Pupillary contagion is independent of the emotional expression of the face

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Running title: Pupillary contagion is independent of emotion

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Contributions
CD and TC are responsible for the conception, design and data collection. TC is responsible for statistical analysis and manuscript writing. CD and TC are responsible for the interpretation of results. CD, RMK and MB provided critical revisions of the manuscript. All authors approved the final manuscript before submission.

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Abstract

The concept of pupillary contagion refers to the automatic imitation of observed pupil size and reflects shared autonomic arousal. Previous studies linked the experience of sadness to changes in pupil size. Accordingly, Harrison, Singer, Rotshtein, Dolan and Critchley found evidence for pupillary contagion when the observed face expresses sadness, but not for neutral, happy or angry expressions [*Social Cognitive and Affective Neuroscience, 1*(1), 5–17. (2006)]. However, differences in eye movements might have influenced previous results. Furthermore, the relatively small sample size of the study merits additional replication. In the current study, we modified the previous experimental design (Harrison et al., 2006) by requiring high attention towards the eye region of the face, which minimized differences in eye movements between facial expressions. In doing so, we demonstrate that the degree of pupillary contagion is independent of the observed emotional expression. Instead, pupil size and emotional expression of the model independently contribute to the observer's pupil size. The role of pupillary contagion for social communication is discussed.

key words: autonomic contagion, empathy, eye tracking, facial expression, pupil

Introduction

An important social ability is to emphasize with other people (Morelli, Ong, Makati, Jackson, & Zaki, 2017). Empathy is the ability to experience feelings in line with the feelings expressed by another person (Davis, 1983; Preston & De Waal, 2002). The role of body signals in revealing emotions to others has gained attention in recent research on empathy (for a review: Kret, 2015). Indeed, different emotions are experienced at different parts of the body (Nummenmaa, Glerean, Hari, & Hietanen, 2014), which is reflected in phrases such as "hot under the collar" (DeWall & Bushman, 2009) or "getting cold feet" (Vinkers et al., 2013). Bodily symptoms of emotional arousal are blushing, heavy breathing, increased pupils and sweat on palms and forehead (Critchley & Nagai, 2012; Koelstra et al., 2012; Kreibig, 2010). Such emotional displays accompany cognitive and action-related components of emotional experience (Scherer, 2005). These signs of inner turmoil are initiated by the autonomic nervous system (ANS) and prepare for further action (Barrett, 2012). In accordance with subjective experience, evidence shows that different emotions are associated with distinctive patterns of ANS activity (Kreibig, 2010; Levenson, Ekman, & Friesen, 1990; Stemmler, Aue, & Wacker, 2007).

The coupling of emotions to bodily states allows to experience emotions on a holistic basis (Critchley, 2009), while it may also display emotions to others more effectively (Barrett, 2012; Critchley, 2009). Indeed, several studies have shown that patterns of autonomic arousal align, when one person observes or interacts with another (Cooper et al., 2014; Ebisch et al., 2012; Engert, Plessow, Miller, Kirschbaum, & Singer, 2014; Messina et al., 2013). This coupling of emotion-contingent body signs has been described as "autonomic contagion", suggesting that autonomic states can directly or indirectly "spread" from one person to another. One straightforward explanation for these findings is the fact that similar emotional experiences can

result in corresponding autonomic responses (see Golland, Arzouan, & Levit-Binnun, 2015). In addition, autonomic contagion might also contribute to the understanding of other people's inner states. In line with findings on the automatic imitation of muscle movements (see Heyes, 2011; for a review), autonomic contagion might promote empathic understanding from a direct, first-person perspective. Indeed, patients with primary autonomic failure show lower empathy scores than healthy controls (Chauhan, Mathias, & Critchley, 2008).

Research on the question how autonomic contagion can contribute to emotional understanding between interacting individuals can profit from the unique role of the eyes in communicating emotions. Indeed, while muscle activity around the eyes greatly defines the portrayed emotional expression (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Ekman & Friesen, 1978; Schurgin et al., 2014; Wells, Gillespie, & Rotshtein, 2016), increased pupil size can signal heightened autonomic arousal during emotional experience (Bradley, Miccoli, Escrig, & Lang, 2008; Partala & Surakka, 2003). This is because pupil diameter is highly correlated with activity in the locus coeruleus under constant light conditions (Aston-Jones & Cohen, 2005). This noradrenergic nucleus plays a key role in allocating attention to stimuli of interest (Sara & Bouret, 2012) and regulates arousal through widespread projections to various parts of the nervous system, including hypothalamus, brainstem and spinal cord (Samuels & Szabadi, 2008). Crucially, locus coeruleus also strongly innervates the Edinger–Westphal nucleus, which is ultimately responsible for regulating pupil dynamics (Barbur, 2004). The pupil thus not only regulates the amount of light which enters the eye, but serves as doorway for visual information entering the nervous system (e.g. Bombeke, Duthoo, Mueller, Hopf, & Boehler, 2016).

Importantly, several studies have shown that perceived pupil size is imitated automatically, demonstrating that pupillary dynamics of others are not only perceived, but also shared: As a first, Hess (1975) showed that schematic drawings of eyes elicit pupillary contagion when presented as pairs of eyes, but not when shown in isolation or as triplets. Similarly, infants showed pupillary contagion with circles, but not squares representing schematic "eyes" (Fawcett, Wesevich, & Gredebäck, 2016; see also Fawcett, Arslan, Falck-Ytter, Roeyers, & Gredebäck, 2017; for pupillary contagion in infants using photographs), demonstrating that pupillary contagion is not merely the byproduct of altered picture brightness by depicted pupil size. Instead, pupillary contagion is a social phenomenon: Not only is pupillary contagion stronger within-species than across species (Kret, Tomonaga, & Matsuzawa, 2014; comparing humans and chimpanzees), but pupillary contagion is associated with trust, which is modulated by oxytocin intake and group membership (Kret, Fischer, & De Dreu, 2015; Kret & De Dreu, 2017). Accordingly, asynchrony of own and observed pupil dynamics activates brain regions related to social salience (Harrison, Gray, & Critchley, 2009). Moreover, electric stimulation of the amygdala, a brain area responsible for identifying biologically relevant events (Pessoa & Adolphs, 2010; for a review), leads not only to pupil dilation when stimulated (Applegate, Kapp, Underwood, & McNall, 1983; Ursin & Kaada, 1960), but the amygdala also shows sensitivity to dilated pupils of others (Amemiya & Ohtomo, 2011; Demos, Kelley, Ryan, Davis, & Whalen, 2008).

