants. Error bars indicate SEMs and p-values were obtained by Pairwise comparison (Bonferroni corrected). (c) Psychometric functions from a naïve subject with low AQ score (AQ = 13). (d) Psychometric functions from a naïve subject with high AQ score (AQ = 26). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

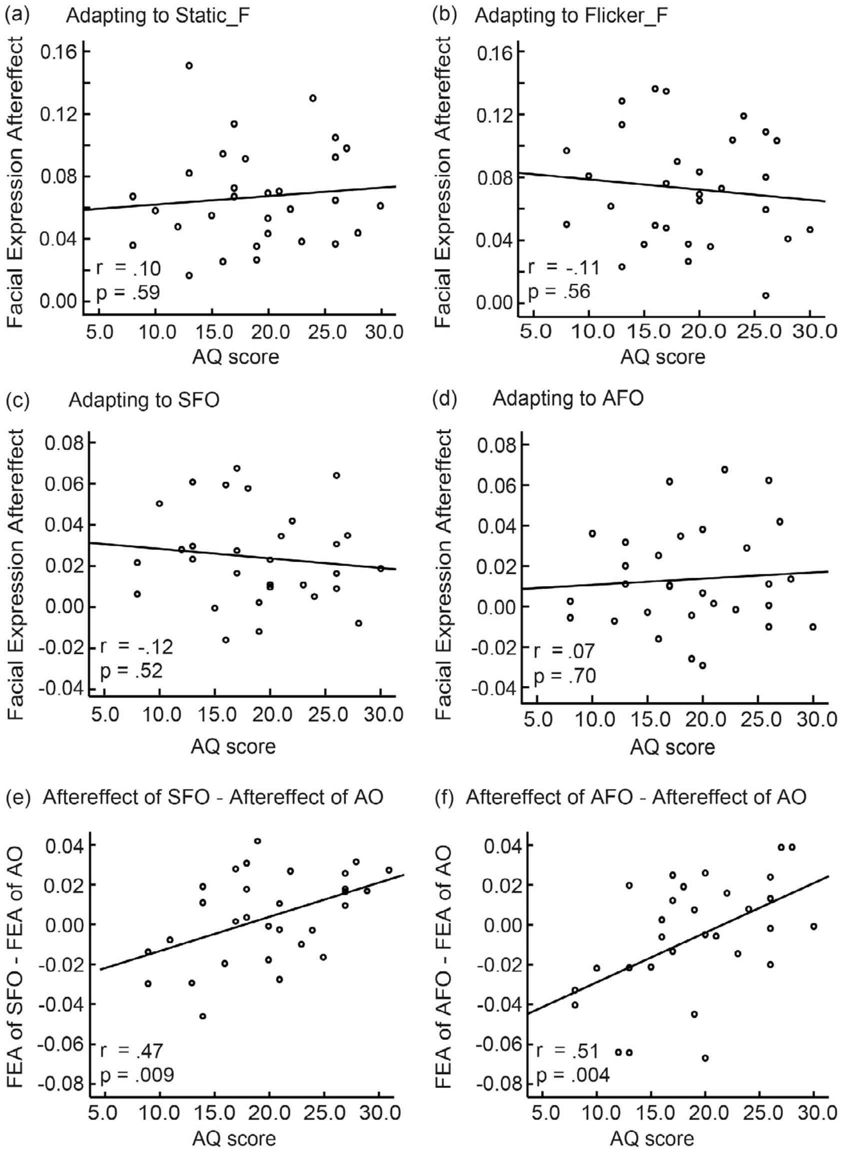


**Fig. 7.** Relationship between AQ and FEA magnitude after adapting to full and occluded flickering faces. In the first four figures, aftereffect amplitudes were plotted as a function of individual AQ. Adapting to the: (a) Static full face (Static_F condition); (b) Flickering full face (Flick_F condition); (c) Synchronized flickering occluded face (SFO condition); (d) Asynchronized flickering occluded face (AFO condition). In the last two figures, aftereffect differences were plotted as a function of AQ: (e) Aftereffect difference between SFO and AO; (f) Aftereffect difference between AFO and AO.

**Table 2**
Correlation coefficient between AQ and FEA to full and obscured flickering faces.

| | Flicker_F | Static_F | SFO | AFO |
|---|---|---|---|---|
| AQ score | 0.10 (0.59) | −0.11 (56) | −0.12 (0.52) | 0.07 (0.70) |
| 1: Social skill | 0.13 (0.50) | 0.10 (0.59) | −0.11 (0.55) | 0.21 (0.28) |
| 2: Attention switching | 0.05 (0.81) | −0.20 (0.30) | −0.20 (0.27) | −0.09 (0.66) |
| 3: Attention to detail | 0.05 (0.80) | −0.15 (0.42) | 0.14 (0.48) | 0.06 (0.76) |
| 4: Communication | 0.05 (0.81) | 0.06 (0.75) | −0.09 (0.66) | 0.12 (0.54) |
| 5: Imagination | 0.001 (1.00) | −0.14 (0.45) | −0.13 (0.50) | −0.13 (0.50) |

Flicker_F, flickering full face adaptation; Static_F, static full face adaptation; SFO, synchronized flickering occluded face adaptation; AFO, asynchronized flickering occluded face adaptation. All *ps* > 0.2.

and FEA. This may be due to high AQ participants relying more on the local mouth information in the fully viewable face during adaptation. To investigate any effect of gender, we also conducted further correlational analyses on FEA and AQ for each gender. These analyses yielded no significant associations either (all *ps* > 0.36).

