



## Brief article

## Preferential awareness of protofacial stimuli in autism



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## ABSTRACT

It has been suggested that a subcortically mediated, innate sensitivity to protofacial stimuli leads to specialized face processing and to the development of the social brain. A dysfunction of this face-processing pathway has been associated with atypical social development in individuals with autism spectrum disorder (ASD). This study investigated whether individuals with ASD exhibit primary sensitivity to monochrome protoface stimuli using continuous flash suppression (CFS). Under CFS, visual stimuli are suppressed from awareness, and cortical processing is strongly reduced while subcortical regions continue to respond to invisible stimuli. We found that both adolescents with ASD and typically developing adolescents showed preferential detection of upright protoface stimuli under CFS but not in a non-CFS control condition. These results challenge the notion that a primitive sensitivity to protoface stimuli is essential for typical social development. Rather, our findings suggest such sensitivity is not a sufficient condition for typical social development and that the presence of other complementary factors is necessary for the development of the social brain.

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## 1. Introduction

Faces contain a wealth of essential information for social communication, and facial perception is one of the most highly specialised perceptual skills in humans (Haxby, Hoffman, & Gobbini, 2000). Sensitivity (i.e. preferential looking) to face-like or protofacial stimuli (i.e. schematic faces) is already present in newborns (Farroni et al., 2005; Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991). This innate preference of stimuli with face-like features, which is presumably mediated by a subcortical pathway, possibly lays the foundation for the development of specialized face processing and the networks of the social brain (Johnson, 2005) that are key for social cognition and behaviour (Brothers, 1990). Although the innate preference to protofacial stimuli declines at two months of age the underlying subcortical

face detection system continuous to be present (Nakano & Nakatani, 2014) and can be studied even in adults by testing subcortically mediated behaviour such as saccadic responses (Tomalski, Csibra, & Johnson, 2009). A dysfunction of this innate face detection mechanism has been suggested to play a major role in the atypical social development characteristic of autism spectrum disorder (ASD) (Johnson, 2005). ASD is a developmental disorder characterised by difficulties with social interaction and communication and restricted and repetitive behaviours (American Psychiatric Association, 2013). Whereas in typically developing (TD) individuals, human faces are a powerful stimulus capable of capturing and holding visual attention (Bindemann, Burton, Hooge, Jenkins, & de Haan, 2005; Langton, Law, Burton, & Schweinberger, 2008), children and adolescents with ASD do not show such preferential attention to faces (Chawarska, Volkmar, & Klin, 2010; Kikuchi, Senju, Tojo, Osanai, & Hasegawa, 2009; Kikuchi et al., 2011). It has been proposed that their atypical responses to faces could be a consequence of a lack of sensitivity to social stimuli, including protofacial stimuli, in early infancy (Johnson, 2005; Klin, Jones, Schultz, & Volkmar, 2003).

Recent findings, however, contradict this hypothesis: Adults with ASD have been found to show intact attentional orienting to

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peripherally presented protofacial stimuli (Shah, Gaule, Bird, & Cook, 2013). As these protofacial stimuli have previously been shown to optimally drive neonates' preferential looking (Farroni et al., 2005) and the underlying face detection system is presumably preserved in adults (Tomalski et al., 2009), this finding represents a challenge to the hypothesis that alterations in the innate sensitivity to such protofacial stimuli are associated with the atypical development of the social brain in ASD (Johnson, 2005). In reaction to this result, Johnson (2014) stressed that it is still possible that individuals with ASD lack this sensitivity at early ages, leading to the atypical development of social behaviour, though it may emerge later in life. Since the study by Shah et al. (2013) measured attentional orienting by manual responses and did not record more reflexive saccadic eye movements driven by the superior colliculus (Lee, Rohrer, & Sparks, 1988) or other responses that are likely to be mediated by the subcortical face detection pathway, it remains unclear whether individuals with ASD have an intact subcortical face detection pathway that is sensitive to protofacial stimuli. Furthermore, as Johnson (2014) pointed out, it would be important to test very young infants, because preferential looking to protofaces declines at two months of age (Johnson et al., 1991). However, it is difficult to collect such data because children with ASD are rarely diagnosed before the age of three (Fountain, King, & Bearman, 2011).