There is thus considerable evidence that pupillary contagion plays a role in nonverbal communication. However, the question arises what is actually being communicated? Evidence suggests that small pupils are associated with negative emotions: Sad facial expressions are rated as more intense when shown with constricted pupils, and more so when participants score high

on empathy (Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006; Harrison, Wilson, & Critchley, 2007). Also angry faces are associated with smaller pupils (Hess, 1975; Kret, 2017). Accordingly, in a reported case of Holmes-Adie syndrome, which is characterized by tonically dilated pupils, pupils constricted to normal when the patient was sad (del Valle Loarte & Garcia Ruiz, 2009), suggesting a link between experienced sadness and pupil constriction. Thus, if pupillary dynamics specifically signal and alter the experience of negative emotions, one would expect stronger pupillary contagion if the implicated emotion of these pupillary changes is supported by the accompanied facial expression. In line with this prediction, Harrison, Singer, Rotshtein, Dolan and Critchley (2006) reported that pupillary contagion occurred exclusively for sad facial expressions, but not for neutral, happy or angry facial expressions.

However, the interpretation of findings in Harrison et al. (2006) is difficult since statistical tests were conducted for each facial expression separately. Thus, it remains unclear whether pupillary responses were statistically different between facial expressions and hence, whether pupillary contagion is differentially enhanced for processing sad expressions (see Nieuwenhuis, Forstmann, & Wagenmakers, 2011). Moreover, with nine participants the studied sample size was small, increasing the likelihood that significant findings do not reflect a true effect but rather a false positive finding (Button et al., 2013). Furthermore, as discussed by Harrison and colleagues, a possible confound was the fact that participants were allowed to freely move their eyes. Since different areas of the face are required to identify different facial expressions (Ebner, He, & Johnson, 2011; Smith, Cottrell, Gosselin, & Schyns, 2005; Sullivan, Ruffman, & Hutton, 2007), the relative amount of time spent in the eye region of the face might differ considerably between facial expressions. If participants spent more time looking at the eye region of sad facial expressions as compared to other expressions, it might explain why pupillary

contagion was only found for processing sadness. This is because pupillary contagion might require sufficient processing of the eyes to emerge. Additionally, in common eye tracking systems measurements of pupil size are substantially distorted by eye gaze (Choe, Blake, & Lee, 2016; Hayes & Petrov, 2015). Thus, larger eye movements decrease reliability of pupil size measurements by distorting estimated means and increasing variance. Variance of pupil measurements was not reported in Harrison et al. (2006), therefore it is not clear whether variance was smaller for sad as compared to other expressions. Importantly, the only other study testing whether the degree of pupillary contagion depends on the facial expression found no difference in pupillary dynamics in response to angry and happy faces of varying pupil size (Kret et al., 2015). However, the use of grayscale images of the eye region might have diminished the emotional content of these stimuli. Taken together, while there are theoretical arguments for the hypothesis that pupillary contagion is influenced by the emotional expression and should be particularly strong for sad faces, the empirical evidence supporting this hypothesis is inconclusive.

With the current study, we wanted to test whether pupillary contagion depends on the emotional expression of the face under more controlled conditions. For this purpose, we asked a larger sample of 40 participants to observe photographs of various facial expressions and pupil sizes while controlling for individual eye movements. Photographs depicted neutral, sad, happy and angry facial expressions with small, medium and large pupil sizes. Participants had to indicate which eye appeared to be more widely opened in each photograph, to make sure that participants keep attending the eyes. On a subset of trials, participants had to indicate the facial expression of the previous photograph to ensure that the emotional content of the picture was processed. Since we expect stronger effects of shared emotional arousal in more empathic

people, an empathy questionnaire was included. If pupillary dynamics signal the experience of sadness, we expected the degree of pupillary contagion to be enhanced when the emotional expression of the observed face matches the signaled emotion.

Method

Subjects

40 undergraduate psychology students at Ghent University, Belgium participated. Sample size was predetermined on the basis of preliminary data of an unpublished study, while taking into account that the allowance of free eye movements might introduce more variance.[1] One participant (male) was excluded from data analysis because more than half of his trials did not meet the inclusion criteria (see below). The remaining 39 participants (5 male) were between 19 and 37 years of age (M = 23.18, SD = 3.68). All participants had normal or corrected-to-normal vision, received 10 Euro for participation and read and signed the informed consent before participation.

Stimuli

Figure 1A provides an example of the picture stimuli used in this study. To create the picture stimuli, four male and four female faces were selected from the Radboud Faces Database (Langner et al., 2010). Photographs were shot from a frontal angle and depicted neutral, sad, happy and angry facial expressions. Pictures were cropped to 400 x 400 pixels, so that pupils

[1] In a preliminary study (unpublished data), 20 participants of the same cohort conducted a comparable task on the same eye tracking system. Besides the manipulation of depicted pupil size, stimuli were presented bottom-up, color-inversed or in regular manner. There was a significant interaction between presentation type and depicted pupil size with $F(4,76) = 3.31$, $p = .02$ and $\eta^2_p = .15$, demonstrating that pupillary contagion differed as a function of presentation type. Since in our current study we wanted to test for a similar interaction between pupillary contagion and emotional expression, but anticipated that free eye movements might increase noise, sample size was doubled.

were in symmetrical position and approximately 80 pixels above the horizontal midline. In Adobe Photoshop Elements 11, for each photograph contrast was increased and mean brightness was matched. Original pupils were replaced with the texture of the iris, then black circles of 10, 20 or 30 pixels in diameter were superimposed. As a final layer corneal reflections, which were cropped from the original photograph, were superimposed to make the pictures appear natural. Finally, mean brightness was matched once again to guarantee comparable overall brightness levels for each photograph. Differences in mean brightness between two pictures were not larger than 0.5 %. For the training of the task, 8 different photographs were selected and edited in a similar manner, with the exception that original pupils of the pictures were kept. Images were presented on a 24-inch display at a resolution of 1600 by 900 pixels, resulting in approximately life-sized stimuli of 13 x 13 cm.

Questionnaire

The Interpersonal Reactivity Index (IRI) is a multidimensional questionnaire of empathy, which assesses both cognitive and emotional aspects of empathy (Davis, 1983). The subscales "perspective taking" and "fantasy" assess the degree to which we can identify with and adapt perspectives of people of the real life (perspective taking) or fictional situations (fantasy). Two other subscales assess individual emotional reactivity to the negative experiences of others. While the "empathic concern" scale assesses feelings of warmth, compassion and concern for others, the personal distress scale measures own personal feelings of anxiety and discomfort as reaction to other's negative experiences.

Procedure

The experiment took place in a window-free, sound-attenuated room. After filling in the informed consent and the Dutch version of the IRI, the chin rest was adjusted and the computer

task was explained to the participants. To hide the true purpose of the study, participants were told that eye movements were recorded, whereas in reality also pupil size was recorded. Participants were instructed to concentrate on the photographs, since questions regarding these pictures would be asked both during and after the experiment. The task of the participant was to compare left and right eyes of each picture in order to decide which eye appeared to be more widely opened (see Figure 1B). This was illustrated with an example: Raising the eyelids reveals more of the eyeball's surface than squinting the eyes. In addition, for a subset of trials the emotional expression of the face had to be identified, which could be sad, neutral, happy or angry. The experiment started with a short training session of 16 trials in which all emotional expressions were portrayed by 4 male and 4 female actors and repeated once.