In Experiment 2, we had predicted that flickering in synchrony would lead to greater FEA in comparison to the FEA in the static, aligned occluding (AO) adaptation condition in Experiment 1 for those high in AQ. Similarly, those low in AQ would probably experience little benefit to such a manipulation due to ceiling effects in their ability to glean emotion from the occluded adaptor. To test for any differences in these conditions across experiments that may not have been apparent in our ANOVA or correlations analyses, we subtracted the FEA in the static aligned condition in Experiment 1 from the flickering condition's FEA for each participant and found a significant correlation between these values and AQ for both synchronous flickering face adaptation (SFO: Fig. 7e, $r(30) = 0.47$, $p = 0.009$) and asynchronous flickering face (AFO: Fig. 7f, $r(30) = 0.51$, $p = 0.004$). This suggests that the emotion perception benefits of flickering as indexed by FEA relative to the aligned adaptor in Experiment 1 were greater for high AQ participants, in comparison to low AQ participants who seemed to exhibit diminished FEA to flickering. These converse effects across high and low AQ participants can therefore explain why the association between AQ and FEA in Experiment 1 was abolished in the flickering conditions. This improvement in emotion processing in high AQ participants may be through the temporal integration of consecutive frames as a dynamic image which incorporates the regions of the brain involved in facial movement and emotion, such as the superior temporal sulcus (STS) (Winston, Henson, Fine-Goulden, & Dolan, 2004). The "Law of Common Fate" (Levinthal & Franconeri, 2011) therefore seems to have differential effects across AQ depending upon the experimental manipulations.

#### 3.2.2. Emotion sensitivity, attention and AQ

As in the case of Experiment 1, we decided to examine our participants' sensitivity in perceiving emotion in the test faces after adaptation by performing a correlation on the slope values of the psychometric curves at PSE and AQ. We found that AQ was not correlated with sensitivity of emotion for any condition (all $ps > 0.23$). This suggests that participants' sensitivity in judging the emotion of the test faces was similar across all levels of autistic traits regardless of adaptation condition. The correlation analyses were then conducted by gender, and found a significant correlation between AQ and sensitivity in the static full face condition (Static_F) in females ($r(16) = -0.64$, $p = 0.01$), but not males ($r(14) = 0.24$, $p = 0.42$). No significant correlations were observed in either gender for all other conditions (all $ps > 0.16$). This suggests that adapting to a fully viewable static face diminishes subsequent sensitivity to facial emotion in the test faces in women as AQ increases, but not in men.

In Experiment 2, flickering might draw the attention of those high in AQ more than those with low AQ. The overall PBF in experiment 2 was 1.94%, and was similar to the PBF in Experiment 1 ($t(29) = 0.89$, $p = 0.38$, Cohen's d = 0.20). The PBF in the baselines were comparable between experiment 1 and 2 ($t(29) = 1.64$, $p = 0.11$, Cohen's d = 0.40). We subtracted the PBF of each condition from its corresponding baseline and performed a one-way repeated measures ANOVA. Results showed that PBFs were similar across all conditions ($F(3.28, 95.16) = 0.51$, $p = 0.69$, $\eta^2 = 0.02$, Greenhouse-Geisser corrected as Mauchly's sphericity test had been violated, $\chi^2(14) = 44.32$, $p < 0.001$). We then examined the relationship between attention on fixation, AQ and FEA. As in Experiment 1, we did not observe a significant correlation between AQ and the tendency to break fixation (PBF) in general ($r(30) = 0.20$, $p = 0.30$), nor AQ with PBF in any condition (all $ps > 0.13$). The tendency to break fixation for each condition relative to baseline was also not correlated with the FEA induced by the static full face and the flickering full face ($r(30) = -0.02$, $p = 0.91$ and $r(30) = -0.01$, $p = 0.95$, respectively), nor the two occluded flickering conditions (AFO and SFO, $r(30) = 0.16$, $p = 0.26$ and $r(30) = -0.04$, $p = 0.83$, respectively). This suggests that FEA was not associated with the breaking of fixation. Similarly, there did not seem to be any relationship between this drawing of attention by the adaptor and AQ. Therefore, the lack of association between AQ and FEA in Experiment 2 cannot be explained by increased attention in the high AQ participants. As mentioned earlier, we are unable to tell whether covert attention, whereby the eyes do not break fixation, may in some way be influencing our results. It will therefore be interesting for future work to test the extent to which attention facilitates the processing of contrast flickering stimuli.

## 4. Experiment 3

We have argued that increasing AQ is associated with diminishing FEA in Experiment 1 due to increasingly weaker holistic processing. To provide more direct evidence for this suggestion, we have to quantify holistic processing. While we have mentioned criticisms of the face inversion and composite tasks, they are still the two most widely used paradigms to test holistic processing. To this end, we decided to use the face inversion task to index holistic processing of our adapting faces across AQ. If the inversion effects for our adapting faces in Experiment 1 become smaller as AQ increases, then this could be taken as evidence that those high in AQ experience decreased holistic perception of the adapting faces' emotions. Such cases must therefore rely more heavily upon featural information when perceiving emotion. We chose this task because at least in comparison to the composite task, it still keeps the canonical configuration of the faces intact similar to our adapting faces, albeit upside down.

