



Reduced Pupil Oscillation During Facial Emotion Judgment in People with Autism Spectrum Disorder

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Abstract

People with autism spectrum disorder (ASD) show abnormal face perception and emotion recognition. However, it remains largely unknown whether these differences are associated with abnormal physiological responses when viewing faces. In this study, we employed a sensitive emotion judgment task and conducted a detailed investigation of pupil dilation/constriction and oscillation in high-functioning adult participants with ASD and matched controls. We found that participants with ASD showed normal pupil constriction to faces; however, they demonstrated reduced pupil oscillation, which was independent of stimulus properties and participants' perception of the emotion. Together, our results have revealed an abnormal physiological response to faces in people with ASD, which may in turn be associated with impaired face perception previously found in many studies.

Keywords Autism spectrum disorder · Pupil · Face Perception · Eye Tracking · Emotion · Ambiguity

Introduction

The majority of people with autism spectrum disorder (ASD) demonstrate deficits in recognizing emotions from facial expressions (Kennedy & Adolphs, 2012; Law Smith et al., 2010; Loth et al., 2018; Philip et al., 2010; Wallace et al., 2011). In particular, many studies have documented abnormal eye movement patterns when people with ASD view faces (Adolphs et al., 2001; Kliemann et al., 2010; Klin et al., 2002; Neumann et al., 2006; Pelphrey et al., 2002; Spezio et al., 2007a, 2007b), which may account for such impaired face perception or emotion recognition. For example, people with ASD tend to have reduced fixations on the eyes (Spezio et al., 2007b) but increased fixations on the mouth (Joseph & Tanaka, 2003; Neumann et al., 2006). When viewing photos of posed expressions of 6 basic emotions, control participants demonstrated a strategic viewing pattern targeting the eyes, nose, and mouth while adults with ASD had an erratic viewing pattern and looked less often than controls at the eyes, mouth and nose, but looked more often than controls at non-core feature areas (e.g., ear, chin, hairline) (Pelphrey et al., 2002). Additionally, adults with ASD demonstrate active avoidance of the eyes, which negatively influences emotion recognition (Kliemann et al., 2010). At the time of diagnosis, some studies have shown that 2-year olds with ASD are similar to controls when either

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directly or indirectly cued to look at the eyes (Moriuchi et al., 2017), but other studies have shown gaze differences in young children (see Dawson et al. (2005) for a review). The mixed findings in the literature are likely because individuals with ASD are actively trained to look at the eyes as part of their behavioral interventions.

Atypical functioning of the autonomic nervous system (ANS) may lead to altered arousal and atypical processing of emotional stimuli. Therefore, in this study, we explored whether atypical physiological response such as pupil dilation is associated with impaired emotion processing observed in people with ASD. While changes in pupil size are known to be modified by the amount of light in the environment, other factors such as visual attention and imagining changes in luminance (Hartmann & Fischer, 2014) as well as processing load and mental efforts (Beatty, 1982) have also been shown to alter pupil size. In healthy individuals, pupil dilation reflects the temporal dynamics of emotion recognition (Oliva & Anikin, 2018) as well as the level of uncertainty and surprise in the stimulus and outcome (de Berker et al., 2016). Pupil dilation has also been associated with face processing (Proulx et al., 2017). In those with ASD, it has been shown that children exhibit a larger baseline (tonic) pupil size compared to age-matched controls (Anderson & Colombo, 2009) but a decreased pupil size to human faces (Anderson et al., 2006). In adolescents with ASD, there is an altered pupil dilation during watching scenes of human interactions (Bast et al., 2019); and in children with ASD, there are linear associations between tonic pupil size and autism symptom severity (Anderson et al., 2013). In particular, adults with ASD demonstrate attenuated pupil response to static emotional faces (Gotham et al., 2018), suggesting an aberrant physiological reactivity during emotion processing. However, this literature is discrepant (see Arora et al. (2021), Lydon et al. (2016), and Nuske et al. (2013) for reviews). In a large sample of 152 children with ASD and 116 controls, the ASD group showed significantly longer pupillary light reflex latency, reduced relative constriction amplitude, and shorter constriction/redilation time than controls, suggesting abnormal functioning of the ANS (Daluwatte et al., 2013). Conversely, one study found that young children with ASD showed similarly dilated pupillary responses to real-world face stimuli, suggesting typical processing of faces (Nuske et al., 2015). Furthermore, a meta-analysis has shown that while only half the studies using pupillometry found group differences, all the ones that found group differences demonstrated evidence of hyperarousal (Arora et al., 2021). Notably, as pupil measures emotional arousal (Bradley et al., 2008), some studies (Anderson et al., 2006; Kuchinke et al., 2011) have revealed a group difference in pupil response during implicit emotional appraisal but not the others (Falck-Ytter, 2008; Wagner et al., 2013) (see Nuske et al., (2013) for a review).

We have previously shown that people with ASD have reduced specificity in emotion judgment, an impairment that is independent of eye movement (Wang & Adolphs, 2017a). Although eye movement patterns have been well explored in relation to impaired emotion processing, physiological / autonomic responses associated with impaired emotion processing has been significantly under-explored in ASD. Therefore, the present study further investigates physiological aspects of visual processing that may underlie differences seen in those with ASD when viewing faces expressing basic emotions. To investigate autonomic responses associated with impaired emotion processing in autism, we employed a sensitive facial emotion judgment task with well-controlled face stimuli. In particular, we focused on pupil dilation, constriction, and oscillation. Pupil dilation relies on a sympathetic circuit originating in the hypothalamus, then projecting to the superior cervical ganglion, after descending in the spinal cord and climbing along the internal carotid artery and the ophthalmic artery and ending in the pupillary dilator muscle (Kardon, 2005; Lamirel et al., 2018; Loewenfeld, 1999). Pupil dilation arises from both an excitation of the sympathetic nerve and a central inhibition of the parasympathetic pathway; and the labile, dynamic equilibrium of sympathetic and parasympathetic innervation in the pupil light reflex pathway may underlie pupil oscillation (Kardon, 2005; Longtin & Milton, 1989). In this study, we investigated whether adults with ASD showed abnormal changes in pupil size in general and whether pupil dilation, constriction, and oscillation were modulated by the face stimuli or behavioral responses (judging whether the face was happy or fearful as well as confidence ratings of their own judgments).

Methods

Participants

We recruited 18 high-functioning participants with ASD (15 male; ASD diagnosis confirmed by both the DSM-V/ ICD-10 and the Autism Diagnostic Observation Schedule-2 [ADOS-2]) and 15 matched controls (Table 1). The behavioral and eye movement data have been described in detail in a previous study (Wang & Adolphs, 2017a). Participants provided written informed consent and were paid for their time according to protocols approved by the Institutional Review Board of the California Institute of Technology. All participants had self-reported normal or corrected-to-normal visual acuity.