As shown in Figure 1C, each trial started with the presentation of a fixation cross for 2 seconds. The fixation cross was located in the center of the horizontal axis, but positioned on the same level as the pupils of the photographs on the vertical axis. The fixation cross was replaced by a photograph, which was shown for 3 seconds. Afterwards, the phrase "Larger?" was displayed, which remained present until a response was registered or 2 seconds passed. The words "Left" and "Right" were displayed to the left and right of the screen. Responses were given with the left and right arrow keys of the keyboard. A rectangular frame moving from the central phrase to one of the two response options served as visual feedback of a registered response for 0.2 seconds. Every 4 trials on average (range: 1-7) a second question appeared after the first, requiring participants to recall the facial expression of the pervious photograph. In these trials the prompt "Emotion?" replaced the first one and was surrounded by four response options. Participants had to press the left arrow key for "neutral", the right key for "angry", the upper key for "happy" and the lower key for "sad". There was a time limit of 4 seconds to answer the

second question. Once a response key was registered visual feedback was given for 0.2 seconds by moving the rectangular frame to the chosen answer. If no response was registered within the time limits of the two questions, instead of response feedback the phrase “TOO SLOW!” was presented for 1 second. With the exception of the photographs themselves, all other stimuli (including text) were presented in a green color (RGB: 34, 255, 1) in front of a gray background (RGB: 160, 160, 160).

Participants performed three blocks of 96 trials and approximately 10 minutes. Between blocks a short break was provided before the camera was recalibrated with a randomized 9-point sequence. Each photograph was shown once per block and showed one of 4 male and 4 female models with 4 different facial expressions and 3 different pupil sizes. Presentation within each block was randomized with the restriction that no model was repeated in immediate succession. After the computer task, participants were asked to rate photographs of neutral facial expressions on attractiveness on a 7- point visual analog scale ranging from -3 (*very unattractive*) to +3 (*very attractive*) by moving the computer mouse (0 (*neutral*) formed the center of the scale and visual anchors marked every whole step). Attractiveness ratings were included since earlier studies suggest that attractiveness of the face depends on pupil size (Simms, 1967; Tombs & Silverman, 2004).

Pupil size recording and pre-processing

Pupil area of the right eye was recorded with an infrared eye tracker with a sample rate of 1000 Hz (Eyelink 1000 Plus, SR-Research Ltd.). The preprocessing of the pupil data was conducted in R with a custom-written script. Final statistical analysis was conducted in SPSS 23.

Because of the high sample rate, the opening and closing of eyelids during eye blinks was registered as a rapid change in pupil size before and after temporal loss of the pupil signal. To

remove these artifacts in R, data points 100 ms prior and after sequences of missing pupil values were removed. Since the pupil size is registered as the number of pixels falling below a brightness threshold of the camera picture, partial occlusion of the eye by eyelids can lead to abnormally high or low pupil values. Therefore, data points falling outside a range of ± 3 standard deviations above and below the block mean were removed from each block. Subsequently, data was restricted to segments ranging from the onset of the fixation cross to photograph offset. Furthermore, all missing data points were linearly interpolated using the "na.approx"- function from the "zoo"- package (Zeileis & Grothendieck, 2005). The average percentage of interpolated data points for our interval of interest -500 to 3000 ms relative to picture onset was 7.96 % per participant (*SD* = 5.91 %). Data was normalized by calculating the percent change of the average pupil during picture presentation with respect to a 500 ms interval before picture onset, which served as baseline (see Figure 2A; compare Wierda, van Rijn, Taatgen, & Martens, 2012).

Trials were excluded from data analysis if one or more of the following exclusion criteria were met: 1) 50% or more of the data points during either baseline or picture presentation were interpolated (compare Fawcett et al., 2016; Harrison et al., 2006a; Kret et al., 2015), 2) participants did not fixate the fixation cross prior to picture onset, as defined by a deviation of the average gaze by more than ± 3 standard deviations of the mean during that period 3) Eye gaze fell less than 1000 ms in total in the eye region of the face, which covered an area of 100 x 260 pixels around fixation (see Figure 1A). One participant (male) was excluded from data analysis since more than half of the trials met these exclusion criteria. For the remaining 39 participants, 16.82 % (*SD* = 12.14 %) of all trials met the exclusion criteria on average (range = 3.82- 44.79%). Finally, for each participant the average percent change was computed for each

cell of the 3 (pupil size) x 4 (emotion) experimental design, based on the trials that were not excluded. The number of excluded trials did not differ between conditions, as indicated in a repeated-measures ANOVA including the same factors (all *p*'s > .35). Finally, data in R was exported to text-files to allow for statistical testing in SPSS 23.

Results

All post-hoc tests reported in this manuscript were corrected for multiple comparisons by the method of Bonferroni.

Manipulation check

For each trial, dwell time in the eye region was computed, which is the relative duration in which participants eye gaze was within the boundaries of the eye region (see Figure 1A). Dwell time was high for each facial expression (sad: 86.20 %, neutral: *M* = 87.48 %, happy: 84.81 %, angry: 85.59 %), indicating that our manipulation successfully led to high attention towards the eyes. Participants spend more time looking in the eyes of neutral expressions as compared to other expressions (all *p*'s ≤ .05), as indicated in a repeated-measures ANOVA with the factors pupil size and emotion. There was a trend for a main effect of pupil size, which did not reach significance (*p* = .08; small: 86.41 %; medium: 85.77 %; large: 85.87 %). There was no interaction (*p* = .32).

To test whether participants processed the emotional expression of the face despite of the high dwell time in the eye region, we tested whether participants were able to correctly identify facial emotional expressions above chance. Indeed, accuracy was above chance for each facial expression (all *p* < .001). Moreover, in a repeated-measures ANOVA with the factors emotion (4) and pupil size (3) it was tested whether there were systematic differences in emotion identification between conditions. There was a main effect of emotion with $F(2.45,1.87) = 31.76$,

$p < .001$ and $\eta^2_p = .46$. Post-hoc comparisons revealed that emotion identification was higher for happy faces and lower for angry faces as compared to the rest (all $p < .01$). However there was no effect of pupil size ($F(1.53,58.04) = 1.52$, $p = .22$ and $\eta^2_p = .04$) nor an interaction ($F(4.59,174.57) = 0.87$, $p = .52$ and $\eta^2_p = .02$). See Table 1 for an overview on the distribution of responses given for each facial expression.

Since participants classified facial expressions as "sad" more often as compared to the reported norms (Langner et al., 2010), we additionally tested whether the tendency to classify expressions as sad was affected by the factors emotion (4) and pupil size (3). Besides a main effect of emotion ($p < .001$), we found a significant interaction between emotion and pupil size in this analysis ($p = .04$). Separate ANOVA's for each emotional expression indicated that pupil size affected the amount of sadness classifications for angry, but not other facial expressions (angry: $p < .05$; all other p's $\geq .14$). Post-hoc tests indicated that there was a trend for a *decrease* in sadness classifications for small as compared to large pupils in angry faces ($p = .10$).