An alternative interpretation for why AQ is associated with FEA in Experiment 1 is that those high in AQ have reduced perception of the adapting faces' emotional intensity; for example, low AQ participants may perceive the same faces as being happier than high AQ participants, thus leading to greater adaptation aftereffects. This association is then abolished in Experiment 2, due to high AQ participants perceiving the adapting faces' emotions as being more intense, and thus making their judgments more similar to low AQ participants. In this perspective, perception of the adaptors' emotional intensity can explain our findings rather than increased holistic processing *per se*. To test this, we asked our participants to rate the emotional intensity of the adapting faces used in Experiments 1 & 2.

Finally, it may also be that increasing levels of AQ are associated with decreasing abilities to explicitly recognize the emotion conveyed by the adaptors in Experiment 1. We therefore decided to ask our participants to recognize the emotion of our adaptors from the previous experiments, along with additional versions created using a sad face.

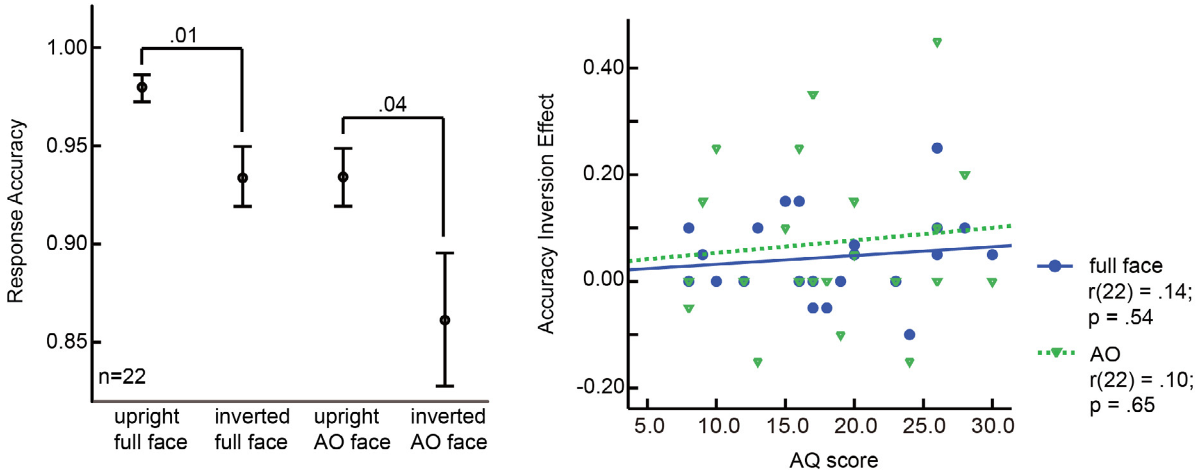
### 4.1. Methods

#### 4.1.1. Subjects

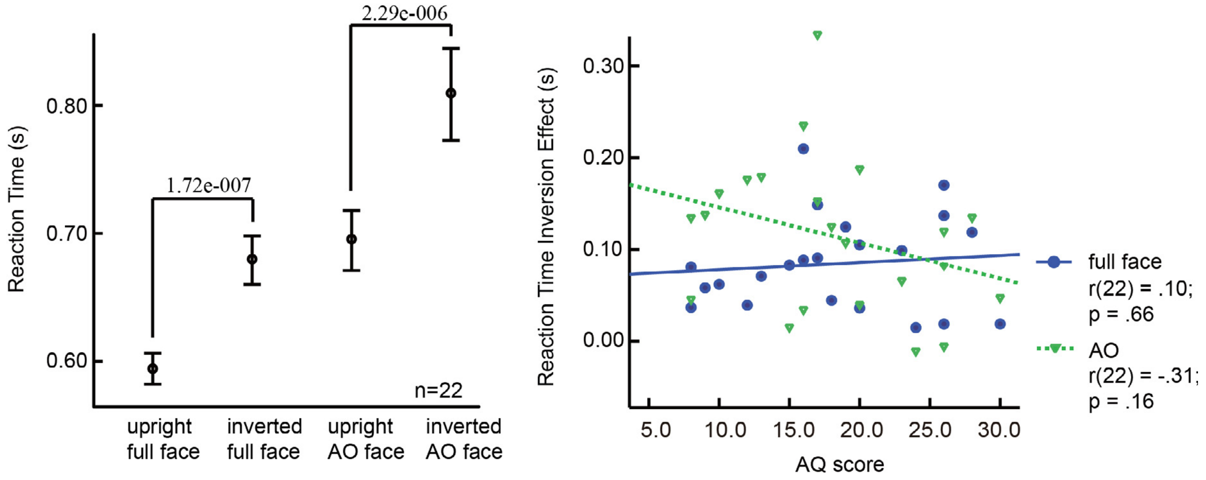
A number of months after the first two experiments, we invited all of our participants to return for Experiment 3. Due to many having graduated, only 19 could participate, so we recruited a further 3 new participants to take part, making a total of 22 participants (10 males, mean age 26.2 ± 2.57 years). As before, we asked our new participants to complete the AQ. Eye tracking data was recorded during all tasks. Participants were informed to respond as accurately and quickly as possible during the inversion tasks, whereas for the recognition and intensity tasks, they merely had to respond as accurately as they could. The tasks were completed in a random order with the caveat that the emotion recognition task was always completed at an earlier stage than the intensity judgment task. Participants were also given a 3-minute break between consecutive tasks.