In the present study, continuous flash suppression (CFS) (Tsuchiya & Koch, 2005) was used to investigate the initial primary processing of protofacial stimuli at the threshold of conscious awareness in individuals with ASD. CFS is a binocular-rivalry technique in which a target stimulus is continuously presented to one eye while dynamic, high-contrast masks are flashed into the other eye. With this CFS technique, the target can be suppressed from awareness (i.e. rendered invisible) for several seconds, enabling researchers to study the processes that precede and lead to stimulus awareness for complex stimuli such as faces (Axelrod, Bar, & Rees, 2015) over extended periods of time. During CFS, visual cortex responses to the target are strongly suppressed (Hesselmann, Hebart, & Malach, 2011; Yuval-Greenberg & Heeger, 2013), while subcortical regions exhibit comparably robust responses to facial stimuli (Jiang & He, 2006; Troiani & Schultz, 2013). This pattern of activation bears a striking similarity to the structure of the newborn brain, in which subcortical regions are already well developed but cortical regions are anatomically (Barkovich, Kjos, Jackson, & Norman, 1988; Paus et al., 2001) and functionally immature (Muir, Clifton, & Clarkson, 1989). Indeed, for TD adults in the breaking CFS task (Jiang, Costello, & He, 2007), upright protofaces overcome CFS and emerge into awareness more quickly than inverted protofaces (Stein, Peelen, & Sterzer, 2011). This preferential processing of protofacial stimuli under CFS in adults is similar to newborns' looking preferences, suggesting that preferential responses in both adults and newborns are based on the same inborn face detection system involving subcortical regions such as the amygdala and pulvinar (Jiang & He, 2006; Johnson, 2005; Troiani & Schultz, 2013). Moreover, research using CFS to study access to awareness of protoface stimuli in individuals with ASD will provide new insight into the basic perceptual mechanisms of face processing in ASD that goes beyond previous studies on attentional orienting to protofaces (Shah et al., 2013), as attention and conscious awareness are thought to be related but distinct processes (Koch & Tsuchiya, 2007; Lamme, 2003).

In the present study, three experiments examining adolescents with ASD and TD adolescents were conducted, in order to study the initial processing of protofaces. We recruited adolescents rather than younger children as participants because testing of children with the CFS setup poses logistic and practical challenges (e.g. stable fusion, fixation and vigilance) that may undermine the quality of the acquired data and has therefore, to the best of our

knowledge, not been done in any previous CFS study except for one study utilising a specific and non-standard equipment (Sylvers, Brennan, & Lilienfeld, 2011). In Experiment 1, the well-known advantage of higher-contrast over lower-contrast Gabor-patches in breaking CFS (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006) was investigated to ensure that participants showed overall normal behavioural performance in the breaking CFS task with non-facial stimuli. Experiment 2 addressed the central question of the present study: whether the advantage of upright versus inverted (i.e. non-face-like) protofaces in breaking CFS (Stein, Peelen et al., 2011) would be present or absent in adolescents with ASD. Finally, Experiment 3 was designed as a control experiment to test whether the findings in Experiment 2 could be explained by non-specific differences unrelated to access to awareness under CFS. To this end, Experiment 3 used the same stimuli and task, and was designed to resemble the visual appearance in Experiment 2, but it did not involve interocular suppression, i.e. CFS. We hypothesised that if individuals with ASD did not have the subcortically mediated primary sensitivity to protofaces, they should not show the advantage of upright over inverted protofaces in breaking CFS. Alternatively, if their primary sensitivity to protofacial stimuli was intact, they should show an advantage of upright protofaces.

## 2. Material and methods

### 2.1. Participants

Ten adolescents with ASD (12–21 years old, 10 males) and 10 TD adolescents (12–20 years old, 9 males) participated in Experiments 1, 2, and 3 (Table 1). Participants with ASD had been previously diagnosed with autistic disorder ( $N = 4$ ), Asperger syndrome ( $N = 1$ ), or pervasive developmental disorder without a detailed diagnosis ( $N = 5$ ) according to the DSM-IV (American Psychiatric Association, 1994). The Japanese version of the Social Communication Questionnaire (SCQ) (Rutter, Bailey, & Lord, 2003) was completed by all parents and the Autism Diagnostic Observation Schedule (ADOS) (Lord et al., 2000) was administered for all participants with ASD. All participants with ASD scored above the ASD cut-off points on both SCQ (15) and ADOS (7, social communication). An abbreviated version of the Japanese Wechsler Intelligence Scale for Children (WISC) (Japanese WISC-III Publication Committee, 1998; Wechsler, 1992) or Wechsler Adult Intelligence Scale (WAIS) (Shinagawa, Kobayashi, Fujita, & Maekawa, 1990; Wechsler, 1981) was administered to all participants to measure their IQ (the WISC for those younger than 16.9 years old and the WAIS for those older than 16.9 years old). There were no significant difference between groups regarding chronological age, IQ, and sex ratio (all  $ps > .05$ ). All participants had normal or corrected-to-normal visual acuity. One participant with ASD had esotropia, but excluding him did not change the statistical significance of the key results (i.e. the inversion effect for protofaces under CFS). Written informed consent was obtained from all participants and their parents. This study was approved by the Research Ethics Committee of the University of Tokyo.