Pupillary response

In order to test our main hypothesis that pupillary contagion might be enhanced for sad facial expressions as compared to other expressions, in a repeated-measures ANOVA it was tested whether individual pupil sizes differed significantly as a function of pupil size and emotion in the photographs (see Figure 2B). There was a main effect of emotion ($F(3,114) = 11.10$, $p < .001$ and $\eta^2_p = .23$), demonstrating that pupil sizes dilated significantly more during angry facial expressions as compared to other expressions (all $p \leq .001$). Moreover a significant effect of pupil size was found ($F(2,76) = 8.03$, $p = .001$ and $\eta^2_p = .17$). Post-hoc comparisons revealed that small pupil sizes in the photographs indeed led to smaller pupil sizes in the observer as compared to large or medium-sized pupils (both $p < .01$; see Figure 2A). There was

no significant difference between large and medium-sized pupil conditions with $p > .99$. There was no interaction between emotion and pupil size ($F(6,228) = 1.54$, $p = .17$ and $\eta^2_p = .04$).

Even though there was no significant interaction between emotion and pupil size, we conducted additional statistical tests to determine whether pupillary responses for each facial expression could be considered similar. Classical frequentist statistical tests allow the rejection, but not the approval of the null hypothesis. However, a Bayesian approach to statistical testing allows to compare the likelihood of both null and alternative hypothesis given the data provided (Jarosz & Wiley, 2014). A Bayesian repeated-measures ANOVA confirmed "strong" to "decisive" evidence for a model with the two factors emotion and pupil size as compared to all reduced models, including the null model (all *BF*'s ≥ 24; see Jarosz & Wiley, 2014). Critically, there was "positive" to "strong" evidence (*BF* = 12) for the two-factor model in comparison to a model with an additional interaction term. Importantly, removing angry faces from the analysis only increased evidence against an interaction (*BF* = 34), while maintaining a main effect of pupil size (*BF* = 67), but providing no evidence for a main effect of emotion (*BF* = 13).

Relation of pupillary adaptations to empathy

We tested whether the degree of pupillary contagion was associated with individual empathy scores as measured by the Interpersonal Reactivity Index. For this purpose, for each participant the degree of pupillary contagion was summarized by computing the difference of pupil size in reaction to observed large and small pupils. This "contagion score" was subsequently correlated with the subscales of the IRI. Pupillary contagion across all facial expressions did not correlate with any of the subscales of the IRI (all $p \geq .27$), nor the aggregated total of the IRI ($p = .26$). Also testing this relationship specifically with pupillary responses to

sad faces led to null results (all $p \geq .26$), even though multiple comparisons were not corrected in this correlational analysis.

Attractiveness ratings

Previous research indicates that observed pupil size affects perceived attractiveness (Simms, 1967; Tombs & Silverman, 2004), which provides an alternative explanation to the phenomenon of pupillary contagion. Therefore, we additionally tested whether depicted pupil size altered perceived attractiveness in our stimulus set. One participant was excluded from this analysis because she decided to skip all attractiveness ratings. In a repeated-measures ANOVA with the factors "pupil size" and "gender of the model" on the dependent variable "attractiveness rating" there was no effect of pupil size in our sample ($F(2,76) = 2.13$, $p = .13$ and $\eta^2_p = .05$). Neither was there an interaction between pupil size and gender of the model with $F(1.68, 63.70) = 0.72$, $p = .49$ and $\eta^2_p = .02$. Similar findings were obtained when removing the six male participants from analysis (indicating that the gender of participants did not affect these results).

Discussion

Pupillary contagion describes a phenomenon of corresponding pupillary adaptations between two persons, reflecting shared autonomic arousal. We tested whether pupillary contagion depends on the observed expression of the face when potential differences in eye movements are taken into account. For this purpose, we conducted a variation of the original study by Harrison, Singer, Rotshtein, Dolan and Critchley (2006) by using a different filler task as compared to the original study. In doing so, we demonstrate that the degree of pupillary contagion does not differ between facial expressions. Even though pupillary contagion was numerically largest for sad facial expressions, Bayesian statistics indicate that both facial expressions and pupil sizes of the picture uniquely contributed to the pupillary response of the

observer, while present data strongly speaks against an interaction of these two effects. Taken together, our study resolves inconsistencies in the literature on pupillary contagion regarding the question whether pupillary contagion is influenced by emotion expression (Fawcett et al., 2017, 2016, Harrison et al., 2006, 2007; Hess, 1975; Kret & De Dreu, 2017; Kret et al., 2015, 2014; Simms, 1967) demonstrating that pupillary contagion is a mechanism which occurs independently of emotional context.

Even though our main findings speak against a role of the facial expression on the emergence of pupillary contagion, some patterns in our data require closer discussion. One possible concern with regards to our results is that pupillary responses of participants did not differ between medium-sized or large pupils in the pictures. The stimulus material used in our study might have prevented such a distinction. While a pupil diameter of 10 pixels was used for small pupil sizes, medium-sized pupils were 20 pixels wide and large pupils were 30 pixels wide. However, a linear increase in diameter generates a nonlinear increase in pixels covering the pupil area. While the pupil area was 4 times larger for medium-sized as compared to small pupils, the relative area increase from medium-sized to large pupils was 2.25. Thus, pupil areas of medium-sized and large pupils were more similar in size than medium-sized and small pupils by experimental design. Moreover, pupil diameter has a natural range of 2 to 4 mm during bright light and 4 to 8 mm during dark (Spector, 1990). Since our photographs were displayed at a size of approximately 13 x 13 cm, small, medium and large pupils were displayed approximately at 3.3 mm, 6.6 mm and 9.9 mm in diameter, respectively. Since maximum available illumination was used during data acquisition to match brightness of the presented stimulus material, the natural range of the pupil during these light conditions might have restricted reactivity to

medium and large pupils as compared to small pupils. Future studies on pupillary contagion should take pupil adaptability into careful consideration.