#### 4.1.2. Stimuli and procedure

*4.1.2.1. Inversion task: fully viewable faces.* Face inversion is thought to disrupt the holistic processing of facial emotion, with any differences in response times between upright and inverted faces


(a) Response accuracy for the inversion tasks.

(b) Correlation between the accuracy inversion effect and AQ.


(c) Reaction time for the inversion tasks.

(d) Correlation between the reaction time inversion effect and AQ.

**Fig. 8.** Inversion effects and the correlations with AQ score. (a) Accuracy for the inversion tasks. Error bars indicate SEM. (b) The correlation between the accuracy inversion effect (AIE) and AQ scores. AIE was calculated by subtracting the accuracy of the inverted faces from the accuracy of the upright faces. Blue dots and solid line are judgments to the fully viewable face and its linear regression line, and green triangles and dotted line are judgments to the aligned occluded face and its linear regression line. (c) Reaction time for the inversion tasks. Error bars indicate SEM. (d) The correlation between the reaction time inversion effect (RTIE) and AQ scores. RTIE was calculated by subtracting the reaction time of the upright faces from the reaction time of the inverted faces. Blue dots and solid line are reaction times to the fully viewable face and its linear regression line, and green triangles and dotted line are reaction times to the aligned occluded face and its linear regression line. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

believed to crudely index a participant's ability to holistically process a face. Under such circumstances, a smaller inversion effect suggests greater employment of featural processing. Thus, if the inversion effect were to diminish as AQ increases, then this would suggest that high AQ participants had reduced levels of holistic processing for that particular face. We therefore decided to ask participants to judge the emotion of fully viewable, upright or inverted, sad and happy faces (4 faces) presented in the same location as where the adaptors were presented during Experiments 1 and 2, while participants fixated on a central cross. Each face was randomly presented 10 times with a total of 40 trials overall for each participant.

*4.1.2.2. Inversion task: occluded faces.* The present task was the same as the previous one, except we asked participants to rate faces that had been partially occluded in the same way as the aligned occluder adaptor in Experiment 1. As featural processing of the mouth is disrupted in these faces, we anticipate that the face inversion effect should diminish as AQ increases.

*4.1.2.3. Emotion recognition task.* In our first task, we tested whether AQ was associated with the recognizability of the emotions conveyed by the adaptors. Participants were required to judge the emotion of the 6 adaptor types (AO, MO, Static_F, Flicker_F, SFO, AFO) while maintaining their fixation on the central cross throughout. There were 12 faces, half of which were the original happy versions of the adaptors used in the previous experiments with the other half sad, taken from the same identity as the adaptors. Each face appeared in a randomized order for 5 times, thus a total of 60 trials for each participant. The location and duration of the stimuli were the same as the adaptors used in previous experiments (2 s), with participants judging their facial expression as happy or sad via a key press. After pressing the key, participants had a 500 ms inter-trial interval until the start of the next trial.

*4.1.2.4. Emotional intensity task.* Upon completion of the recognition task, participants judged the perceived emotional intensity of the faces used in the Emotion Recognition Task using a 7-point Likert Scale, with 1 representing the lowest intensity and 7 the highest. The paradigm was the same as the Emotion Recognition Task, except participants had to judge the faces' emotional intensity instead. There were 60 trials for each participant.

### 4.2. Results and discussion

#### 4.2.1. Inversion task: fully viewable faces

The mean accuracy for upright faces was 97.96%, and 93.41% for inverted faces. To investigate the inversion effect, we performed a paired samples *t*-test between the two face viewpoints (upright vs inverted). The upright faces were identified more accurately than their inverted counterparts ($t(21) = 2.71$, $p = 0.01$, Cohen's d = 0.50, Fig. 8a). The mean correct responses' reaction times for upright and inverted faces were 0.60 s and 0.68 s, respectively. The same *t*-test was performed on reaction times for inversion effect. Again, reaction times also revealed an inversion effect, with upright faces identified faster than inverted ($t(21) = 7.64$, $p < 0.001$, Cohen's d = 1.99, Fig. 8c).

We quantified the inversion effect for both the accuracy and response times by subtracting the upright measures from the inverted responses. These inversion effects showed no associations with AQ (all *ps* > 0.54, Fig. 8b & d). This is perhaps unsurprising, as the mouth region is still in view for all participants and can strongly assist in recognition judgments.