### 2.2. Apparatus and stimuli

Stimuli were presented on a 17-inch CRT monitor (1024 × 768 pixel resolution, 60-Hz frame rate), using Matlab (The MathWorks, Natick, MA) with the Cogent 2000 toolbox ([www.vislab.ucl.ac.uk/cogent.php](http://www.vislab.ucl.ac.uk/cogent.php)) on a desktop PC. Participants viewed the screen from a distance of 50 cm with their head stabilized by a chin-and-head rest. Two fusion contours (visual angle:  $8.1^\circ \times 8.1^\circ$ ) consisting of random black and white pixels (width

**Table 1**  
Participant characteristics.

	ASD ( <i>n</i> = 10, no female)		TD ( <i>n</i> = 10, 1 female)		<i>p</i> -value
	<i>M</i> (SD)	Range	<i>M</i> (SD)	Range	
Age, years	16.7 (3.6)	12–21	15.5 (2.6)	12–20	.395
IQ	101.4 (19.8)	73–124	101.8 (15.1)	73–131	.962
SCQ	25.8 (3.8)	18–31	2.6 (2.5)	0–8	<.001
ADOS, social communication	12.6 (3.3)	9–18			

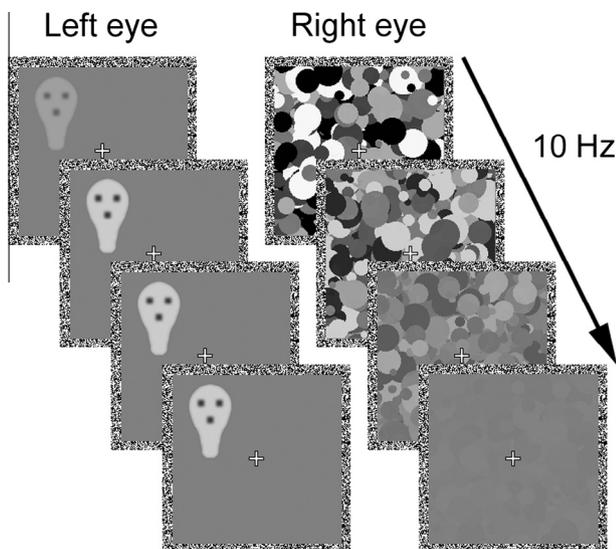
*p*-Values reflect the levels of significance from independent samples *t*-tests. ASD, autism spectrum disorder; TD, typically developing; SCQ, Social Communication Questionnaire; ADOS, Autism Diagnostic Observation Schedule.

0.5°) were presented side-by-side, dichoptically through a custom-built mirror stereoscope (i.e. one frame was visible to one eye), against a uniform grey background. A white fixation cross (0.6° × 0.6°) was displayed in the centre of each frame. High-contrast, randomly positioned greyscale circles (diameter 0.3–1.6°) updated at 10 Hz were presented as masks.

In Experiment 1 (Contrast, CFS), the well-established typical effect of luminance contrast on suppression durations was investigated using vertically and horizontally oriented Gabor-patches (2.6° × 2.6°) as targets; half were high contrast (Michelson contrast = 1) and the other half were low contrast (Michelson contrast = 0.37). For Experiments 2 (Protiface, CFS) and 3 (Protiface, non-CFS), protofacial stimuli were created according to previous studies (Farroni et al., 2005; Johnson et al., 1991; Mondloch et al., 1999; Stein, Peelen et al., 2011). Protofacial stimuli (2.0° × 3.3°) consisted of a white head-shaped contour and three black blobs. In face-like upright protofaces these blobs were arranged such that they represented the eyes and the mouth (two dark blobs over one dark blob, see Fig. 1). Suppression durations for these upright protofaces were compared to non-face-like stimuli in which the orientation of the three dark blobs was vertically inverted, such that the typical spatial arrangement of the eyes above the mouth was disrupted while all pixel values remained constant. All stimuli were greyscale.

### 2.3. Procedure

Before the experiment, participants were shown example pictures of the target stimuli from all conditions. They were instructed



**Fig. 1.** Example of the experimental procedure in the CFS experiment with protofaces (Experiment 2). In each trial, flashing masks were presented to one eye while a target stimulus was presented to the other eye. Participants pressed one of four buttons to indicate in which quadrant any part of the target stimulus became visible.

to respond as soon as a target stimulus or any part of the target became visible. Trials started with a 1-s presentation of the fusion contours and the fixation cross only. Next, in the CFS experiments (Experiments 1 and 2) CFS masks refurbished at 10 Hz were presented to one randomly selected eye. A target stimulus was gradually faded into the other eye by increasing its contrast over the first second of each trial and then remained constant until the participants responded or for a maximum of 10 s. Target stimuli were presented in one of the four quadrants (centred at eccentricities of 2.5°). Participants were asked to press one of four keys on the keyboard (F, V, J, N) to indicate in which quadrant the target stimulus appeared. Beginning 1.1 s after trial onset, the contrast of the masks was linearly decreased to zero over 6.9 s. In the non-CFS control experiment (Experiment 3), the design, the task, and the display layout were identical to the CFS experiment (Experiment 2), but the protofacial stimuli and the masks were presented to both eyes simultaneously. To approximate the perceptual experience in this control experiment to that under CFS, the transparency of the protofacial stimuli was reduced linearly from 100% to 0% over 10 s by alpha blending. This resulted in gradual visibility of the protofacial stimuli against the masks (Jiang et al., 2007; Stein, Peelen et al., 2011; Stein, Sterzer, & Peelen, 2012; Yang, Zald, & Blake, 2007; Zhou, Zhang, Liu, Yang, & Qu, 2010).

Participants completed 32 trials in Experiment 1 and 64 trials each in Experiments 2 and 3. The order of trials was randomised in each experiment and across participants, and each combination of two Gabor contrasts (Experiment 1, high or low), two Gabor orientations (Experiment 1, vertical or horizontal), or two vertical orientations of the protofacial stimuli (Experiments 2 and 3, upright or inverted) occurred equally often within each experiment.