Stimuli and Task

Participants provided trial-by-trial judgments of two emotions (fear and happiness). The anchor faces (100% fear or

Table 1 Demographic data

	ASD (<i>n</i> = 18)	Controls (<i>n</i> = 15)	<i>t</i> -test (<i>p</i>)
Age (years)	30.8 ± 7.40	35.1 ± 11.4	0.20
WASI-II FSIQ	105 ± 13.3	107 ± 8.69	0.74
AQ	29.3 ± 8.28	17.7 ± 4.29	4.62 × 10 ⁻⁵
SRS-A-SR	84.6 ± 21.5	51.0 ± 30.3	0.0039
Benton Score	46.1 ± 3.89	n.a	n.a
ADOS-2 CSS SA	8.00 ± 1.71	n.a	n.a
ADOS-2 CSS RRB	7.13 ± 1.36	n.a	n.a
ADOS-2 CSS CSS SA&RRB	7.88 ± 1.54	n.a	n.a

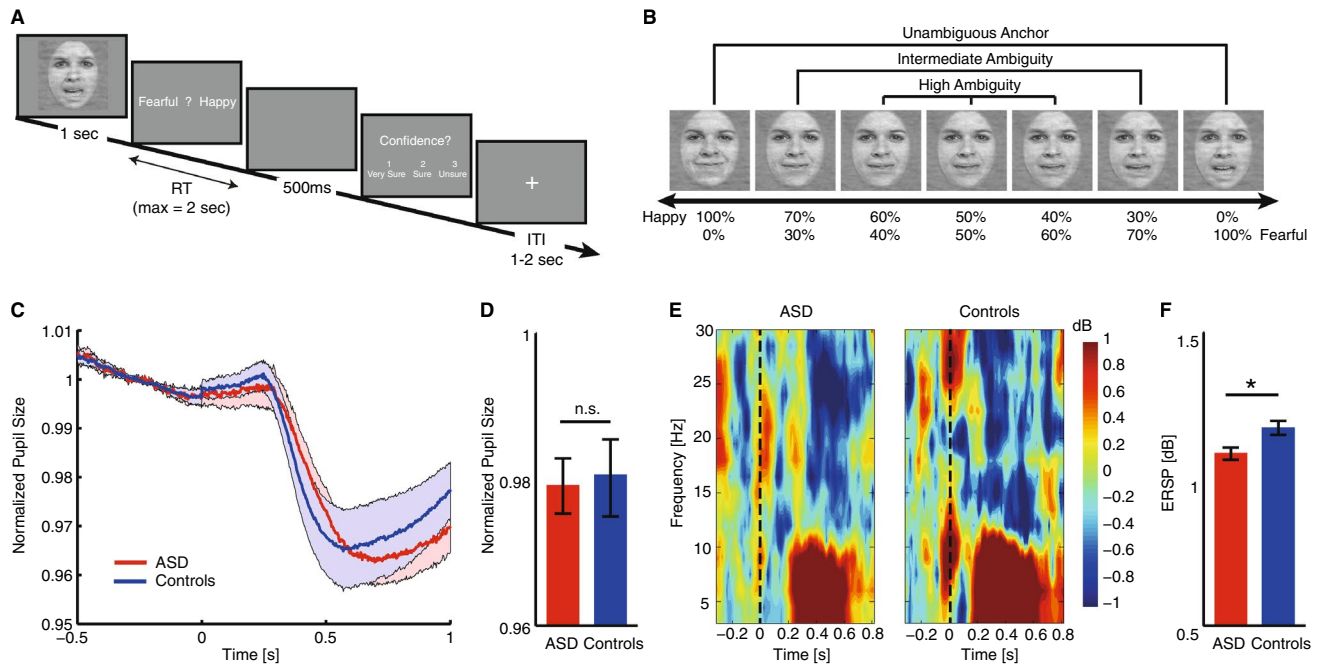


Fig. 1 Task, sample stimuli, and pupil response. **A** Task. A face was presented for 1 s followed by a question asking participants to identify the facial emotion (fearful or happy) within 2 s. After a blank screen was presented for 500 ms, a subset of 11 participants from each group indicated their confidence in their decision ('1' for 'very sure', '2' for 'sure', or '3' for 'unsure'). **B** Sample stimuli of one female identity ranging from 0% fear/100% happy to 100% fear/0% happy. **C** Normalized pupil size for all trials. Shaded areas

denote $\pm$ SEM across participants for each group (red: ASD; blue: controls). **D** Mean normalized pupil size averaged in the time interval 0 ms to 1000 ms after stimulus onset. Error bars denote $\pm$ SEM across participants. **E** Time–frequency plots depicting the power of pupil oscillations for each group of participants. Black dashed line denotes stimulus onset (Time=0). **F** Mean power of pupil oscillation in the 3 Hz to 12 Hz frequency range between 200 to 600 ms after stimulus onset. Error bars denote $\pm$ SEM across participants

100% happy) were from four people (2 female) and had clear expressions of fear or happiness (Roy et al., 2007). We further created a gradient of morphed faces based on the anchor faces (Fig. 1; see Wang et al. (2017) for details). We grouped the two highest fearful levels (100% and 70% fearful) as most fearful (least happy), the middle three fearful levels (60%, 50%, and 40% fearful) as intermediate fearful, and the last two fearful levels (30% and 0% fearful) as the least fearful (most happy). Moreover, we grouped the faces into three ambiguity levels: Unambiguous (100% fearful or 100% happy), Intermediate Ambiguity (70% / 30% morphs), and High Ambiguity (60% / 40% morphs and a 50% / 50%

morph). Importantly, to analyze pupil response, we equalized low-level image properties (luminance and contrast) using the MATLAB SHINE toolbox (Willenbockel et al., 2010).

In each trial, a face was shown for 1 s and then participants made their best guess using a keyboard regarding the facial emotion expressed (fearful or happy) (Fig. 1A; maximum reaction time allowed = 2 s). Participants were not provided with any feedback regarding their selection of perceived emotion expressed in the face stimuli. A central fixation cross was presented for 1 to 2 s during the inter-trial-interval (ITI). There were 36 trials for each of the 7

emotion morph levels constituting a total of 252 trials in 3 consecutive blocks for each participant (Fig. 1B). The trial order was completely randomized within each block and trials were pooled across blocks for analysis. Before the experiment began, each participant practiced 5 trials to make sure they understood the directions and to familiarize them with the task. Stimuli ($11.9^\circ \times 11.9^\circ$ visual angle) were presented at a 60 Hz refresh rate using MATLAB's Psychtoolbox 3 (Brainard, 1997) (<http://psychtoolbox.org>).

Confidence ratings were also provided by a subset of the participants (11 participants from each group) after emotion judgment and following a 500 ms blank screen (Fig. 1A). Participants were instructed to indicate their confidence level in their emotion judgment via button press within 2 s after the face image disappeared to indicate either '1' for 'very sure', '2' for 'sure' or '3' for 'unsure'.

Eye Tracking and Apparatus

Participants sat in a testing room with stable and constant lighting condition throughout the experiment. The lighting condition was also consistent across all participants. Binocular gaze (300 Hz) was recorded for all participants using a non-invasive infrared remote Tobii X300 system which enables recording of eye movements and pupil size as well as detection of visual fixations (sliding window averaging method; velocity threshold = 35 pixels/sample). The valid recording duration per trial (and thus eye movement recording quality) was comparable between groups (ASD: 947 ± 27.8 ms, controls: 959 ± 32.5 ms; $t(31) = 1.10$, $P = 0.28$). It is worth noting that although there may be systematic errors of pupil size estimation using the Tobii eye tracker (Brisson et al., 2013), similar fixation patterns across stimulus levels (Wang & Adolphs, 2017a; Wang, 2018) would minimize the influence of gaze directions on our results. We excluded all trials where only one eye was tracked, which indicated head turning that could introduce error from ambient light exposure. Blinks were detected by Tobii Studio and were labeled as missing data, so we excluded all blinks from analysis.

Data Analysis

We first computed the mean waveform of pupil size for each condition within each participant. All waveforms were time-locked to the stimulus onset. We then computed the group mean waveforms for each condition by averaging across participants.