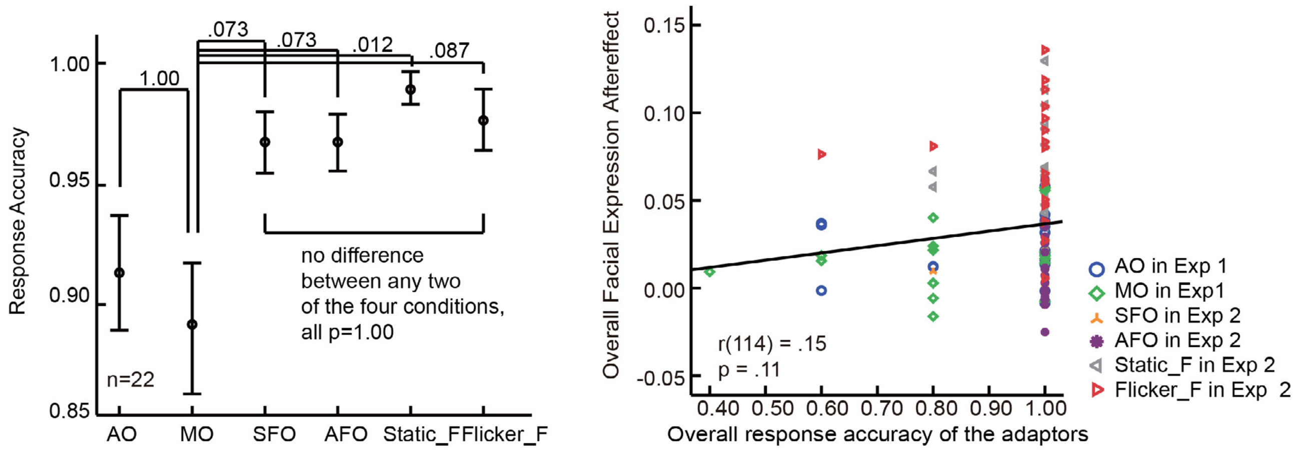
#### 4.2.2. Inversion task: occluded faces

The mean accuracy for upright and inverted occluded faces was 93.41% and 86.14%, respectively. The upright faces were identified more accurately than their inverted counterparts ($t(21) = 2.21$, $p = 0.04$, Cohen's d = 0.054, paired *t*-test, Fig. 8a). This is interesting as it suggests the presence of a holistic effect in the occluded faces.

Response times for upright and inverted faces were 0.70 s and 0.81 s, respectively. Reaction times were faster for upright faces than the inverted ($t(21) = 6.42$, $p < 0.001$, Cohen's d = 1.93, paired *t*-test, Fig. 8c). To examine whether there was association between

(a) Response accuracy for the emotion recognition task

(b) Correlation between overall accuracy of the adaptors and the FEAs.



(c) Perceived emotion intensity.

(d) Correlation between perceived emotion intensity and the FEAs.

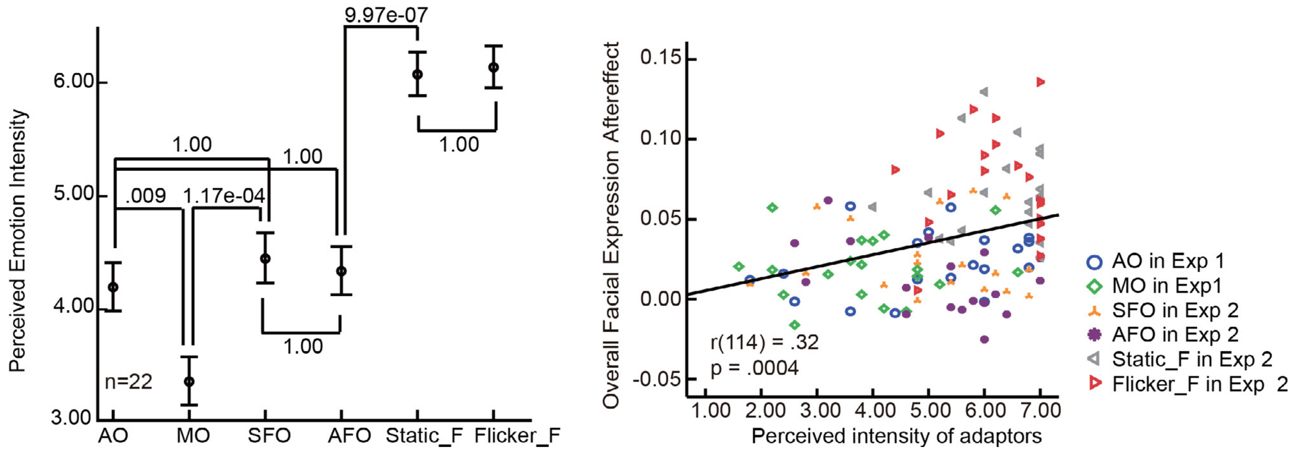


**Fig. 9.** (a) Accuracy for the emotion recognition task. Aligned occluded (AO), Misaligend occluded (MO); Synchronized flickering occluded face (SFO condition), Asynchronized flickering occluded face (AFO condition), Static full face (Static_F condition), Flickering full face (Flick_F condition). Error bars indicate SEM. (b) The correlation between overall accuracy of the adaptors used in experiments and the FEAs. The blue circle indicates aligned occluded face used as adaptor in Experiment 1; the green diamond indicates misaligned occluded face used as adaptor in Experiment 1; the orange triangle indicates synchronous flickering occluded face used as adaptor in Experiment 2; the purple asterisk indicates asynchronous flickering occluded face used as adaptor in Experiment 2; the gray triangle indicates static full face used as adaptor in Experiment 2; and the red triangle indicates flickering full face used as adaptor in Experiment 2. The straight line is the simple linear regression line of all the faces. (c) Perceived emotion intensity of the different types of adaptors. Error bars indicate SEM. (d) The correlation between perceived emotion intensity of the adaptors used in experiments and the FEAs. The different color and shape of dots and line indicate the same faces as in the (b). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