### 2.4. Design and analysis

The mean response times (RTs, seconds) were compared by a two-way mixed analysis of variance (ANOVA) with group (ASD or TD) as the between-participant factor and contrast (high or low) in Experiment 1 or vertical orientation (upright or inverted) in Experiments 2 and 3 as the within-participant factor. Additionally, to compare the inversion effect for protofaces between the CFS condition and the binocular non-CFS control condition, a three-way mixed ANOVA including experiment as an additional within-participant factor (Experiment 2 or 3) was conducted. Trials with no responses and trials with incorrect responses (Experiment 1, 0.2%, 1.7%; Experiment 2, 0.0%, 2.0%; Experiment 3, 0.0%, 1.3%, respectively) were excluded from the calculation of mean RTs. Trials with RTs of more than 2 standard deviations (SDs) above or below the mean of each individual in each condition (Experiment 1, 2.2%; Experiment 2, 2.1%; Experiment 3, 2.3%) were excluded from the RT analysis (see also Supplementary Material, Table S1). The number of trials with no responses or incorrect responses did not differ between groups or conditions in any experiment (Supplementary Material, Table S2; all *ps* > .05).

### 3. Results

#### 3.1. Experiment 1 (Contrast, CFS)

An ANOVA revealed a significant main effect of contrast ( $F_{(1, 18)} = 52.73, p < .001, \eta_p^2 = .75$ ). As predicted, high-contrast Gabor-patches ( $M = 5.78, SEM = 0.51$ ) were localised faster than were low-contrast patches (Table 2;  $M = 6.78, SEM = 0.55$ ). Neither the main effect of group nor the interaction was significant ( $ps > .10$ ).

#### 3.2. Experiment 2 (Orientation, CFS)

Under CFS, there was a significant main effect of vertical orientation ( $F_{(1, 18)} = 12.25, p = .003, \eta_p^2 = .40$ ). Upright protofaces ( $M = 2.66, SEM = 0.34$ ) were localised faster than were inverted protofaces (Fig. 2;  $M = 2.88, SEM = 0.35$ ). Neither the main effect of group nor the interaction between group and orientation were significant (both  $ps > .10$ ).

#### 3.3. Experiment 3 (Orientation, non-CFS)

In the control non-CFS experiment, there were no significant effects (all  $ps > .10$ ).

#### 3.4. Experiments 2 and 3 (Orientation, CFS and non-CFS)

The main effect of vertical orientation was significant ( $F_{(1, 18)} = 16.33, p = .001, \eta_p^2 = .48$ ). Upright protofaces ( $M = 2.91, SEM = 0.22$ ) were localised faster than were inverted protofaces ( $M = 3.06, SEM = 0.23$ ). The interaction between group and experiment was also significant ( $F_{(1, 18)} = 5.30, p = .034, \eta_p^2 = .23$ ). A simple effect analysis revealed a significant main effect of experiment in the ASD group ( $F_{(1, 9)} = 10.12, p = .011, \eta_p^2 = .53$ ) but not in the TD group ( $F_{(1, 9)} = 0.18, p = .683, \eta_p^2 = .02$ ). In the ASD group, target stimuli were detected faster in the CFS condition ( $M = 2.31, SEM = 0.41$ ) than in the non-CFS condition ( $M = 3.34, SEM = 0.21$ ). Finally, the interaction between experiment and orientation approached statistical significance ( $F_{(1, 18)} = 3.29, p = .086, \eta_p^2 = .15$ ). An exploratory simple effect analysis revealed a significant simple main effect of protoface orientation in the CFS condition ( $F_{(1, 18)} = 12.25, p = .003, \eta_p^2 = .40$ ) but not in the non-CFS condition ( $F_{(1, 18)} = 2.75, p = .115, \eta_p^2 = .13$ ). The three-way interaction was not significant ( $p > .10$ ).

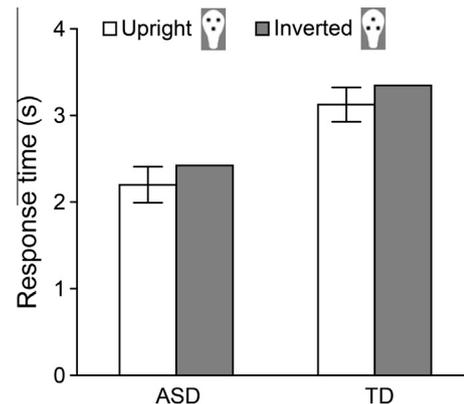
### 4. Discussion

This study investigated whether a primary sensitivity to protofacial stimuli is intact in adolescents with ASD by measuring the time until target stimuli gained access to visual awareness under CFS. In Experiment 1, the well-known advantage of higher- relative to lower-contrast Gabor-patches under CFS (Tsuchiya & Koch, 2005) was observed in both groups, replicating previous results (Akechi et al., 2014). In the non-CFS control experiment (Experiment 3), detection speed did not differ between upright and inverted protofaces, suggesting that sensitivity to protofaces is not mediated by ordinary non-CFS specific visual processing or by differences in response criteria (Stein, Peelen et al., 2011). In the critical CFS experiment (Experiment 2), both groups showed a detection advantage for upright relative to inverted protofaces under CFS. This suggests that the primary sensitivity to protofaces, possibly supported by the subcortical face detection pathway (Johnson et al., 1991; Mondloch et al., 1999; Morton & Johnson, 1991), is intact in individuals with ASD. As the pattern of neural activity under CFS resembles brain function in newborns, with

**Table 2**

Means and standard errors of mean (SEMs) of reaction times (s) for each experiment.