Moreover, observer's pupils were significantly increased during the presentation of angry faces as compared to other emotional expressions. This is in line with a study by Kret, Roelofs, Stekelenburg, & de Gelder (2013), who found that pupil size was largest in reaction to angry faces and body poses in comparison to happy or fearful faces and body poses. This finding parallels data on the "anger superiority effect", which demonstrates that angry facial expressions are detected faster than happy facial expressions (Hansen & Hansen, 1988; Pinkham, Griffin, Baron, Sasson, & Gur, 2010). Even outside conscious awareness angry faces modulate early emotion-sensitive ERP-signals (Lyyra, Hietanen, & Astikainen, 2014). Interestingly, the eye region itself is sufficient to evoke the anger superiority effect (Fox & Damjanovic, 2006). From an evolutionary perspective, angry faces propose threat signals whose early detection is crucial for preparing defense responses. Dilating pupils in response to angry faces might reflect heightened attention or action readiness in response to threat. An alternative explanation for larger pupils during the observation of angry faces is the finding that angry faces possessed greater emotional ambiguity than other facial expressions. This is reflected by the finding that accuracy of emotion identification was lower for angry faces as compared to other facial expressions. Indeed, in circa 27 % of the trials where an angry face had to be identified, participants indicated to have seen a sad face (see table 1). This ambiguity of angry expressions could have led to increased task difficulty for emotion identification. It has been shown that both increased cognitive workload and uncertainty leads to pupil dilation (Laeng, Ørbo, Holmlund, & Miozzo, 2011; Lavín, San Martín, & Rosales Jubal, 2014; Zekveld, Kramer, & Festen, 2010). Even though participants needed to make an emotional judgment on only a subset of trials, the

fact that these trials were randomized made it necessary to process the emotional expression of every photograph for optimal performance.

Another potential concern regarding our results is to what extend the findings depend on the specific tasks we used. One might argue that the identification of emotional expressions is an elemental component of social interaction (task 2) whereas the comparison of exposed eyeball surfaces is not (task 1). Since surface comparison had to be performed on every trial and emotion identification only on a subset, it begs the question whether our task setting prevented participants from adequately processing the emotional content of the photograph, which may in turn result in a null finding regarding the interaction. There are several aspects speaking against this. First of all, the task of emotion identification was randomly presented so that participants did not know whether they had to perform the emotion identification task or not. Furthermore, it was always presented after the other task. Therefore, participants always had to identify the emotion in order to be able to carry out the emotion identification task. Secondly, even though overt attention towards the eyes was indeed very high with ca. 86 % of presentation time on average, participants identified the emotional expression highly above chance with ca. 83 % accuracy on average. Since no performance feedback was provided throughout the task, these identification rates truly reflected individual impressions of faces and were not merely the result of learning. Crucially, with the exception of angry facial expressions, identification rates were in line with those reported in the validation study of the used data set (Langner et al., 2010). While a certain ambiguity of emotional expressions is likely a property of emotional expressions in general (e.g. Alves, Koch, & Unkelbach, 2017), high performance levels in this secondary task might have been reached because we presented life-size, fully colored photographs for a sufficiently long duration of 3 seconds.

Nevertheless, there remains a possibility that pupillary dynamics are at least partially driven by identified rather than depicted emotional expressions. This is especially the case since in contrast to the norm ratings misclassifications of emotional expressions as "sad" were overrepresented. However, we deem this possibility rather unlikely. On the one hand, despite for a trend for a *decrease* in sadness classifications for angry faces with small pupils as compared to large pupils, we did not find that depicted pupil sizes altered the tendency to report "sad" (in contrast to Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006; Harrison, Wilson, & Critchley, 2007). Moreover, if pupillary contagion was merely driven by perceived sadness, we would expect a clear decline in the degree of pupillary contagion from presenting sad faces to angry, neutral and happy faces. Bayesian statistics clearly speak against this assumption, showing that these null findings are legitimate, and not merely the result of lacking power. In addition, even though the IRI assesses empathy towards primarily negative emotions of others and partially shows a strong overlap with the empathy scale used in the original study by Harrison, Wilson and Critchley (2007; see Davis, 1983), we have no indication that participants with higher empathy scores showed stronger pupillary contagion than others, even when testing this relationship specifically for pupillary reactions to sad faces. Taken together, we propose that pupillary contagion is not specifically engaged in sadness processing, but is independent of the emotional expression of the face.

What do these findings imply for the functional role of pupillary contagion? Our study demonstrates that signals stemming from pupil size and facial expressions seem to be processed independently, so that no specific facial expression is required for pupillary contagion to occur. More strictly speaking, it is also not the case that the *degree* of pupillary contagion is enhanced for specific emotional expressions. Interestingly, earlier work demonstrates that pupillary

contagion can be observed as early as 4- to 9- months of age (Fawcett et al., 2017, 2016), a period in life during which other socially relevant skills such as attention to faces (Frank, Amso, & Johnson, 2014; Frank, Vul, & Johnson, 2009), emotion recognition (Grossmann, 2010) or joint attention (Cleveland, Schug, & Striano, 2007; Cleveland & Striano, 2007) are still under development. The fact that infants with poor discrimination of facial expressions show pupillary contagion as long as stimulus material resembles human eyes further supports our interpretation that pupillary contagion is not critically reliant upon emotional processing of faces. Instead, pupillary contagion seems to reflect a rather elementary process which occurs at early age, outside of awareness and voluntary control and is independent of emotional context. However this is not to say that pupillary contagion may not form an integral aspect of social interaction. Indeed, previous studies have shown that the degree of pupillary contagion predicts trust (Kret, Fischer, & De Dreu, 2015; Kret & De Dreu, 2017), which itself relies upon the ability to anticipate another person's true intentions, and hence might benefit from a more holistic internal model of the other.

Overall, more research is needed to further specify the functional role of pupillary contagion. In line with research on the relationship between embarrassment and blood flow of the face (Drummond & Lazaroo, 2012), the temporal restriction of pupillary flexibility by use of mydriatic eye drops or face illumination might allow to determine the involvement of pupillary contagion in other processes, such as emotion identification or trust.

Conclusion

By using Bayesian statistics, our study is the first to demonstrate that pupillary contagion occurs independently of the emotional expression of the face. In doing so, we provide strong evidence against the idea that pupillary contagion is specifically engaged in the processing of sad

faces. Future studies should aim to better identify the functional role of “pupillary contagion” and test whether it contributes to the understanding of others just as the term implies.

References

Alves, H., Koch, A., & Unkelbach, C. (2017). Why Good Is More Alike Than Bad: Processing Implications. *Trends in Cognitive Sciences*.

Amemiya, S., & Ohtomo, K. (2011). Effect of the observed pupil size on the amygdala of the beholders. *Social Cognitive and Affective Neuroscience*, *7*(3), 332–341.

Applegate, C. D., Kapp, B. S., Underwood, M. D., & McNall, C. L. (1983). Autonomic and somatomotor effects of amygdala central N. stimulation in awake rabbits. *Physiology & Behavior*, *31*(3), 353–360.

Aston-Jones, G., & Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: adaptive gain and optimal performance. *Annu. Rev. Neurosci.*, *28*(1), 403–450. http://doi.org/10.1146/annurev.neuro.28.061604.135709

Barbur, J. L. (2004). Learning from the pupil-studies of basic mechanisms and clinical applications. *The Visual Neurosciences*, *1*, 641–656.

Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The "Reading the Mind in the Eyes" test revised version: A study with normal adults, and adults with Asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry*, *42*(2), 241–251.

Barrett, L. F. (2012). Emotions are real. *Emotion*, *12*(3), 413.