To calculate the time–frequency spectrum for each trial, we employed a Morlet wavelet transform (MWT) where the cycle number increased with frequency linearly (Fuentemilla et al., 2006) (see Sun, Yu, et al. (2017), Sun, Zhen, et al. (2017)) for details). Briefly, we generated 200 time points

for each epoch and estimated 19 linearly spaced frequencies from 3.0 Hz to 30.0 Hz for each trial. The spectrum was log-transformed (in Decibel [dB]) and a common mean baseline spectrum (starting from -315 ms to -115 ms relative to stimulus onset) for all conditions was subtracted to derive the baseline-normalized event related spectral perturbation (ERSP). ERSPs were subsequently averaged for each condition, in the time window from -315 ms to 815 ms relative to stimulus onset. The mean activity was assessed between 200 and 600 ms in the 3–12 Hz frequency range.

Results

Normal Pupil Constriction but Reduced Pupil Oscillation in ASD

With the present data, we previously showed that people with ASD demonstrate reduced specificity in emotion judgment, an impairment that is independent of eye movement (Wang & Adolphs, 2017a). In the present study, we further investigated whether people with ASD demonstrated abnormal pupil response to faces with emotional expressions.

We first showed that pupils constricted as a response to faces for both groups (Fig. 1C), and the magnitude of pupil constriction was similar between participants with ASD and controls (Fig. 1D; mean constriction in the time interval 0 ms to 1000 ms after stimulus onset: two-tailed two-sample t -test: $t(31) = 0.051$, $P = 0.96$, Cohen's $d = 0.009$; similar results were derived using different time intervals for analysis), suggesting that people with ASD had a normal pupil constriction in response to face stimuli. In addition to pupil constriction, we found that pupil dilation (in a time window 200 to 300 ms after stimulus onset) did not differ between groups either ($t(31) = 0.78$, $d = 0.14$). However, notably, we found that compared with controls, participants with ASD had a reduced power of oscillation in the 3 Hz to 12 Hz frequency range in a time window 200 ms to 600 ms after stimulus onset (Fig. 1E, F; two-tailed two-sample t -test: $t(31) = 2.63$, $P = 0.013$, $d = 0.47$). Similar results were derived if we removed trials that participants did not subsequently respond with a button press for emotion judgment ($P < 0.01$). We next explored whether any stimulus properties or behavioral responses would modulate pupil response.

Pupil Response as a Function of Emotion Content

For both participants with ASD and controls, their judgment of fear increased as a function of fearfulness shown in the morphed face (Fig. 2A, B; mixed-measures ANOVA: ASD: $F(6,102) = 304.8$, $P < 0.001$, $\eta_p^2 = 0.95$; controls: $F(6,84) = 251.6$, $P < 0.001$, $\eta_p^2 = 0.95$), showing that both groups could track the gradual change in

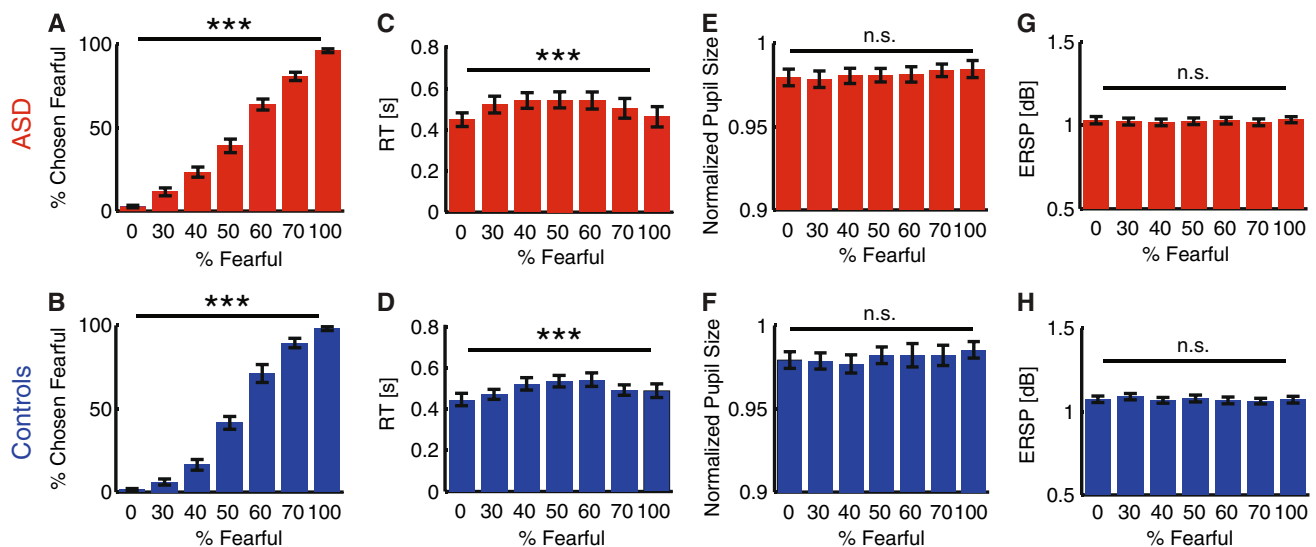


Fig. 2 Pupil constriction and oscillation as a function of stimulus levels. **A, C, E, G** Participants with ASD. **B, D, F, H** Controls. **A, B** The proportion of trials judged as fearful as a function of morph levels (ranging from 0% fearful [100% happy] on the left to 100% fearful [0% happy] on the right). **C, D** The reaction time (RT; relative to stimulus offset) for the fear/happy decision, which can be considered as an implicit measure of confidence in their judgments. **E, F** Mean

normalized pupil size averaged in the time interval 0 ms to 1000 ms after stimulus onset. **G, H** Mean power of pupil oscillation in the 3 Hz to 12 Hz frequency range between 200 to 600 ms after stimulus onset. Error bars denote $\pm$ SEM across participants. Asterisks indicate a significant difference between stimulus levels within each group using a one-way repeated-measures ANOVA: *** $P < 0.001$. n.s.: not significant

emotions (our desired behavioral effects). Furthermore, we found that for both participants with ASD and controls, reaction time (RT) varied as a function of stimulus levels, with more ambiguous expressions of emotion (40%, 50%, and 60% fearful) being judged more slowly than less ambiguous expressions of emotion (e.g., 0% and 100% fearful) (Fig. 2C, D; ASD: $F(6,102) = 6.99$, $P < 0.001$, $\eta_p^2 = 0.29$; controls: $F(6,84) = 4.98$, $P < 0.001$, $\eta_p^2 = 0.26$). However, we found that for both participants with ASD and controls, neither pupil constriction (Fig. 2E, F; ASD: $F(6,102) = 0.64$, $P = 0.70$, $\eta_p^2 = 0.036$; controls: $F(6,84) = 1.54$, $P = 0.17$, $\eta_p^2 = 0.099$) nor pupil oscillation (Fig. 2G, H; ASD: $F(6,102) = 0.48$, $P = 0.82$, $\eta_p^2 = 0.028$; controls: $F(6,84) = 1.04$, $P = 0.40$, $\eta_p^2 = 0.069$) differed between stimulus levels, suggesting that pupil response was not modulated by emotional content of the face stimuli. We further confirmed the group difference in pupil oscillation using a two-way repeated-measures ANOVA (main effect of participant group: $F(1,186) = 3.35$, $P = 0.069$).