		ASD (n = 10)	TD (n = 10)
Experiment 1 (Gabor-patch)	High contrast	5.05 (0.87)	6.52 (0.49)
	Low contrast	5.82 (0.93)	7.73 (0.43)
Experiment 2 (Protoface)	Upright	2.20 (0.39)	3.12 (0.53)
	Inverted	2.42 (0.44)	3.34 (0.53)
Experiment 3 (Protoface)	Upright	3.28 (0.21)	3.05 (0.21)
	Inverted	3.40 (0.22)	3.07 (0.23)



**Fig. 2.** The results of the CFS protoface experiment (Experiment 2). The bar plots depict the mean response times for protofacial stimuli, separately for upright protofaces and inverted protofaces in each group. The error bars indicate 95% confidence intervals for the mean difference between the upright and inverted conditions in each group. ASD, autism spectrum disorder; TD, typically developing; CFS, continuous flash suppression.

visual cortex activity being significantly suppressed during CFS (Hesselmann et al., 2011; Yuval-Greenberg & Heeger, 2013) while subcortical regions continue to respond to facial stimuli despite CFS (Jiang & He, 2006; Troiani & Schultz, 2013), this result could suggest that sensitivity to protofacial stimuli is intact in individuals with ASD from their early infancy, although the present study did not test infants.

This interpretation would challenge the notion that the innate sensitivity to protofacial stimuli is crucial for the typical development of social brain networks (Johnson, 2005). Several accounts of ASD assume that an innate or ontogenetically early sensitivity to social stimuli such as faces and eyes, supported by subcortical regions including the amygdala, is crucial for typical social development, while its early disruption is associated with atypical social development in individuals with ASD (Klin et al., 2003; Schultz, 2005). The present results demonstrate that adolescents with ASD show preferential processing of protofaces under CFS, just as TD adolescents do. Thus, our findings provide no evidence for disturbed initial processing of face-like stimuli in ASD. This is consistent with recent work showing that adults with ASD also have an attentional bias to peripherally presented protofacial stimuli (Shah et al., 2013), suggesting that “the subcortical social orienting system is intact in adults with autism” (Johnson, 2014, p. R30). Because our study investigated the subcortical face detection pathway otherwise by using CFS, our findings strengthen the possibility that individuals with ASD also have an innate face detection system. As it remains possible that the subcortical face detection system “is impaired or delayed around the time of birth” (Johnson, 2014, p. R30), it will still be necessary to test newborns who will later be diagnosed with ASD to provide unequivocal evidence for intact inborn face sensitivity in ASD. Hence, a promising avenue for future studies is to study the younger siblings of individuals with ASD, who are themselves at high risk of developing ASD (Jones, Gliga, Bedford, Charman, & Johnson, 2014).

One limitation of the present study is that recent work suggests that detection under CFS does not exclusively reflect subcortical processing. For example, it has been found that suppression durations are influenced by facial properties that may be too subtle to be processed by a coarse subcortical pathway, such as a face's race, age (Stein, End, & Sterzer, 2014), or a face's familiarity to the observer (Gobbini et al., 2013). Also, detection of stimuli containing high spatial frequencies that are thought to be processed by cortical areas overcome CFS relatively quickly (Stein, Seymour, Hebart, & Sterzer, 2014; Yang & Blake, 2012). Furthermore, whereas earlier neuroimaging studies indicated that neural activity under interocular suppression is largely confined to subcortical areas (Jiang & He, 2006; Pasley, Mayes, & Schultz, 2004; Troiani & Schultz, 2013; Williams, Morris, McGlone, Abbott, & Mattingley, 2004), the extent and location of residual neural processing in cortical areas – especially in the dorsal visual processing stream – is still a matter of debate (Ludwig & Hesselmann, 2015; Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014), with some imaging studies showing preserved cortical responses despite interocular suppression (e.g. Fang & He, 2005; Sterzer, Haynes, & Rees, 2008). At the same time, recent results from monkey neurophysiology show that face-like patterns such as those used in the present study elicit responses in the pulvinar (thought to be part of the subcortical face detection pathway) at extremely short latencies of about 50 ms (Nguyen et al., 2013), likely reflecting direct feedforward ascending input from the retina. Thus, it remains possible that with the specific protofaces used in the present study suppression durations under CFS mainly reflect subcortical processing.