Bombeke, K., Duthoo, W., Mueller, S. C., Hopf, J.-M., & Boehler, C. N. (2016). Pupil size directly modulates the feedforward response in human primary visual cortex independently of attention. *NeuroImage*, *127*, 67–73.

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*(4), 602–607.

Button, K. S., Ioannidis, J. P. A., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S. J., & Munafò, M. R. (2013). Power failure: why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, *14*(5), 365–376.

Chauhan, B., Mathias, C. J., & Critchley, H. D. (2008). Autonomic contributions to empathy: evidence from patients with primary autonomic failure. *Autonomic Neuroscience*, *140*(1), 96–100.

Choe, K. W., Blake, R., & Lee, S.-H. (2016). Pupil size dynamics during fixation impact the accuracy and precision of video-based gaze estimation. *Vision Research*, *118*, 48–59.

Cleveland, A., Schug, M., & Striano, T. (2007). Joint attention and object learning in 5-and 7-month-old infants. *Infant and Child Development*, *16*(3), 295–306.

Cleveland, A., & Striano, T. (2007). The effects of joint attention on object processing in 4-and 9-month-old infants. *Infant Behavior and Development*, *30*(3), 499–504.

Cooper, E. A., Garlick, J., Featherstone, E., Voon, V., Singer, T., Critchley, H. D., & Harrison, N. A. (2014). You turn me cold: evidence for temperature contagion. *PloS One*, *9*(12), e116126.

Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorials in Quantitative Methods for Psychology*, *1*(1), 42–45.

Critchley, H. D. (2009). Psychophysiology of neural, cognitive and affective integration: fMRI and autonomic indicants. *International Journal of Psychophysiology*, *73*(2), 88–94.

Critchley, H. D., & Nagai, Y. (2012). How emotions are shaped by bodily states. *Emotion Review*, *4*(2), 163–168.

Davis, M. H. (1983). Measuring individual differences in empathy: Evidence for a

multidimensional approach. *Journal of Personality and Social Psychology*, *44*(1), 113.

del Valle Loarte, M., & Garcia Ruiz, P. J. (2009). A new clinical sign in Holmes-Adie syndrome. *Journal of Neurology*, *256*(1), 127–128.

Demos, K. E., Kelley, W. M., Ryan, S. L., Davis, F. C., & Whalen, P. J. (2008). Human amygdala sensitivity to the pupil size of others. *Cerebral Cortex*, *18*(12), 2729–2734.

DeWall, C. N., & Bushman, B. J. (2009). Hot under the collar in a lukewarm environment: Words associated with hot temperature increase aggressive thoughts and hostile perceptions. *Journal of Experimental Social Psychology*, *45*(4), 1045–1047.

Drummond, P. D., & Lazaroo, D. (2012). The effect of niacin on facial blood flow in people with an elevated fear of negative evaluation. *European Neuropsychopharmacology*, *22*(3), 200–204.

Ebisch, S. J., Aureli, T., Bafunno, D., Cardone, D., Romani, G. L., & Merla, A. (2012). Mother and child in synchrony: thermal facial imprints of autonomic contagion. *Biological Psychology*, *89*(1), 123–129.

Ebner, N. C., He, Y. I., & Johnson, M. K. (2011). Age and emotion affect how we look at a face: Visual scan patterns differ for own-age versus other-age emotional faces. *Cognition & Emotion*, *25*(6), 983–997.

Ekman, P., & Friesen, W. V. (1977). Facial action coding system.

Engert, V., Plessow, F., Miller, R., Kirschbaum, C., & Singer, T. (2014). Cortisol increase in empathic stress is modulated by emotional closeness and observation modality. *Psychoneuroendocrinology*, *45*, 192–201.

Fawcett, C., Arslan, M., Falck-Ytter, T., Roeyers, H., & Gredebäck, G. (2017). Human eyes with dilated pupils induce pupillary contagion in infants. *Scientific Reports*, *7*.

Fawcett, C., Wesevich, V., & Gredebäck, G. (2016). Pupillary Contagion in Infancy Evidence for Spontaneous Transfer of Arousal. *Psychological Science*, 956797616643924.

Fox, E., & Damjanovic, L. (2006). The eyes are sufficient to produce a threat superiority effect. *Emotion*, *6*(3), 534.

Frank, M. C., Amso, D., & Johnson, S. P. (2014). Visual search and attention to faces during early infancy. *Journal of Experimental Child Psychology*, *118*, 13–26.

Frank, M. C., Vul, E., & Johnson, S. P. (2009). Development of infants' attention to faces during the first year. *Cognition*, *110*(2), 160–170.

Golland, Y., Arzouan, Y., & Levit-Binnun, N. (2015). The Mere Co-Presence: Synchronization of Autonomic Signals and Emotional Responses across Co-Present Individuals Not Engaged in Direct Interaction. *PloS One*, *10*(5), e0125804.

Grossmann, T. (2010). The development of emotion perception in face and voice during infancy. *Restorative Neurology and Neuroscience*, *28*(2), 219–236.

Hansen, C. H., & Hansen, R. D. (1988). Finding the face in the crowd: an anger superiority effect. *Journal of Personality and Social Psychology*, *54*(6), 917.

Harrison, N. A., Gray, M. A., & Critchley, H. D. (2009). Dynamic pupillary exchange engages brain regions encoding social salience. *Social Neuroscience*, *4*(3), 233–243.

Harrison, N. A., Singer, T., Rotshtein, P., Dolan, R. J., & Critchley, H. D. (2006). Pupillary contagion: central mechanisms engaged in sadness processing. *Social Cognitive and Affective Neuroscience*, *1*(1), 5–17. http://doi.org/10.1093/scan/nsl006

Harrison, N. A., Wilson, C. E., & Critchley, H. D. (2007). Processing of observed pupil size modulates perception of sadness and predicts empathy. *Emotion*, *7*(4), 724. http://doi.org/10.1037/1528-3542.7.4.724

Hayes, T. R., & Petrov, A. A. (2015). Mapping and correcting the influence of gaze position on pupil size measurements. *Behavior Research Methods*, 1–18.

Hess, E. H. (1975). The role of pupil size in communication. *Scientific American*, *233*(5), 110–112.

Heyes, C. (2011). Automatic imitation. *Psychological Bulletin*, *137*(3), 463.

Jarosz, A. F., & Wiley, J. (2014). What are the odds? A practical guide to computing and reporting Bayes factors. *The Journal of Problem Solving*, *7*(1), 2.

Koelstra, S., Muhl, C., Soleymani, M., Lee, J.-S., Yazdani, A., Ebrahimi, T., … Patras, I. (2012). Deap: A database for emotion analysis; using physiological signals. *IEEE Transactions on Affective Computing*, *3*(1), 18–31.

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. *Biological Psychology*, *84*(3), 394–421.

Kret, M. E. (2015). Emotional expressions beyond facial muscle actions. A call for studying autonomic signals and their impact on social perception. *Frontiers in Psychology*, *6*(May), 711. http://doi.org/10.3389/fpsyg.2015.00711

Kret, M. E. (2017). The role of pupil size in communication. Is there room for learning? *Cognition and Emotion*, 1–7.