Pupil Response as a Function of Face Stimuli Emotion Ambiguity Level

We next explored whether pupil response was modulated by the level of ambiguity of the emotion expressed. As expected, both participants with ASD and controls showed a longer RT for more ambiguous facial expressions (Fig. 3A, B; mixed-measures ANOVA: ASD: $F(2,34) = 21.7$,

$P < 0.001$, $\eta_p^2 = 0.56$; controls: $F(2,28) = 8.85$, $P = 0.001$, $\eta_p^2 = 0.39$). We also found that pupil constriction did not differ between ambiguity levels for both participants with ASD and controls (Fig. 3C-F; ASD: $F(2,34) = 0.088$, $P = 0.92$, $\eta_p^2 = 0.005$; controls: $F(2,28) = 0.53$, $P = 0.60$, $\eta_p^2 = 0.036$), nor did pupil oscillation (Fig. 3G-J; ASD: $F(2,34) = 2.35$, $P = 0.11$, $\eta_p^2 = 0.12$; controls: $F(2,28) = 1.58$, $P = 0.22$, $\eta_p^2 = 0.10$), suggesting that pupil response was not modulated by emotional ambiguity of the face stimuli. We further confirmed the group difference in pupil oscillation using a two-way repeated-measures ANOVA (main effect of participant group: $F(1,62) = 5.47$, $P = 0.023$).

Pupil Response as a Function of Behavioral Judgment of Facial Emotions

Lastly, we explored whether pupil response differed between behavioral judgments. Controls but not participants with ASD showed a significantly different RT between fearful vs. happy judgments (Fig. 4A, B; two-tailed paired t -test: ASD: $t(17) = 0.83$, $P = 0.42$, $d = 0.20$; controls: $t(14) = 3.70$, $P = 0.002$, $d = 0.99$). However, we found that for both groups, neither pupil size (Fig. 4C-F; ASD: $t(17) = 1.11$, $P = 0.282$, $d = 0.269$; controls: $t(14) = 0.54$, $P = 0.60$, $d = 0.14$) nor pupil oscillation (Fig. 4G-J; ASD: $t(17) = 1.108$, $P = 0.283$, $d = 0.268$; controls: $t(14) = 0.003$, $P = 0.998$, $d = 8.01 \times 10^{-4}$) differed between behavioral judgments of the emotion expressed, suggesting that pupil response was not modulated

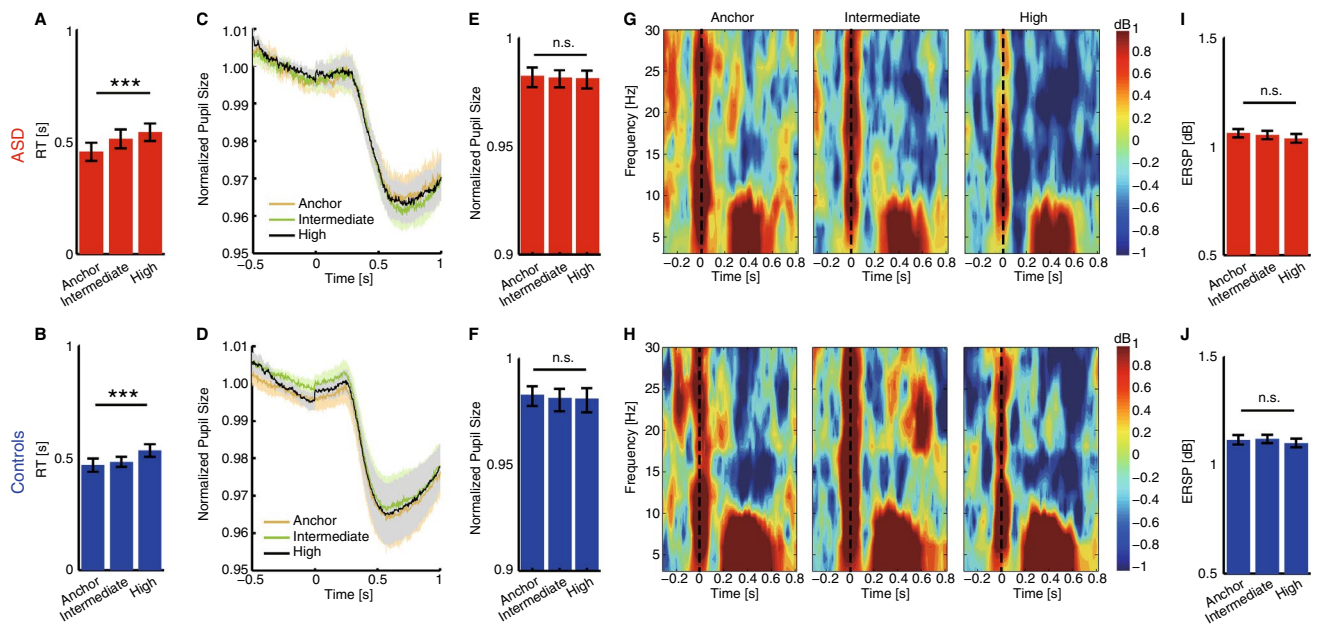


Fig. 3 Pupil constriction and oscillation as a function of emotion ambiguity levels. **A, C, E, G, I** Participants with ASD. **B, D, F, H, J** Controls. **A, B** The reaction time (RT; relative to stimulus offset) for the fear/happy decision. **C, D** Normalized pupil size for each ambiguity level. Shaded area denotes $\pm$ SEM across participants. **E, F** Mean normalized pupil size averaged in the time interval 0 ms to 1000 ms after stimulus onset. **G, H** Time–frequency plots depicting the power

of pupil oscillations for each ambiguity level. **I, J** Mean power of pupil oscillation in the 3 Hz to 12 Hz frequency range between 200 to 600 ms after stimulus onset. Error bars denote $\pm$ SEM across participants. Asterisks indicate a significant difference between ambiguity levels within each group using a one-way repeated-measures ANOVA: *** $P < 0.001$. n.s.: not significant