Another current debate revolves around the logic of including a non-CFS control condition to exclude that the findings obtained with CFS were due to non-specific differences unrelated to access to awareness under CFS (e.g. Gayet, Van der Stigchel, & Paffen, 2014; Jiang et al., 2007; Stein, Hebart, & Sterzer, 2011; Stein & Sterzer, 2014). Because it is hard to fully match these conditions, it is possible that the non-CFS control condition did not capture all non-specific differences between conditions that might have contributed to the effects obtained with CFS, e.g. response biases due to strategic differences. In fact, in the ASD group overall RTs were faster in the control condition than in the CFS condition, indicating that the conditions were not fully matched. Due to enormous inter-individual variability in suppression times, depending on factors such as relative eye dominance, brain structure, and genetics (e.g. Kleinschmidt, Sterzer, & Rees, 2012), the direct comparison of overall RTs between the CFS and control condition is difficult to interpret. Importantly, however, there were no significant differences in overall RTs between ASD and TD individuals in either the CFS or in the non-CFS experiment, meaning that overall RT differences are unlikely to account for the present findings.

If it is true that individuals with ASD have normal primary subcortically mediated sensitivity to protoface stimuli, it remains an outstanding question why such sensitivity does not necessarily lead to the typical development of the social brain. Given that children and adults with ASD reportedly lack preferential behavioural and neural responses to faces (Pelphrey, Shultz, Hudac, & Vander Wyk, 2011; Weigelt, Koldewyn, & Kanwisher, 2012), the primary sensitivity to protofacial stimuli could be a necessary condition—but might not be a sufficient condition—for typical social development. For example, early preferential responses to socially important signals (e.g. protofaces) may not turn into sustained, attentive preferential looking later in life if these social signals were not paired with sufficient reward values for the perceiver early in life. Up-to-date evidence from prospective longitudinal studies suggests that individuals with ASD have an innate preference for social stimuli, but that they lose sensitivity to the same stimuli during infancy. For instance, infants who are later diagnosed as ASD look at other people's faces as frequently as TD

infants at 6 months, but subsequently the frequency of looking significantly decreases (Ozonoff et al., 2010). The gaze duration of infants with ASD towards other person's eyes is comparable with that of TD infants at first, but continuously declines from 2 to 24 months old (Jones & Klin, 2013). Since early experience is crucial for the development of important social skills such as configural face processing (Le Grand, Mondloch, Maurer, & Brent, 2001) and language perception (Kuhl, Williams, Lacerda, Stevens, & Lindblom, 1992), identifying other factors which are essential to social development (e.g. gaze duration towards other people) will be an important avenue for future research. The present study revealing intact preferential detection of protofaces in individuals with ASD demonstrates how research using state-of-the-art vision sciences techniques such as continuous flash suppression to study basic perceptual processes can advance our understanding of the nature of typical as well as atypical social development in humans.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.cognition.2015.06.016>.

## References

- Akechi, H., Stein, T., Senju, A., Kikuchi, Y., Tojo, Y., Osanai, H., et al. (2014). Absence of preferential unconscious processing of eye contact in adolescents with autism spectrum disorder. *Autism Research*, 7, 590–597.
- American Psychiatric Association (1994). *Diagnostic and statistical manual of mental disorders* (4th ed.). Washington, DC: American Psychiatric Association.
- American Psychiatric Association (2013). *Diagnostic and statistical manual of mental disorders* (5th ed.). Washington, DC: American Psychiatric Association.
- Axelrod, V., Bar, M., & Rees, G. (2015). Exploring the unconscious using faces. *Trends in Cognitive Sciences*, 19, 35–45.
- Barkovich, A. J., Kjos, B. O., Jackson, D. E., & Norman, D. (1988). Normal maturation of the neonatal and infant brain: MR imaging at 1.5 T. *Radiology*, 166, 173–180.
- Bindemann, M., Burton, A. M., Hooge, I. T. C., Jenkins, R., & de Haan, E. H. F. (2005). Faces retain attention. *Psychonomic Bulletin & Review*, 12, 1048–1053.
- Brothers, L. (1990). The social brain: A project for integrating primate behavior and neurophysiology in a new domain. *Concepts in Neuroscience*, 1, 27–51.
- Chawarska, K., Volkmar, F., & Klin, A. (2010). Limited attentional bias for faces in toddlers with autism spectrum disorders. *Archives of General Psychiatry*, 67, 178–185.
- Fang, F., & He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neuroscience*, 8, 1380–1385.
- Farroni, T., Johnson, M. H., Menon, E., Züljan, L., Faraguna, D., & Csibra, G. (2005). Newborns' preference for face-relevant stimuli: Effects of contrast polarity. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 17245–17250.
- Fountain, C., King, M. D., & Bearman, P. S. (2011). Age of diagnosis for autism: Individual and community factors across 10 birth cohorts. *Journal of Epidemiology and Community Health*, 65, 503–510.
- Gayet, S., Van der Stigchel, S., & Paffen, C. L. E. (2014). Breaking continuous flash suppression: Competing for consciousness on the pre-semantic battlefield. *Frontiers in Psychology*, 5, 460.

