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Pupil Mimicry Correlates With Trust in In-Group Partners With Dilating Pupils

M. E. Kret[1,2], A. H. Fischer[1,2], and C. K. W. De Dreu[1,2,3]
[1]Psychology Department, University of Amsterdam; [2]Amsterdam Brain and Cognition Center, University of Amsterdam; and [3]Center for Experimental Economics and Political Decision Making, University of Amsterdam

Abstract
During close interactions with fellow group members, humans look into one another's eyes, follow gaze, and quickly grasp emotion signals. The eye-catching morphology of human eyes, with unique eye whites, draws attention to the middle part, to the pupils, and their autonomic changes, which signal arousal, cognitive load, and interest (including social interest). Here, we examined whether and how these changes in a partner's pupils are processed and how they affect the partner's trustworthiness. Participants played incentivized trust games with virtual partners, whose pupils dilated, remained static, or constricted. Results showed that (a) participants trusted partners with dilating pupils and withheld trust from partners with constricting pupils, (b) participants' pupils mimicked changes in their partners' pupils, and (c) dilation mimicry predicted trust in in-group partners, whereas constriction mimicry did not. We suggest that pupil-contingent trust is in-group bounded and possibly evolved in and because of group life.

Keywords
cooperation, contagion, groups, theory of mind, emotion

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Across human evolution, cooperation and trust have enabled groups and institutions to function and prosper (Bowles & Gintis, 2011; De Dreu et al., 2010; Parks, Joireman, & Van Lange, 2013). However, within groups and institutions, individuals also need to be prepared to detect noncooperators and withhold trust, so as to avoid exploitation and betrayal (Axelrod & Hamilton, 1981; Cosmides & Tooby, 2005; Komorita & Parks, 1995). To tackle this evolutionary exchange problem, humans rely on neurocognitive architectures that help them to quickly evaluate another's emotions and trustworthiness (Adolphs, Tranel, & Damasio, 1998; Cosmides & Tooby, 2005; Tamietto & de Gelder, 2010; Winston, Strange, O'Doherty, & Dolan, 2002). During close interactions, individuals orient to a partner's tractable characteristics, such as facial features and emotion expressions. By attending to the stream of subtle moment-to-moment facial reactions during an interaction, people "feel themselves into" the emotional landscapes inhabited by their partners; they rely on, and are influenced by, implicit signals from the partner's face that are autonomic (not under someone's control) yet reflective of his or her emotions and intentions (Hatfield, Cacioppo, & Rapson, 1994; U. Hess & Fischer, 2013).

Among the many implicit cues that may inform assessments of someone's trustworthiness, the human eye region stands out as particularly salient and powerful. Both infants and adults focus on their interaction partner's eyes, grasp emotion signals, and follow gaze (Farroni, Csibra, Simion, & Johnson, 2002). It has been suggested that the unique morphology of the human eye, including the fine muscles around the eyes to express emotional signals (Lee, Susskind, & Anderson, 2013) and the eyes' large white sclera, which sets off the darker iris and makes it easier for an observer to follow another person's gaze (Kobayashi & Kohshima, 1997; Lee et al., 2013), sensitizes observers to others' pupils, their size, and the changes they undergo (Kret, Tomonaga, &

Corresponding Author:
M. E. Kret, Leiden University, The Faculty of Social and Behavioural Sciences, Institute of Psychology, Cognitive Psychology Unit, Room 2B.16, Wassenaarseweg 52, 2333 AK, Leiden, The Netherlands
E-mail: m.e.kret@umail.leidenuniv.nl

Matsuzawa, 2014). Here, we examined whether humans infer assessments of trustworthiness and untrustworthiness from their partner's eyes and base their decisions to cooperate and trust on changes in their partner's pupils.

Pupil size is autonomic and not controllable, yet it reflects ongoing cognitive effort, social interest, surprise, or uncertainty, as well as other emotions (Bradshaw, 1967; E. H. Hess, 1975; Lavin, San Martin, & Jubal, 2014). Precisely because pupil changes are unconscious, they provide an honest reflection of the person's inner state and thus may be a particularly relevant source of information for observers when making decisions to trust and cooperate. Because the pupil provides a very reliable signal, and the development of new techniques facilitates its measurement, the number of pupillometry studies are increasing. However, research to date has mainly focused on what the pupil signals, and relatively few studies have investigated how those signals are perceived and how people react to their partners' pupil size (Kret, 2015). The few studies that did examine this question have consistently shown that pupillary changes are indeed processed by observers and influence evaluations: Partners with large pupils are judged to be positive and attractive, and those with small pupils to be cold and distant (Amemiya & Ohtomo, 2012; Demos, Kelley, Ryan, Davis, & Whalen, 2008; E. H. Hess, 1975). In addition, and of interest for the present research, E. H. Hess (1975) anecdotally introduced the topic of *pupil mimicry*, which suggests that partners' pupil sizes converge during an interaction (E. H. Hess, 1975). To date, only three published studies have confirmed the existence of this phenomenon (Harrison, Gray, & Critchley, 2009; Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006; Kret et al., 2014). Two of these studies were neuroimaging studies showing that humans process partner's pupil size in the amygdala, which projects to the observer's brainstem autonomic nuclei, inducing pupil mimicry in the observer (Harrison et al., 2009; Harrison et al., 2006).