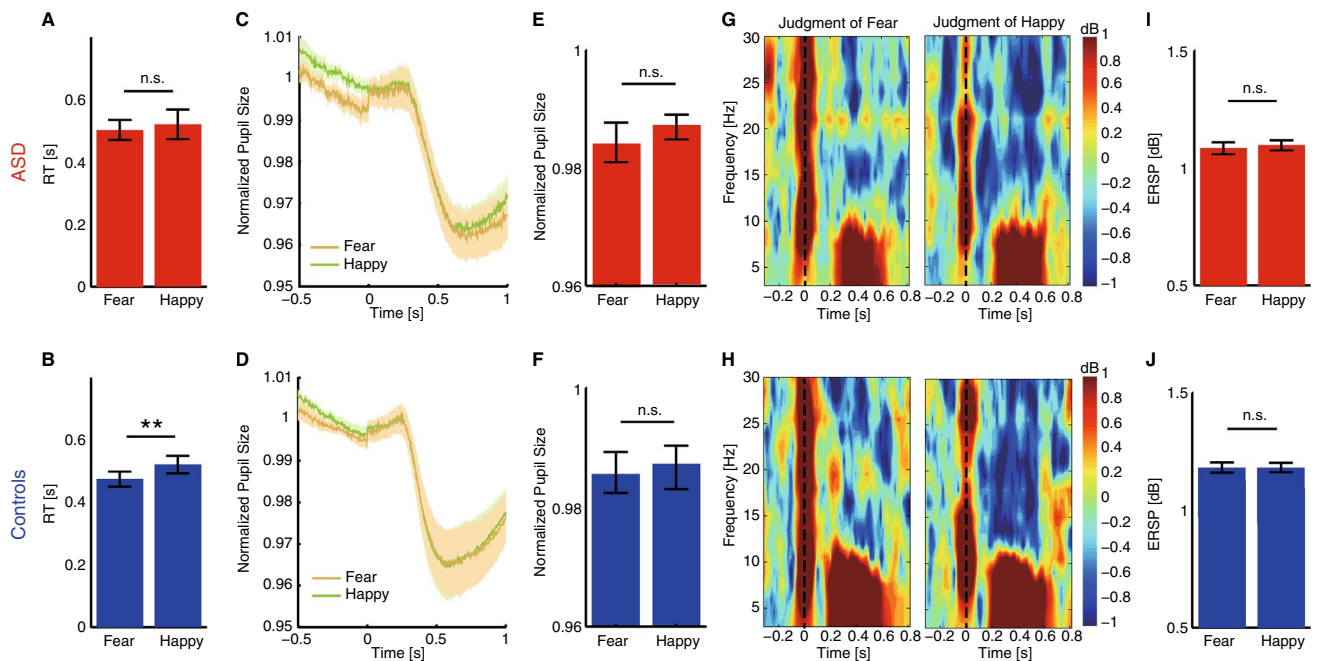


Fig. 4 Pupil constriction and oscillation as a function of behavioral judgment. **A, C, E, G, I** Participants with ASD. **B, D, F, H, J** Controls. **A, B** The reaction time (RT; relative to stimulus offset) for the fear/happy judgment. **C, D** Normalized pupil size for each behavioral judgment. Shaded area denotes $\pm$ SEM across participants. **E, F** Mean normalized pupil size averaged in the time interval 0 ms to 1000 ms after stimulus onset. **G, H** Time–frequency plots depicting the power

of pupil oscillations for each behavioral judgment. **I, J** Mean power of pupil oscillation in the 3 Hz to 12 Hz frequency range between 200 to 600 ms after stimulus onset. Error bars denote $\pm$ SEM across participants. Asterisks indicate a significant difference between behavioral judgments within the groups using two-tailed paired t -test: ** $P < 0.01$. n.s.: not significant

by behavioral judgments. We further confirmed the group difference in pupil oscillation using a two-way repeated-measures ANOVA (main effect of participant group: $F(1,31)=8.12$, $P=0.0077$).

Discussion

In this study, we investigated a physiological response (changes in pupil size) when viewing static images of faces with expressions of fear or happiness. Participants with ASD and controls indicated which emotion was being presented while undergoing eye tracking. Our data showed that pupil oscillation was reduced in people with ASD compared to controls. However, neither pupil constriction nor oscillation was modulated by stimulus properties or behavioral response.

Possible Caveats

In our task, we did not include a scrambled image/control image of matched luminance, therefore, the response to the face involved pupillary light reflex. However, all of our stimuli were equated in luminance and our comparison was across stimuli (rather than to baseline). Therefore, even if our analysis involved light reflex response, such response was equal across our stimuli and thus did not affect our conclusions. Furthermore, the pupil constriction following stimulus onset (e.g., from 0 to 500 ms after stimulus onset; Fig. 1C) may involve not only pupillary light reflex but also multiple cognitive processes such as attention, emotion processing, and ambiguity processing, given the face processing stages (Duchaine & Yovel, 2015; Latinus & Taylor, 2006); a future study using luminance-equated preceding control stimuli is thus needed to dissociate light reflex and cognitive processes.

It is worth noting that we observed pupil oscillation in a cognitive task (i.e., emotion judgment of faces) without using frequency tagging (Naber et al., 2013); and there are other forms of pupil oscillation (see Kardon et al. (2005) for a review). For example, irregular variations in pupil area (i.e., hippus or physiologic pupillary unrest) occur spontaneously, whereas regular pupil oscillations (i.e., pupil cycling) can be induced by focusing a small light beam at the pupillary margin (Longtin & Milton, 1989). Furthermore, distinct from physiologic pupillary unrest, other spontaneous pupil oscillations like sleepiness-related fluctuations in the dark (sleepiness waves) can occur during decreased central nervous activation (Lowenstein et al., 1963; Warga et al., 2009). Therefore, a future study is needed to systemically investigate different forms of pupil oscillation in ASD.

In contrast to previous studies showing that emotional valence modulates evoked pupil responses (Bradley et al., 2008; Nuske et al., 2014), in this study, we found that pupillary response (both pupil size and oscillation) did not vary as a function of emotional content, likely because we used morphed faces and we did not include emotionally neutral faces (note that all morphed faces had an emotional content, and 50% fear/50% happy faces should not be considered as emotionally neutral; also note that our task did not ask participants to judge whether the face had an emotion [i.e., emotional vs. neutral] but the emotional content of the face [i.e., fearful vs. happy]). Our present result is consistent with a study showing no modulation of pupil size by facial emotional stimuli (Wang et al., 2018); and our present findings need to be contextualized.

Lastly, it is worth noting that our present results could only speak to high-functioning adults with ASD. A future study will thus need to take development trajectory as well as cognitive ability into consideration. Furthermore, it has been argued that emotion-processing impairments may not be universal in ASD and emotion-processing impairments may not be specific to ASD (Nuske et al., 2013). Notably, it has been suggested that individuals with ASD have fewer abnormalities in neural and autonomic responding during explicit emotion tasks (e.g., emotion labelling) compared to implicit emotion tasks (e.g., gender labelling of emotional facial expressions), which is likely because implicit processing of emotion is more difficult (Nuske et al., 2014). This also indicates that cognitive ability may influence emotion processing. Together, comparing our findings with studies measuring pupillary reactivity to emotions in cognitive delayed children will not only reveal the specificity of this physiological deficit but also shed light on the role of cognitive ability in emotion processing.

Pupil Response and ASD

Prior studies have shown that ASD symptoms such as altered states of arousal and aberrant processing of stimuli may be the result of atypical functioning of the ANS (Daluwatte et al., 2013). One study showed that in the absence of any task demands, children with ASD exhibit a larger baseline (tonic) pupil size compared to age-matched controls (Anderson & Colombo, 2009). When undergoing cognitive testing, young children with ASD show decreased pupil size to human faces, whereas age-matched controls conversely show an increase in pupil size, which was especially true when looking at the internal region of the faces (eyes, nose, and mouth) (Anderson et al., 2006). Conversely, when viewing a hand gesture (pointing) thought to have social communicative value, participants with ASD show increased pupil size compared to controls, which is thought to reflect greater emotional arousal (Aldaqr et al., 2016). In 2-year-olds with

ASD, task-evoked, phasic pupil responses, a sensitive and involuntary measure of mental effort, are associated with better performance in a visual search task (Blaser et al., 2014). Interestingly, when healthy adults view a bistable-rotating cylinder, pupil diameter oscillate in phase with the ambiguous perception and the magnitude of oscillation is correlated with autistic traits (Turi et al., 2018), consistent with deficits in global and holistic perception in ASD, as described by a key theory of autism, weak central coherence (Happé & Frith, 2006). Together, pupillometry has been shown to effectively index physiological and cognitive differences in autism when processing socially relevant and non-social stimuli.