- Gobbini, M. I., Gors, J. D., Halchenko, Y. O., Rogers, C., Guntupalli, J. S., Hughes, H., et al. (2013). Prioritized detection of personally familiar faces. *PLoS One*, 8, e66620.
- Goren, C. C., Sarty, M., & Wu, P. Y. (1975). Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics*, 56, 544–549.
- Haxby Hoffman & Gobbini (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4, 223–233.
- Hesselmann, G., Hebart, M., & Malach, R. (2011). Differential BOLD activity associated with subjective and objective reports during “blindsight” in normal observers. *Journal of Neuroscience*, 31, 12936–12944.
- Japanese WISC-III Publication Committee (1998). *Nihonban WISC-III chinou kensahou [Japanese Wechsler Intelligence Scale for Children 3rd ed.]*. Tokyo: Nihon Bunka Kagakusha.
- Jiang, Y., Costello, P., & He, S. (2007). Processing of invisible stimuli: Advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychological Science*, 18, 349–355.
- Jiang, Y., & He, S. (2006). Cortical responses to invisible faces: Dissociating subsystems for facial-information processing. *Current Biology*, 16, 2023–2029.
- Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience*, 6, 766–774.
- Johnson, M. H. (2014). Autism: Demise of the innate social orienting hypothesis. *Current Biology*, 24, R30–R31.
- Johnson, M. H., Dziurawiec, S., Ellis, H., & Morton, J. (1991). Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition*, 40, 1–19.
- Jones, E. J. H., Gliga, T., Bedford, R., Charman, T., & Johnson, M. H. (2014). Developmental pathways to autism: A review of prospective studies of infants at risk. *Neuroscience and Biobehavioral Reviews*, 39, 1–33.
- Jones, W., & Klin, A. (2013). Attention to eyes is present but in decline in 2–6-month-old infants later diagnosed with autism. *Nature*, 504, 427–431.
- Kikuchi, Y., Senju, A., Akechi, H., Tojo, Y., Osanai, H., & Hasegawa, T. (2011). Atypical disengagement from faces and its modulation by the control of eye fixation in children with autism spectrum disorder. *Journal of Autism and Developmental Disorders*, 41, 629–645.
- Kikuchi, Y., Senju, A., Tojo, Y., Osanai, H., & Hasegawa, T. (2009). Faces do not capture special attention in children with autism spectrum disorder: A change blindness study. *Child Development*, 80, 1421–1433.
- Kleinschmidt, A., Sterzer, P., & Rees, G. (2012). Variability of perceptual multistability: From brain state to individual trait. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 367, 988–1000.
- Klin, A., Jones, W., Schultz, R., & Volkmar, F. (2003). The enactive mind, or from actions to cognition: Lessons from autism. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 358, 345–360.
- Koch, C., & Tsuchiya, N. (2007). Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Sciences*, 11, 16–22.
- Kuhl, P. K., Williams, K. A., Lacerda, F., Stevens, K. N., & Lindblom, B. (1992). Linguistic experience alters phonetic perception in infants by 6 months of age. *Science*, 255, 606–608.
- Lamme, V. A. F. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, 7, 12–18.
- Langton, S. R. H., Law, A. S., Burton, A. M., & Schweinberger, S. R. (2008). Attention capture by faces. *Cognition*, 107, 330–342.
- Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Neuroperception. Early visual experience and face processing. *Nature*, 410, 890.
- Lee, C., Rohrer, W. H., & Sparks, D. L. (1988). Population coding of saccadic eye movements by neurons in the superior colliculus. *Nature*, 332, 357–360.
- Lord, C., Risi, S., Lambrecht, L., Cook, E. H., Jr., Leventhal, B. L., DiLavore, P. C., et al. (2000). The autism diagnostic observation schedule-generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders*, 30, 205–223.
- Ludwig, G., & Hesselmann, G. (2015). Weighing the evidence for a dorsal processing bias under continuous flash suppression. *Consciousness and Cognition*, 35, 251–259.
- Mondloch, C. J., Lewis, T. L., Budreau, D. R., Maurer, D., Dannemiller, J. L., Stephens, B. R., et al. (1999). Face perception during early infancy. *Psychological Science*, 10, 419–422.
- Morton, J., & Johnson, M. H. (1991). CONSPEC and CONLERN: A two-process theory of infant face recognition. *Psychological Review*, 98, 164–181.
- Muir, D. W., Clifton, R. K., & Clarkson, M. G. (1989). The development of a human auditory localization response: A U-shaped function. *Canadian Journal of Psychology*, 43, 199–216.
- Nakano, T., & Nakatani, K. (2014). Cortical networks for face perception in two-month-old infants. *Proceedings of the Royal Society B: Biological Sciences*, 281. <http://dx.doi.org/10.1098/rspb.2014.1468>.
- Nguyen, M. N., Hori, E., Matsumoto, J., Tran, A. H., Ono, T., & Nishijo, H. (2013). Neuronal responses to face-like stimuli in the monkey pulvinar. *European Journal of Neuroscience*, 37, 35–51.