holistic processing and AQ, we correlated the inversion effect with AQ. These analyses again showed no associations for either the response times or accuracy with AQ (both $ps > 0.16$, Fig. 8b & d). Overall, these results suggest that it is not entirely clear that the relationship between FEA and AQ in Experiment 1 was due to diminishing levels of holistic processing as autistic traits increased, at least as indexed by the inversion effects.

### 4.2.3. Emotion recognition task

Results showed that participants were able to easily recognize the emotions of all adaptors, with accuracy ranging from 86.36% (happy MO) to 100% (happy AFO), and an overall mean accuracy of 95.15%. We averaged the happy and sad emotions together and performed an ANOVA on the recognizability of the different conditions (static full, dynamic full, static occluded aligned, static occluded misaligned, occluded synchronized and unsynchronized). This analysis revealed a significant main effect ($F(3.36, 60.52) = 6.21$, $p = 0.001$, $\eta^2 = 0.23$) (Fig. 9a). Pairwise comparisons with Bonferroni corrections revealed no differences in the recognition of the occluded aligned and misaligned adapting facial types in Experiment 1 (the accuracy for the AO and MO were 91.36% and 89.09%, respectively, $p = 1.00$). No differences were found among any pair of the 4 adapting facial types in Experiment 2 either (the mean accuracy for SFO was 96.82%, AFO 96.82%, Static_F 99.09%, and Flicker_F 97.73%, all $ps = 1.00$). Pearson correlations found no association between AQ and recognition accuracy of the types of faces (all $ps > 0.30$). This suggests that the association between AQ and FEA in Experiment 1 was not due to diminishing recognition abilities of the adaptor's emotion as autistic traits increase.

Using Bonferroni-corrections for multiple comparisons, we examined the recognition accuracies of the adaptor types used in Experiment 1 & 2. These analyses revealed that the static occluded faces (AO & MO) were judged less accurately than the occluded flickering faces (SFO & AFO) ($t(21) = -3.89$, $p = 0.002$, Cohen's $d = -0.96$) and the fully viewable faces (Staic_F & Flicker_F) ($t(21) = -3.50$, $p = 0.007$, Cohen's $d = -0.77$). The accuracy of the fully viewable faces were similar to the two occluded flickering adaptors ($t(21) = -0.93$, $p = 1.00$, Cohen's $d = -0.06$).

Pearson correlations found no association between the judgment accuracy of the faces and AQ (all $ps > 0.12$), again indicating that basic recognizability of the adaptors was not related to AQ. FEA was not correlated with recognizability of the adapting faces either ($r(114) = 0.15$, $p = 0.11$, Fig. 9b). However, these interpretations should be taken with caution as ceiling effects may mask a relationship that is not apparent from such a basic task.

### 4.2.4. Emotional intensity task

We performed the same ANOVA on the intensity task by averaging happy and sad emotions to see if there were any differences in the perceived intensity for the different facial types (AO, MO, SFO, AFO, Static_F and Dynamic_F). These results showed a significant main effect ($F(2.65, 55.55) = 66.03$, $p < 0.001$, $\eta^2 = 0.76$, Fig. 9c). Bonferroni corrected comparisons indicated that perceived intensity was highest for the fully viewable faces compared to the occluded faces (all $ps < 0.001$), regardless of dynamic information (mean intensity for Static_F and Flicker_F were 6.07 and 6.14 respectively, with no differences between them, $p = 1.00$). This suggests that the larger FEA in the two fully viewable face conditions in Experiment 2 could have been due to their emotions being perceived as more intense.

The perceived intensity for the aligned condition was higher than that of the misaligned (mean intensity for aligned was 4.20 and for misaligned was 3.38, $p = 0.01$). Perceived intensity between the two occluded dynamic faces was comparable (SFO: 4.46 and AFO: 4.34, $p = 1.00$). Both of the two occluded dynamic faces were judged to be more intense than that of the misaligned (all $ps < 0.001$).

AQ was not correlated with the perceived intensity of any facial type (all $ps > 0.34$). These results suggest that the association between AQ and FEA in Experiment 1 was not due to differences in our participants' perceptions of the adapting faces' emotional intensity. However, a significant correlation was observed between FEAs and the perceived intensity of all of the adapting faces ($r(114) = 0.32$, $p < 0.001$, Fig. 9d), indicating that FEA is strongly dependent upon the emotional intensity of faces.