Reduced Pupil Oscillation May Result from Reduced Saliency for Faces

Although using this task and set of stimuli we show in a prior report that the reduced specificity of emotion judgment in participants with ASD could not be attributed to gross differences in eye movements (Wang & Adolphs, 2017a), we found in the present study a difference in pupil oscillation, suggesting that the impaired emotion processing may arise from central cognitive processing differences. The pupil response reflects cognitive processes and tracks visual attention allocation (Hartmann & Fischer, 2014). Using frequency tagging, luminance-induced pupil oscillations can track allocation of visual attention (Naber et al., 2013). Although without using frequency tagging, we observed stimulus-evoked pupil oscillation, which was reduced in participants with ASD. This might be because the relative saliency of facial features (i.e., eyes vs. mouth) (Kliemann et al., 2010; Neumann et al., 2006; Pelphrey et al., 2002; Spezio et al., 2007b) or the relative saliency of faces as a whole (i.e., faces vs. objects) (Wang et al., 2015) is altered in autism. Reduced attention to faces may lead to noisier face and emotion processing and therefore, the reduced specificity of emotion judgment (Wang & Adolphs, 2017a) as well as the associated deficits in pupil oscillation as observed in the present study may be due to the decreased saliency of faces in general to people with ASD.

Physiologically, pupil response is an important index of ANS functions. Pupil dilation/constriction reflects a balance between the sympathetic and parasympathetic systems (Kardon, 2005) and is mediated by the locus coeruleus-nor-epinephrine (LC-NE) system, which is outlined as a pace-maker of attentional function (see Bast et al. (2019) for a review). Therefore, the weaker pupil oscillation in people with ASD observed in this study may indicate an aberrant attentional function, consistent with the general social attentional deficits in ASD (Wang & Adolphs, 2017b). In line with our present results, atypical LC-NE activity has been proposed as an underlying mechanism of aberrant attentional

function, which may manifest as (i) increased tonic activity with reduced phasic reactivity to exogenous stimuli, (ii) attenuated bottom-up signaling mitigating saliency and predictive reward attribution during phasic alerting, and (iii) reduced activation of the ventral frontoparietal attention system attenuating orienting to exogenous stimuli (Bast et al., 2019). Together, atypical LC-NE activity, and thus LC-NE mediated pupil oscillation, may be a mechanism leading to reduced social attention in ASD.

Pupil Dilation and Decision Making

In this study, we found that pupil response (pupil constriction or oscillation) was not related to decision speed, likely because our task was not a speeded task. In our previous studies using the identical task and stimuli, we found a neural signature originating from the cingulate cortex, the late positive potential (LPP), that encodes perceptual judgment decisions (including emotion judgment decisions) rather than stimulus representations (Sun, Yu, et al., 2017; Sun, Zhen, et al., 2017). Pupil dilation reflects increased mental effort (Beatty, 1982), which is in turn encoded by the cingulate cortex (Alexander & Brown, 2010; Cole et al., 2009; Shackman et al., 2011; Shenhav et al., 2013; Sheth et al., 2012). Therefore, the cingulate cortex may serve as a common neural substrate for both pupil dilation and the LPP under perceptual decision making. This hypothesis is strongly supported by direct recordings from the primate anterior cingulate cortex (ACC) (Joshi et al., 2016), as well as the connectivity between the ACC and the brainstem nucleus locus coeruleus (LC) (Aston-Jones & Cohen, 2005) (note that there is a close direct relationship between pupil diameter and LC tonic activity in the monkey and monkey LC receives prominent, direct inputs from the ACC). Furthermore, it has been shown that pupil dilation alone can predict the timing of decisions and this prediction of timing is distinct from a general arousal or reward-anticipation response (Einhauser et al., 2010). Using a perceptual choice task with dynamic random dots, pupil dilation reflects decision uncertainty and alters serial choice bias (Urai et al., 2017). A future study with a speeded task will be needed to elucidate the relationship between pupil dilation and emotion judgment decisions.

Emotion Processing in Autism

Many individuals with ASD have significant difficulty explaining their own emotions and recognizing or labeling emotions expressed by others. However, results of research investigating emotion recognition in ASD are mixed, with some studies showing deficits in this area (Kennedy & Adolphs, 2012; Law Smith et al., 2010; Philip et al., 2010; Wallace et al., 2011), while outcomes from other studies

have not found significant group differences (Adolphs et al., 2001; Baron-Cohen et al., 1997; Neumann et al., 2006). ASD is a heterogeneous disorder (Happé et al., 2006), which may contribute to these mixed findings. However, the variety of stimuli and tasks used in studies examining facial emotion recognition in ASD may also have contributed to the different outcomes in the published literature. It is expected that behavioral and biological measures with high sensitivity used in facial emotion recognition research can capture group differences (Harms et al., 2010). Additionally, increasing the task demands by using difficult or unfamiliar tasks and manipulating the face stimuli (e.g., morphing the expressions of emotion) can improve task sensitivity (Law Smith et al., 2010; Wallace et al., 2011). In the present study, we parametrically controlled the intensity of the emotions expressed in the face stimuli in order to evaluate emotion recognition in those with ASD at a more fine-grained level. We previously used this task stimuli in an eye-tracking study investigating emotion recognition (fear and happiness) in adults with ASD and found reduced specificity in emotion judgment compared to controls across the range of emotion intensity morphs (Wang & Adolphs, 2017a).

It is worth noting that our findings did not map onto the perception of emotion, suggesting that pupil oscillation was a correlate of implicit rather than explicit emotion processing in autism (see Lane (2000) for a review of implicit vs. explicit emotion processing). Consistent with our result, it has been shown that pupil size could match arousal levels (indexed by heart rate and skin conductance) only before face presentation (i.e., stimulus onset) but not during explicit emotion judgment (Wang et al., 2018). People with ASD have demonstrated difficulties for both implicit and explicit emotion processing (Kana et al., 2016; Lozier et al., 2014; Senju, 2013), which may be attributed to the dysfunction of the cerebellum (Siciliano & Clausi, 2020) or abnormal cerebral effective connectivity (Wicker et al., 2008). In particular, a comprehensive survey of the neural correlates of explicit vs. implicit facial emotion processing in ASD has shown disruptions in early visual processing and top-down attentional processes in ASD (Luckhardt et al., 2017).

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Declarations

Conflict of interest The authors declare no conflict of interest.

References

- Adolphs, R., Sears, L., & Piven, J. (2001). Abnormal processing of social information from faces in Autism. *Journal of Cognitive Neuroscience*, 13, 232–240.
- Aldagre, I., Schuwerk, T., Daum, M. M., Sodian, B., & Paulus, M. (2016). Sensitivity to communicative and non-communicative gestures in adolescents and adults with autism spectrum disorder: Saccadic and pupillary responses. *Experimental Brain Research*, 234, 2515–2527.
- Alexander, W. H., & Brown, J. W. (2010). Computational models of performance monitoring and cognitive control. *Topics in Cognitive Science*, 2, 658–677.
- Anderson, C. J., & Colombo, J. (2009). Larger tonic pupil size in young children with autism spectrum disorder. *Developmental Psychobiology*, 51, 207–211.
- Anderson, C. J., Colombo, J., & Jill, S. D. (2006). Visual scanning and pupillary responses in young children with autism spectrum disorder. *Journal of Clinical and Experimental Neuropsychology*, 28, 1238–1256.
- Anderson, C. J., Colombo, J., & Unruh, K. E. (2013). Pupil and salivary indicators of autonomic dysfunction in autism spectrum disorder. *Developmental Psychobiology*, 55, 465–482.
- Arora, I., Bellato, A., Ropar, D., Hollis, C., & Groom, M. J. (2021). Is autonomic function during resting-state atypical in Autism: A systematic review of evidence. *Neuroscience & Biobehavioral Reviews*, 125, 417–441.
- Aston-Jones, G., & Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive Gain and Optimal Performance. *Annual Review of Neuroscience*, 28, 403–450.
- Baron-Cohen, S., Jolliffe, T., Mortimore, C., & Robertson, M. (1997). Another advanced test of theory of mind: evidence from very high functioning adults with autism or asperger syndrome. *Journal of Child Psychology and Psychiatry*, 38, 813–822.
- Bast, N., Banaschewski, T., Dziobek, I., Brandeis, D., Poustka, L., & Freitag, C. M. (2019). Pupil dilation progression modulates aberrant social cognition in autism spectrum disorder. *Autism Research*, 12, 1680–1692.
- Beatty, J. (1982). Task-evoked pupillary responses, processing load, and the structure of processing resources. *Psychological Bulletin*, 91, 276–292.
- Blaser, E., Eglington, L., Carter, A. S., & Kaldy, Z. (2014). Pupilometry reveals a mechanism for the autism spectrum disorder (ASD) advantage in visual tasks. *Scientific Reports*, 4, 4301.
- Bradley, M. M., Miccoli, L., Escrig, M. A., & Lang, P. J. (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*, 45, 602–607.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436.
- Brisson, J., Mainville, M., Mailloux, D., Beaulieu, C., Serres, J., & Sirois, S. (2013). Pupil diameter measurement errors as a function of gaze direction in corneal reflection eyetrackers. *Behavior Research Methods*, 45, 1322–1331.
- Cole, M. W., Yeung, N., Freiwald, W. A., & Botvinick, M. (2009). Cingulate cortex: Diverging data from humans and monkeys. *Trends in Neurosciences*, 32, 566–574.
- Daluwatte, C., Miles, J. H., Christ, S. E., Beversdorf, D. Q., Takahashi, T. N., & Yao, G. (2013). Atypical pupillary light reflex and heart rate variability in children with autism spectrum disorder. *Journal of Autism and Developmental Disorders*, 43, 1910–1925.
- Dawson, G., Webb, S. J., & McPartland, J. (2005). Understanding the nature of face processing impairment in autism: insights from