Kret, M. E., & De Dreu, C. K. W. (2017). Pupil-mimicry conditions trust in partners: moderation by oxytocin and group membership. In *Proc. R. Soc. B* (Vol. 284, p. 20162554). The Royal Society.

Kret, M. E., Fischer, A. H., & De Dreu, C. K. W. (2015). Pupil mimicry correlates with trust in in-group partners with dilating pupils. *Psychological Science*, *26*(9), 1401–1410.

Kret, M. E., Roelofs, K., Stekelenburg, J., & de Gelder, B. (2013). Emotional signals from faces,

bodies and scenes influence observers' face expressions, fixations and pupil-size. *Frontiers in Human Neuroscience, 7*, 810.

Kret, M. E., Tomonaga, M., & Matsuzawa, T. (2014). Chimpanzees and humans mimic pupil-size of conspecifics. *PloS One*, *9*(8), e104886.

Laeng, B., Ørbo, M., Holmlund, T., & Miozzo, M. (2011). Pupillary stroop effects. *Cognitive Processing*, *12*(1), 13–21.

Langner, O., Dotsch, R., Bijlstra, G., Wigboldus, D. H. J., Hawk, S. T., & van Knippenberg, A. (2010). Presentation and validation of the Radboud Faces Database. *Cognition and Emotion*, *24*(8), 1377–1388.

Lavín, C., San Martín, R., & Rosales Jubal, E. (2014). Pupil dilation signals uncertainty and surprise in a learning gambling task. *Frontiers in Behavioral Neuroscience*, *7*, 218.

Levenson, R. W., Ekman, P., & Friesen, W. V. (1990). Voluntary facial action generates emotion-specific autonomic nervous system activity. *Psychophysiology*, *27*(4), 363–384.

Lyyra, P., Hietanen, J. K., & Astikainen, P. (2014). Anger superiority effect for change detection and change blindness. *Consciousness and Cognition*, *30*, 1–12.

Messina, I., Palmieri, A., Sambin, M., Kleinbub, J. R., Voci, A., & Calvo, V. (2013). Somatic underpinnings of perceived empathy: The importance of psychotherapy training. *Psychotherapy Research*, *23*(2), 169–177.

Morelli, S. A., Ong, D. C., Makati, R., Jackson, M. O., & Zaki, J. (2017). Empathy and well-being correlate with centrality in different social networks. *Proceedings of the National Academy of Sciences*, *114*(37), 9843–9847.

Nieuwenhuis, S., Forstmann, B. U., & Wagenmakers, E.-J. (2011). Erroneous analyses of interactions in neuroscience: a problem of significance. *Nature Neuroscience*, *14*(9), 1105–

1107.

Nummenmaa, L., Glerean, E., Hari, R., & Hietanen, J. K. (2014). Bodily maps of emotions. *Proceedings of the National Academy of Sciences*, *111*(2), 646–651.

Partala, T., & Surakka, V. (2003). Pupil size variation as an indication of affective processing. *International Journal of Human-Computer Studies*, *59*(1), 185–198.

Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: from a'low road'to'many roads' of evaluating biological significance. *Nature Reviews Neuroscience*, *11*(11), 773–783.

Pinkham, A. E., Griffin, M., Baron, R., Sasson, N. J., & Gur, R. C. (2010). The face in the crowd effect: anger superiority when using real faces and multiple identities. *Emotion*, *10*(1), 141.

Preston, S. D., & De Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, *25*(1), 1–20.

Samuels, E. R., & Szabadi, E. (2008). Functional neuroanatomy of the noradrenergic locus coeruleus: its roles in the regulation of arousal and autonomic function part II: physiological and pharmacological manipulations and pathological alterations of locus coeruleus activity in humans. *Current Neuropharmacology*, *6*(3), 254–285.

Sara, S. J., & Bouret, S. (2012). Orienting and reorienting: the locus coeruleus mediates cognition through arousal. *Neuron*, *76*(1), 130–141.

Scherer, K. R. (2005). What are emotions? And how can they be measured? *Social Science Information*, *44*(4), 695–729.

Schurgin, M. W., Nelson, J., Iida, S., Ohira, H., Chiao, J. Y., & Franconeri, S. L. (2014). Eye movements during emotion recognition in faces. *Journal of Vision*, *14*(13), 14.

Simms, T. M. (1967). Pupillary response of male and female subjects to pupillary difference in

male and female picture stimuli. *Perception & Psychophysics*, *2*(11), 553–555.

Smith, M. L., Cottrell, G. W., Gosselin, F., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychological Science*, *16*(3), 184–189.

Spector, R. H. (1990). The Pupils. In H. K. Walker, W. D. Hall, & J. W. Hurst (Eds.), *Clinical Methods: The History, Physical, and Laboratory Examinations. 3rd edition.* (3. edition, p. Chapter 58). Boston: Butterworth.

Stemmler, G., Aue, T., & Wacker, J. (2007). Anger and fear: Separable effects of emotion and motivational direction on somatovisceral responses. *International Journal of Psychophysiology*, *66*(2), 141–153.

Sullivan, S., Ruffman, T., & Hutton, S. B. (2007). Age differences in emotion recognition skills and the visual scanning of emotion faces. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, *62*(1), P53–P60.

Tombs, S., & Silverman, I. (2004). Pupillometry: A sexual selection approach. *Evolution and Human Behavior*, *25*(4), 221–228.

Ursin, H., & Kaada, B. R. (1960). Functional localization within the amygdaloid complex in the cat. *Electroencephalography and Clinical Neurophysiology*, *12*(1), 1–20.

Vinkers, C. H., Penning, R., Hellhammer, J., Verster, J. C., Klaessens, J. H. G. M., Olivier, B., & Kalkman, C. J. (2013). The effect of stress on core and peripheral body temperature in humans. *Stress*, *16*(5), 520–530.

Wells, L. J., Gillespie, S. M., & Rotshtein, P. (2016). Identification of Emotional Facial Expressions: Effects of Expression, Intensity, and Sex on Eye Gaze. *PloS One*, *11*(12), e0168307.

Wierda, S. M., van Rijn, H., Taatgen, N. a., & Martens, S. (2012). Pupil dilation deconvolution

reveals the dynamics of attention at high temporal resolution. *Proceedings of the National Academy of Sciences, 109*(22), 8456–8460. http://doi.org/10.1073/pnas.1201858109

Zeileis, A., & Grothendieck, G. (2005). zoo: S3 infrastructure for regular and irregular time series. *arXiv Preprint math/0505527*.

Zekveld, A. A., Kramer, S. E., & Festen, J. M. (2010). Pupil response as an indication of effortful listening: The influence of sentence intelligibility. *Ear and Hearing, 31*(4), 480–490.