### 4.2.5. Global analyses across experiments

We manipulated the adapting stimuli to either facilitate or disrupt holistic perception of emotion in the above experiments. To investigate the effects of different manipulations on FEA, we analyzed the data of the 19 participants from all 3 experiments. In Experiments 1 and 2, we were interested in whether these manipulations tapped into differences in the holistic perception of emotion. We first conducted a global analysis using a multilevel mixed-effects regression to predict the FEAs from all conditions based on the different factors (e.g., intensity rating, accuracy, eye tracking results, inversion effect and AQ). The results showed that the perceived intensity was a significant predictor for FEA ($\beta = 0.011$, $p < 0.001$). To separately look at the effects in individual conditions, a series of stepwise multiple regressions were performed, with FEA from each condition as a dependent variable and the corresponding intensity rating, accuracy, eye tracking results, inversion effect and AQ as independent variables. If our manipulations were effective and influenced different aspects of facial emotion perception, then we would expect to find FEAs to be predicted by different factors. We found that for Experiment 1, AQ was the only significant predictor for the FEA in the AO condition ($\beta = -0.002$, $p = 0.001$), and explained a significant proportion of variance ($R^2 = 0.50$, $F(1, 17) = 16.91$, $p = 0.001$). For the FEA in the MO condition, occluded face accuracy inversion effect was the only significant predictor ($\beta = -0.07$, $p = 0.02$) and explained 0.27 of the overall variance. For Experiment 2, no factor could significantly predict FEA in the SFO, AFO, Static_F conditions (all $ps > 0.20$); but the full face accuracy inversion effect seemed to predict the FEA in the Flicker_F condition ($\beta = -0.22$, $p = 0.04$). Thus, our findings support the suggestion that our various manipulations led to different predictors for FEA.

To summarize, the perception of emotional intensity in the adapting faces seems to account for the differences in FEA across all conditions in Experiments 1 and 2: the fully viewable faces which produced the largest FEA were also perceived as conveying emotion more intensely. However, the way in which our adapting stimulus manipulations affected subsequent FEA are heterogeneous: AQ was the only significant predictor for FEA in aligned occluded face adaptation; whereas the emotion recognizability inversion effect (a holistic processing index) was the only significant predictor for FEA in misaligned occluded face adaptation in Experiment 1. In Experiment 2, only the accuracy inversion effect for the fully viewable face significantly predicted the FEA in the Flicker_F condition. The other index of holistic processing, the response time related face inversion effect, failed to predict FEA, nor clearly confirm our hypothesis that the FEA in Experiment 1 was due to diminishing holistic perception of the adapting faces as AQ increases. Also, analysis of our eye tracking data showed that none of our findings across the tasks appeared to be due to any relationship with AQ and attention, as indexed by breaking of fixation (all correlations' $ps > 0.31$).

## 5. General discussion

It has been hypothesized that seemingly neurotypical FEA in ASD adults may purely be due to atypical (i.e., non-holistic) face processing strategies (Cook et al., 2014). By contrast, neurotypical individuals are believed to produce FEA mainly through the holistic processing of the adapting face's emotion. The present study set out to test whether this hypothesis held true across varying levels of autistic traits in a neurotypical population, with those high in such traits expected to not produce adaptation aftereffects when required to process emotion in a holistic manner. To accomplish this, we used opaque bars to partially occlude the adapting faces. This meant that any emotion adaption aftereffects would need to be produced through amodal completion of the adapting face's emotion into a coherent, holistic percept. We hypothesized that this ability would diminish as autistic traits increased, and thus produce similarly diminishing FEA.

As we predicted, FEA to the partially occluded faces were indeed associated with autistic traits in Experiment 1. This association was abolished in Experiment 2 when participants could fully view the face; possibly due to increasingly greater reliance upon the happy face's mouth to process emotion as autistic traits increased. Similarly, contrast flickering of the faces also abolished the association between AQ and FEA due to synchronous flickering boosting FEA for high AQ participants, and flickering diminishing FEA for low AQ participants. In our final experiment, we find evidence that any relationship between FEA and AQ in the aligned occluded condition could not be explained by differences in either the recognizability of the adaptors' emotions, nor in their perceived intensity. While we had hypothesized that the relationship between AQ and FEA in Experiment 1 was due to diminishing abilities to code emotion from the adaptors in a holistic fashion, we failed to clearly show this with our face inversion task.

Why is it that higher AQ scores are associated with FEA to the obscured adaptors in Experiment 1? It has been suggested that those with ASD are known to have impaired grouping, or holistic perception, of complex stimuli (Bertone et al., 2005; Sucksmith et al., 2011). In the inversion task in Experiment 3, however, it is not entirely clear that as autistic traits increase, then so too does the ability to code emotion from the occluded adaptors in a holistic fashion decrease. Does this therefore mean that the relationship between AQ and FEA is not related to holistic face perception? We do not believe so. First, this lack of a clear relationship may be due to the fact that the face inversion task itself relies upon unnatural face processing strategies (i.e., those used during inversion) as a way indexing holistic face perception. As earlier mentioned, it is still unclear whether inversion merely disrupts holistic processing in a quantitative (Sekuler et al., 2004) or qualitative (Rossion, 2008) fashion, thus the face inversion effect may not be a true index of holistic perception of emotion. Our occlusion paradigm, however, is arguably a better way of testing holistic perception over inversion and composite tasks as it keeps the face's parts in their canonical formation. Thus, under such circumstances, participants' emotion perception of the adapting faces must be due to the fairly natural strategies used in daily life. We therefore believe that the relationship between AQ and FEA in Experiment 1 is actually a better index of holistic processing than one yielded from inversion or composite paradigms.