- behavioral and electrophysiological studies. *Developmental Neuropsychology*, 27, 403–424.
- de Berker, A. O., Rutledge, R. B., Mathys, C., Marshall, L., Cross, G. F., et al. (2016). Computations of uncertainty mediate acute stress responses in humans. *Nature Communications*, 7, 10996.
- Duchaine, B., & Yovel, G. (2015). A revised neural framework for face processing. *Annual Review of Vision Science*, 1, 393–416.
- Einhauser, W., Koch, C., & Carter, O. (2010). Pupil dilation betrays the timing of decisions. *Frontiers in Human Neuroscience*. <https://doi.org/10.3389/fnhum.2010.00018>
- Falck-Ytter, T. (2008). Face inversion effects in autism: A combined looking time and pupillometric study. *Autism Research*, 1, 297–306.
- Fuentemilla, L., Marco-Pallarés, J., & Grau, C. (2006). Modulation of spectral power and of phase resetting of EEG contributes differentially to the generation of auditory event-related potentials. *NeuroImage*, 30, 909–916.
- Gotham, K. O., Siegle, G. J., Han, G. T., Tomarken, A. J., Crist, R. N., et al. (2018). Pupil response to social-emotional material is associated with rumination and depressive symptoms in adults with autism spectrum disorder. *PLoS ONE*, 13, e0200340.
- Happe, F., Ronald, A., & Plomin, R. (2006). Time to give up on a single explanation for autism. *Nature Neuroscience*, 9, 1218–1220.
- Happé, F., & Frith, U. (2006). The weak coherence account: detail-focused cognitive style in autism spectrum disorders. *Journal of Autism and Developmental Disorders*, 36, 5–25.
- Harms, M., Martin, A., & Wallace, G. (2010). Facial emotion recognition in autism spectrum disorders: A review of behavioral and neuroimaging studies. *Neuropsychology Review*, 20, 290–322.
- Hartmann, M., & Fischer, M. H. (2014). Pupillometry: the eyes shed fresh light on the mind. *Current Biology*, 24, R281–R282.
- Joseph, R. M., & Tanaka, J. (2003). Holistic and part-based face recognition in children with autism. *Journal of Child Psychology and Psychiatry*, 44, 529–542.
- Joshi, S., Li, Y., Kalwani Rishi, M., & Gold, J. I. (2016). Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron*, 89, 221–234.
- Kana, R. K., Patriquin, M. A., Black, B. S., Channell, M. M., & Wicker, B. (2016). Altered medial frontal and superior temporal response to implicit processing of emotions in Autism. *Autism Research*, 9, 55–66.
- Kardon R. 2005. Anatomy and physiology of the autonomic nervous system. *Walsh and Hoyt's Clinical Neuro-Ophthalmology*: 649–714
- Kennedy, D. P., & Adolphs, R. (2012). Perception of emotions from facial expressions in high-functioning adults with autism. *Neuropsychologia*, 50, 3313–3319.
- Kliemann, D., Dziobek, I., Hatri, A., Steimke, R., & Heekeren, H. R. (2010). Atypical reflexive gaze patterns on emotional faces in autism spectrum disorders. *The Journal of Neuroscience*, 30, 12281–12287.
- Klin, A., Jones, W., Schultz, R., Volkmar, F., & Cohen, D. (2002). Visual fixation patterns during viewing of naturalistic social situations as predictors of social competence in individuals with autism. *Archives of General Psychiatry*, 59, 809–816.
- Kuchinke, L., Schneider, D., Kotz, S. A., & Jacobs, A. M. (2011). Spontaneous but not explicit processing of positive sentences impaired in Asperger's syndrome: Pupillometric evidence. *Neuropsychologia*, 49, 331–338.
- Lamirel, C., Ajasse, S., Moulignier, A., Salomon, L., Deschamps, R., et al. (2018). A novel method of inducing endogenous pupil oscillations to detect patients with unilateral optic neuritis. *PLoS ONE*, 13, e0203170.
- Lane RD. 2000. Neural correlates of conscious emotional experience. *Cognitive neuroscience of emotion*: 345–70
- Latinus, M., & Taylor, M. J. (2006). Face processing stages: Impact of difficulty and the separation of effects. *Brain Research*, 1123, 179–187.
- Law Smith, M. J., Montagne, B., Perrett, D. I., Gill, M., & Gallagher, L. (2010). Detecting subtle facial emotion recognition deficits in high-functioning Autism using dynamic stimuli of varying intensities. *Neuropsychologia*, 48, 2777–2781.
- Loewenfeld, I. (1999). *The pupil: Anatomy, physiology, and clinical applications*. Butterworth-Heinemann.
- Longtin, A., & Milton, J. G. (1989). Modelling autonomous oscillations in the human pupil light reflex using non-linear delay-differential equations. *Bulletin of Mathematical Biology*, 51, 605–624.
- Loth, E., Garrido, L., Ahmad, J., Watson, E., Duff, A., & Duchaine, B. (2018). Facial expression recognition as a candidate marker for autism spectrum disorder: How frequent and severe are deficits? *Molecular Autism*, 9, 7.
- Lowenstein O, Feinberg R, Loewenfeld IE. 1963. Pupillary movements during acute and chronic fatigue: A new test for the objective evaluation of tiredness. Federal Aviation Agency, Office of Aviation Medicine.
- Lozier, L. M., Vanmeter, J. W., & Marsh, A. A. (2014). Impairments in facial affect recognition associated with autism spectrum disorders: A meta-analysis. *Development and Psychopathology*, 26, 933–945.
- Luckhardt, C., Kröger, A., Cholemkery, H., Bender, S., & Freitag, C. M. (2017). Neural Correlates of Explicit Versus Implicit Facial Emotion Processing in ASD. *Journal of Autism and Developmental Disorders*, 47, 1944–1955.
- Lydon, S., Healy, O., Reed, P., Mulhern, T., Hughes, B. M., & Goodwin, M. S. (2016). A systematic review of physiological reactivity to stimuli in autism. *Developmental Neurorehabilitation*, 19, 335–355.
- Moriuchi, J. M., Klin, A., & Jones, W. (2017). Mechanisms of diminished attention to eyes in autism. *American Journal of Psychiatry*, 174, 26–35.
- Naber, M., Alvarez, G., & Nakayama, K. (2013). Tracking the allocation of attention using human pupillary oscillations. *Frontiers in Psychology*. <https://doi.org/10.3389/fpsyg.2013.00919>
- Neumann, D., Spezio, M. L., Piven, J., & Adolphs, R. (2006). Looking you in the mouth: Abnormal gaze in autism resulting from impaired top-down modulation of visual attention. *Social Cognitive and Affective Neuroscience*, 1, 194–202.
- Nuske, H. J., Vivanti, G., & Dissanayake, C. (2013). Are emotion impairments unique to, universal, or specific in autism spectrum disorder? A comprehensive review. *Cognition and Emotion*, 27, 1042–1061.
- Nuske, H. J., Vivanti, G., Hudry, K., & Dissanayake, C. (2014). Pupillometry reveals reduced unconscious emotional reactivity in autism. *Biological Psychology*, 101, 24–35.
- Nuske, H. J., Vivanti, G., & Dissanayake, C. (2015). No evidence of emotional dysregulation or aversion to mutual gaze in preschoolers with autism spectrum disorder: An eye-tracking pupillometry study. *Journal of Autism and Developmental Disorders*, 45, 3433–3445.
- Oliva, M., & Anikin, A. (2018). Pupil dilation reflects the time course of emotion recognition in human vocalizations. *Scientific Reports*, 8, 4871.
- Pelphrey, K., Sasson, N., Reznick, J. S., Paul, G., Goldman, B., & Piven, J. (2002). Visual scanning of faces in autism. *Journal of Autism and Developmental Disorders*, 32, 249–261.
- Philip, R. C. M., Whalley, H. C., Stanfield, A. C., Sprengelmeyer, R., Santos, I. M., et al. (2010). Deficits in facial, body movement and vocal emotional processing in autism spectrum disorders. *Psychological Medicine*, 40, 1919–1929.
- Proulx, T., Slegers, W., & Tritt, S. M. (2017). The expectancy bias: Expectancy-violating faces evoke earlier pupillary dilation than