- Ozonoff, S., Iosif, A.-M., Baguio, F., Cook, I. C., Hill, M. M., Hutman, T., et al. (2010). A prospective study of the emergence of early behavioral signs of autism. *Journal of the American Academy of Child and Adolescent Psychiatry*, 49, 256–266e2.
- Pasley, B. N., Mayes, L. C., & Schultz, R. T. (2004). Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron*, 42, 163–172.
- Paus, T., Collins, D. L., Evans, A. C., Leonard, G., Pike, B., & Zijdenbos, A. (2001). Maturation of white matter in the human brain: A review of magnetic resonance studies. *Brain Research Bulletin*, 54, 255–266.
- Pelphrey, K. A., Shultz, S., Hudac, C. M., & Vander Wyk, B. C. (2011). Research review: Constraining heterogeneity: The social brain and its development in autism spectrum disorder. *Journal of Child Psychology and Psychiatry*, 52, 631–644.
- Rutter, M., Bailey, A., & Lord, C. (2003). *Social communication questionnaire*. Los Angeles, CA: Western Psychological Services.
- Schultz, R. T. (2005). Developmental deficits in social perception in autism: The role of the amygdala and fusiform face area. *International Journal of Developmental Neuroscience*, 23, 125–141.
- Shah, P., Gaule, A., Bird, G., & Cook, R. (2013). Robust orienting to protofacial stimuli in autism. *Current Biology*, 23, R1087–R1088.
- Shinagawa, F., Kobayashi, S., Fujita, K., & Maekawa, H. (1990). *Nihonban WAIS-R seijin chinou kensahou [Japanese Wechsler Adult Intelligence Scale - Revised]*. Tokyo: Nihon Bunka Kagakusha.
- Stein, T., End, A., & Sterzer, P. (2014). Own-race and own-age biases facilitate visual awareness of faces under interocular suppression. *Frontiers in Human Neuroscience*, 8, 582.
- Stein, T., Hebart, M. N., & Sterzer, P. (2011). Breaking continuous flash suppression: A new measure of unconscious processing during interocular suppression? *Frontiers in Human Neuroscience*, 5, 167.
- Stein, T., Peelen, M. V., & Sterzer, P. (2011). Adults' awareness of faces follows newborns' looking preferences. *PLoS One*, 6, e29361.
- Stein, T., Seymour, K., Hebart, M. N., & Sterzer, P. (2014). Rapid fear detection relies on high spatial frequencies. *Psychological Science*, 25, 566–574.
- Stein, T., & Sterzer, P. (2014). Unconscious processing under interocular suppression: Getting the right measure. *Frontiers in Psychology*, 5, 387.
- Stein, T., Sterzer, P., & Peelen, M. V. (2012). Privileged detection of conspecifics: Evidence from inversion effects during continuous flash suppression. *Cognition*, 125, 64–79.
- Sterzer, P., Haynes, J.-D., & Rees, G. (2008). Fine-scale activity patterns in high-level visual areas encode the category of invisible objects. *Journal of Vision*, 8(10), 1–12.
- Sterzer, P., Stein, T., Ludwig, K., Rothkirch, M., & Hesselmann, G. (2014). Neural processing of visual information under interocular suppression: A critical review. *Frontiers in Psychology*, 5, 453.
- Sylvers, P. D., Brennan, P. A., & Lilienfeld, S. O. (2011). Psychopathic traits and preattentive threat processing in children: A novel test of the fearlessness hypothesis. *Psychological Science*, 22, 1280–1287.
- Tomalski, P., Csibra, G., & Johnson, M. H. (2009). Rapid orienting toward face-like stimuli with gaze-relevant contrast information. *Perception*, 38, 569–578.
- Troiani, V., & Schultz, R. T. (2013). Amygdala, pulvinar, and inferior parietal cortex contribute to early processing of faces without awareness. *Frontiers in Human Neuroscience*, 7, 241.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, 8, 1096–1101.
- Tsuchiya, N., Koch, C., Gilroy, L. A., & Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *Journal of Vision*, 6, 1068–1078.
- Wechsler, D. (1981). *Wechsler adult intelligence scale - Revised*. San Antonio, TX: Psychological Corporation.
- Wechsler, D. (1992). *Wechsler intelligence scale for children (3rd ed.)*. London, UK: Psychological Corporation.
- Weigelt, S., Koldewyn, K., & Kanwisher, N. (2012). Face identity recognition in autism spectrum disorders: A review of behavioral studies. *Neuroscience and Biobehavioral Reviews*, 36, 1060–1084.
- Williams, M. A., Morris, A. P., McGlone, F., Abbott, D. F., & Mattingley, J. B. (2004). Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *Journal of Neuroscience*, 24, 2898–2904.
- Yang, E., & Blake, R. (2012). Deconstructing continuous flash suppression. *Journal of Vision*, 12, 8.
- Yang, E., Zald, D. H., & Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion*, 7, 882–886.
- Yuval-Greenberg, S., & Heeger, D. J. (2013). Continuous flash suppression modulates cortical activity in early visual cortex. *Journal of Neuroscience*, 33, 9635–9643.
- Zhou, G., Zhang, L., Liu, J., Yang, J., & Qu, Z. (2010). Specificity of face processing without awareness. *Consciousness and Cognition*, 19, 408–412.