Lastly, in Experiment 2 we found evidence to support prior work (e.g. Cook et al., 2014) in suggesting that levels of autism in adulthood are not associated with FEA after adapting to a fully viewable face: as a group, those with both high and low AQ produced comparable FEA in both of these conditions. It is a common finding that adapting to fully viewable faces leads to FEA in neurotypical participants (Webster et al., 2004). Why then can participants high in AQ also generate FEA? One possible explanation is that people with high AQ tend to gaze away from the eye region and spend more time looking at the mouth (Kliemann, Dziobek, Hatri, Steimke, & Heekeren, 2010). In addition, the mouth is typically the most informative region for the perception of happy emotions (Schyns et al., 2007). Our previous findings showed that low level visual stimuli, such as a curved line or a mouth, are sufficient to produce FEA (Xu et al., 2008; Luo, Wang, Schyns, Kingdom, & Xu, 2015). Therefore, high AQ participants may have a greater tendency to focus on the mouth, and thus generate FEA based on local mouth adaptation without any global representation of the face. However, the most informative facial areas for other facial expressions (e.g., angry, surprise, fear) and identity are not the same; therefore extrapolating this possibility to other types of emotion adaptation should be done with caution. However, the fact that our high AQ participants generated FEA to the occluded flickering faces may indicate some ability at being able to extract emotion as a gestalt percept. These dynamic faces may require a different neural network that is sensitive to facial motion (e.g., posterior superior temporal sulcus (pSTS) and anterior STS (aSTS), Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011), in comparison to static faces which might be reliant upon the fusiform gyrus and the occipital face area.

We found that neither the recognizability nor the perceived emotional intensity of the adapting faces can explain the association between FEA and AQ in the aligned condition in Experiment 1. Emotional intensity was, however, linked to the magnitude of the FEA across all adaptation conditions. For example, the fully viewable faces' emotions were rated as being more intense than their obscured counterparts, and thus produced larger aftereffects. This is to our knowledge the first time that the perceived emotional intensity of adapting faces have been shown to produce differential magnitudes of FEA. We also generally found no association between autistic traits and emotion recognition abilities, at least in the baseline conditions. These findings corroborate recent suggestions that levels of autism are not related to emotion recognition (Bird & Cook, 2013).

This final finding may appear at odds with the relationship we have observed between FEA and AQ. However, FEA is measured by visual adaptation, a behavioral technique which probes the short term plasticity of visual perception, where our judgments of the test faces are influenced by our prior exposure to the adapting faces. This technique is actually distinct from purely recognizing the emotion of faces. In addition to the adaption aftereffect, visual adaptation has at least two more consequences: renormalization (extreme stimuli similar to the adaptor become less extreme after adaptation) and sensitivity (increased sensitivity to the stimuli that are similar to the adaptor). Therefore, visual adaptation can actually reveal subtle differences in emotion perception between conditions where recognition alone can fail (Liu et al., 2014). However, intact emotion recognition may only be occurring in the high AQ participants purely due to increased reliance upon the mouth region to judge emotion. If the test faces had their mouths obscured, we would anticipate a relationship between AQ and emotion recognition to emerge.

The fact that that we did find a strong correlation between emotion recognition performance and AQ in the misaligned condition is unusual, particularly as there were no differences between the FEA across the two conditions in Experiment 1. Adapting to misaligned bars must increasingly disrupt emotion recognition strategies when judging the test faces as AQ increases. As those high in AQ appear to judge emotion mainly from the mouth region, it is therefore likely that the corner of the misaligned bar impairs subsequent perception of emotion from the mouth. On a related point, the fact that female, but not male, participants exhibited diminishing sensitivity at judging emotion in the test faces after adapting to the fully viewable static face is also unexpected, particularly as there were no clear gender differences in any other conditions. This finding suggests that adaptation to fully viewable emotional faces can lead to gender specific endophenotypes of emotion recognition across autistic traits, endophenotypes that are not otherwise revealed in a pure recognition paradigm as indexed by our baseline conditions. We therefore support the proposal of gender differences related to autistic traits in similar face identity adaptation work (Rhodes et al., 2013). Both of these findings warrant further investigation as they will surely reveal components of emotion perception and recognition that are both distinct, and shared, across genders with varying levels of autism.

## 6. Conclusions

By manipulating the visibility of emotional faces, we have provided the first evidence of an association between autistic traits and emotion adaptation to static, but not dynamic, occluded faces in neurotypical adults. This association suggests that as autistic traits increase, then so too does the ability to process facial emotion decrease. Our findings offer an explanation as to why those with ASD have been shown to evince neurotypical emotion adaptation aftereffects: it is likely due to featural processing, probably of the mouth region. Coherent and dynamic changes in the contrast of a partially viewable face, however, appear to facilitate the processing of its emotion in those high in autistic traits. This suggests that emotion processing involves distinct cortical pathways for static and contrast dynamic faces, and that the extent to which these pathways are employed is related to the presence of autistic traits.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2016.12.018.

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