- neutral or negative faces. *Journal of Experimental Social Psychology*, 70, 69–79.
- Roy, S., Roy, C., Fortin, I., Ethier-Majcher, C., Belin, P., & Gosselin, F. (2007). A dynamic facial expression database. *Journal of Vision*, 7, 944–1044.
- Senju, A. (2013). Atypical development of spontaneous social cognition in autism spectrum disorders. *Brain and Development*, 35, 96–101.
- Shackman, A. J., Salomons, T. V., Slagter, H. A., Fox, A. S., Winter, J. J., & Davidson, R. J. (2011). The integration of negative affect, pain and cognitive control in the cingulate cortex. *Nature Reviews Neuroscience*, 12, 154–167.
- Shenhav, A., Botvinick Matthew, M., & Cohen, J. D. (2013). The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron*, 79, 217–240.
- Sheth, S. A., Mian, M. K., Patel, S. R., Asaad, W. F., Williams, Z. M., et al. (2012). Human dorsal anterior cingulate cortex neurons mediate ongoing behavioural adaptation. *Nature*, 488, 218–221.
- Siciliano, L., & Clausi, S. (2020). Implicit vs. Explicit emotion processing in autism spectrum disorders: An opinion on the role of the cerebellum. *Frontiers in Psychology*. <https://doi.org/10.3389/fpsyg.2020.00096>
- Spezio, M. L., Adolphs, R., Hurley, R. S. E., & Piven, J. (2007a). Abnormal use of facial information in high-functioning Autism. *Journal of Autism and Developmental Disorders*, 37, 929–939.
- Spezio, M. L., Adolphs, R., Hurley, R. S. E., & Piven, J. (2007b). Analysis of face gaze in autism using “Bubbles.” *Neuropsychologia*, 45, 144–151.
- Sun, S., Yu, R., & Wang, S. (2017). A neural signature encoding decisions under perceptual ambiguity. *Eneuro*, 4, 1–14.
- Sun, S., Zhen, S., Fu, Z., Wu, D.-A., Shimojo, S., et al. (2017). Decision ambiguity is mediated by a late positive potential originating from cingulate cortex. *NeuroImage*, 157, 400–414.
- Turi, M., Burr, D. C., & Binda, P. (2018). Pupillometry reveals perceptual differences that are tightly linked to autistic traits in typical adults. *Life*, 7, e32399.
- Urai, A. E., Braun, A., & Donner, T. H. (2017). Pupil-linked arousal is driven by decision uncertainty and alters serial choice bias. *Nature Communications*, 8, 14637.
- Wagner, J. B., Hirsch, S. B., Vogel-Farley, V. K., Redcay, E., & Nelson, C. A. (2013). Eye-tracking, autonomic, and electrophysiological correlates of emotional face processing in adolescents with autism spectrum disorder. *Journal of Autism and Developmental Disorders*, 43, 188–199.
- Wallace, G. L., Case, L. K., Harms, M. B., Silvers, J. A., Kenworthy, L., & Martin, A. (2011). Diminished sensitivity to sad facial expressions in high functioning autism spectrum disorders is associated with symptomatology and adaptive functioning. *Journal of Autism and Developmental Disorders*, 41, 1475–1486.
- Wang, S. (2018). Face size biases emotion judgment through eye movement. *Scientific Reports*, 8, 317.
- Wang, S., & Adolphs, R. (2017a). Reduced specificity in emotion judgment in people with autism spectrum disorder. *Neuropsychologia*, 99, 286–295.
- Wang, S., Jiang, M., Duchesne Xavier, M., Laugeson Elizabeth, A., Kennedy Daniel, P., et al. (2015). Atypical visual saliency in autism spectrum disorder quantified through model-based eye tracking. *Neuron*, 88, 604–616.
- Wang, S., Yu, R., Tyszka, J. M., Zhen, S., Kovach, C., et al. (2017). The human amygdala parametrically encodes the intensity of specific facial emotions and their categorical ambiguity. *Nature Communications*, 8, 14821.
- Wang S, Adolphs R. 2017b. Social Saliency In *Computational and Cognitive Neuroscience of Vision*, ed. Q Zhao, pp. 171–93. Singapore: Springer Singapore
- Wang C-A, Baird T, Huang J, Coutinho JD, Brien DC, Munoz DP. 2018. Arousal Effects on Pupil Size, Heart Rate, and Skin Conductance in an Emotional Face Task. *Frontiers in Neurology*
- Warga, M., Lüdtke, H., Wilhelm, H., & Wilhelm, B. (2009). How do spontaneous pupillary oscillations in light relate to light intensity? *Vision Research*, 49, 295–300.
- Wicker, B., Fonlupt, P., Hubert, B., Tardif, C., Gepner, B., & Deruelle, C. (2008). Abnormal cerebral effective connectivity during explicit emotional processing in adults with autism spectrum disorder. *Soc Cogn Affect Neurosci*, 3, 135–143.
- Willenbockel, V., Sadr, J., Fiset, D., Horne, G., Gosselin, F., & Tanaka, J. (2010). Controlling low-level image properties: The SHINE toolbox. *Behavior Research Methods*, 42, 671–684.

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