Figures

		Correct answer			
		sad	neutral	happy	angry
Chosen answer	sad	84.15	10.80	0.74	26.72
	neutral	8.47	84.92	1.29	4.88
	happy	0.87	2.01	96.16	0.41
	angry	6.09	2.00	1.80	67.73
	missed	0.42	0.27	0.00	0.25

Table 1. Relative proportion of chosen answers per facial expression. Questions requiring emotion identification occurred every four trials on average, leading to a random number of trials per emotion category. In comparison to other facial expressions, identification rate was lower for angry faces and higher for happy faces.

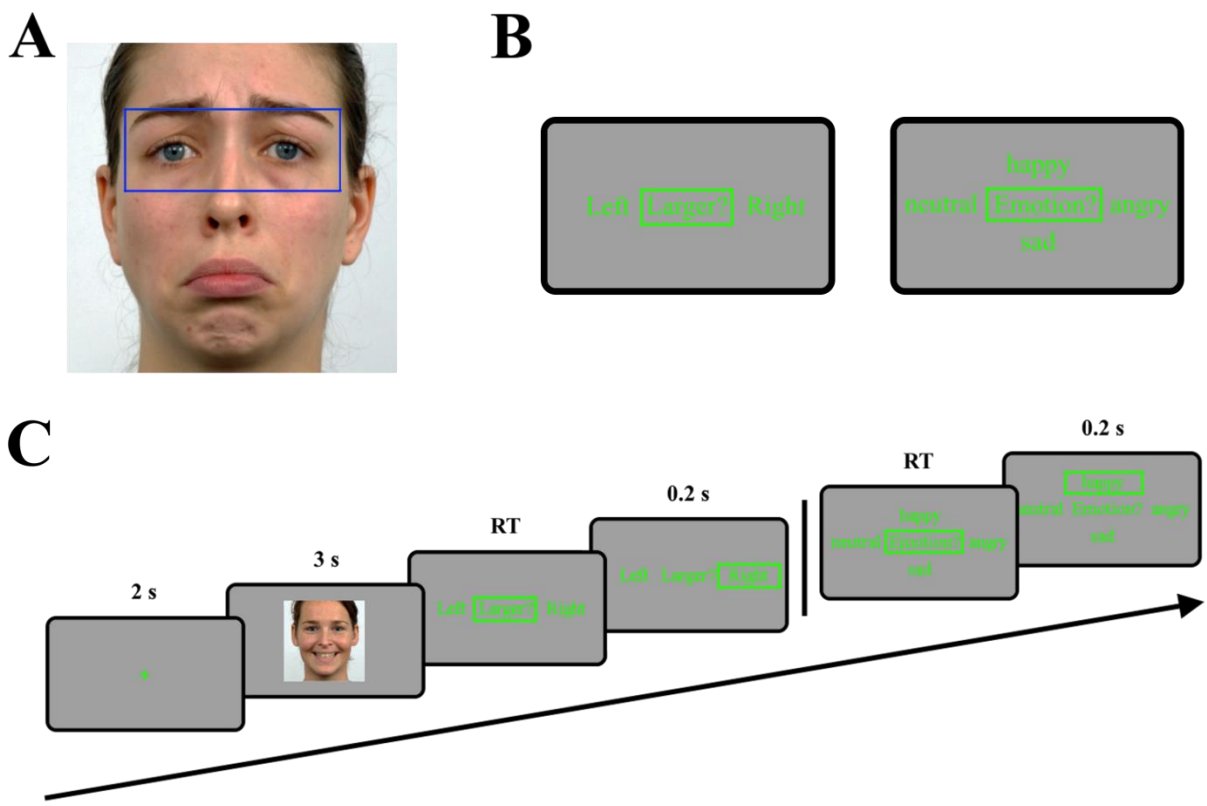

Figure 1. Experimental design. **A)** Example of presented photographs. In this example, a sad facial expression is shown with small pupils. The blue framed area depicts the eye region of the face; eye movements falling within this area were taken as indication that participants looked towards the eyes (see text). The blue frame is only depicted for illustration purposes and was not visible to the participants. Photographs of the Radboud Faces Database are given permission of free use in strictly scientific publications. **B)** Performed tasks. For each prompt, participants had to choose one of the shown answers by pressing the appropriate arrow key. A frame indicated which answer was selected. In case no answer was registered, participants received feedback that their response was "too slow" (see text). **C)** Example of a presented trial. While the first four frames were presented on every trial, the last two frames were only presented every 4 trials on average (see text). RT = reaction time.

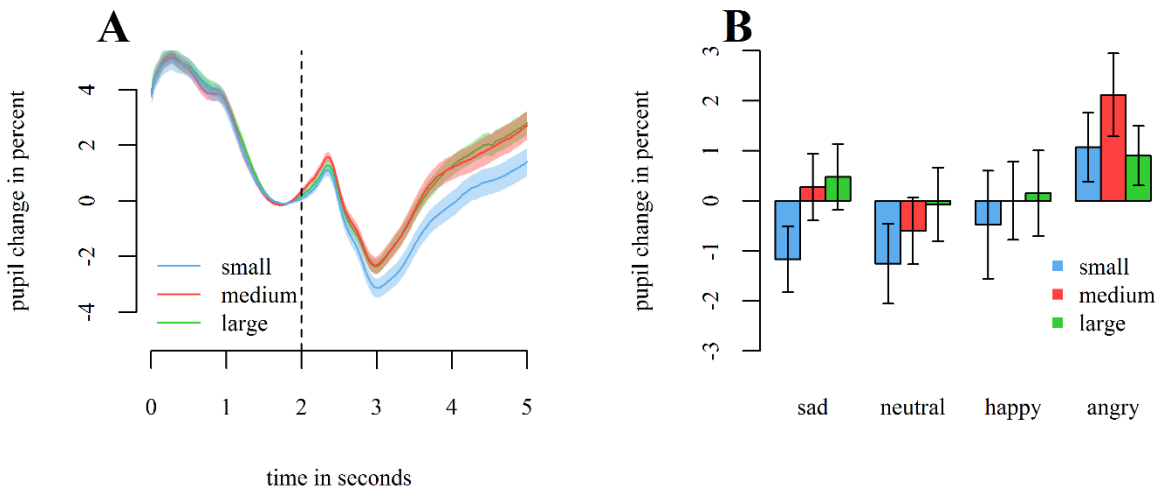

Figure 2. Pupil data. **A)** Grand averages of pupillary responses to pictures containing small, medium and large pupil sizes. Data is normalized with respect to a 500 ms baseline period preceding the picture onset at the 2-second mark (dashed line). Thick lines depict arithmetic means, whereas transparent surfaces cover within-subjects 95%-confidence intervals (Cousineau, 2005). **B)** Mean percent change of the observer's pupil in reaction to sad, neutral, happy and angry facial expressions containing small, medium and large pupils. Percent change is averaged across the 3-second interval of picture presentation. Error bars cover within-subjects 95%-confidence intervals.