The focus of the present research is novel in three ways. First, we systematically examined whether participants' pupil size converges when others' pupils are dilating, constricting, or remain static. Second, we investigated whether this pupil mimicry holds for both in-group and out-group eyes, and third, we examined whether pupil mimicry has an impact on trust. In short, we focused on the social function of pupil mimicry and its implications for trust decisions. The finding that humans process another's pupil size may imply not only that humans attend to their companion's pupils, but also that they automatically synchronize their own pupil movements with them and—via pupil mimicry—quickly and automatically infer whether or not their partner is trustworthy. From this it follows that dilation of a partner's pupils induces dilation in the observer's, referred to as *dilation mimicry*, whereas constriction of a partner's pupils induces constriction in the observer's, henceforth referred to as *constriction mimicry*. If true, the autonomic arousal from dilation mimicry, the synchronization with a positive signal, induces the positive feeling commonly associated with large pupils and should facilitate trust. In contrast, amygdala-driven vigilance from observing constricting pupils, paired with the negative associations with small pupils, should prepare observers to withhold trust.

Recently, we observed that pupil mimicry is stronger between two members of the same species (i.e., human-human, chimpanzee-chimpanzee) than between individuals from different species (i.e., human-chimpanzee; Kret et al., 2014). This within-species advantage fits with the idea that pupil mimicry has adaptive value, in that it enables and promotes swift communication of inner states between conspecifics and facilitates shared understanding and behavioral coordination (Kret et al., 2014). Furthermore, there is abundant evidence that in humans, various forms of mimicry—ranging from body postures and facial expressions of both positive and negative emotions (Chartrand & Bargh, 1999; Dimberg, 1982) to physiological states, such as heartbeat (Levenson & Gottman, 1983)—emerge more with familiar others and in-group members than with strangers (Hess & Fischer, 2013; Norscia & Palagi, 2011; Reed, Randall, Post, & Butler, 2013). It also fits work showing that tendencies to trust and cooperate are more reliable, faster, and more intuitive when partners are considered as in-group members rather than as out-group members (Balliet, Wu, & De Dreu, 2014; Cikara & Van Bavel, 2014; Farmer, McKay, & Tsakiris, 2014). Accordingly, we examined whether pupil mimicry emerges more readily with in-group rather than out-group partners and whether propensity to trust in-group partners especially is conditioned on pupil mimicry.

In sum, the current study examined whether participants trust partners with dilating pupils yet withhold trust from partners with constricting pupils because of dilation mimicry and constriction mimicry, respectively, and whether these tendencies are in-group bounded. We explored whether predicted effects generalized across different emotion expressions (happy vs. angry) and correlated with participant's autonomic arousal and eye fixations. We measured trust by having participants make investments in incentivized trust games (Berg, Dickhaut, & McCabe, 1995). Prior to each investment decision, participants viewed a 4-s, life-size clip of the eye region of a partner from Western European (in-group) or of Asian descent (out-group); in this clip, the partner's eye region expressed a happy or angry state, in which partners' pupils dilated, constricted, or remained static. Participants' own pupils were tracked while they watched these clips and made a trust decision.

Method

Participants

Participants were students at the University of Amsterdam, had no history of neurological or psychiatric disorders, and had normal or corrected-to-normal vision. Earlier work on neurophysiological effects of partner's eye signals (pupil: Harrison et al., 2006; gaze: Schrammel, Pannasch, Graupner, Mojzisch, & Velichkovsky, 2009) included around 40 participants. To ensure enough observations of sufficient quality, we recruited 69 participants in total. Prior to hypothesis testing, we decided to exclude 8 participants because of extremely odd investment response patterns (i.e., always investing; never investing paired with unrealistically fast reaction times). We assumed these participants were not seriously engaged in the task. However, including them in the analyses did not change results or conclusions at all.

The experimental procedures were in accordance with the Declaration of Helsinki and approved by the Ethical Committee of the Faculty of Behavioral and Social Sciences of the University of Amsterdam (EC No. 2012-WOP-2159). Participants provided written informed consent prior to the experiment and received full debriefing and performance-contingent payout on completing the study.

Stimuli

To create virtual partners in the trust game, we selected pictures of four men and four women of Western European descent (in-group) with angry and happy expressions from the Amsterdam Dynamic Facial Expression Set (ADFES; van der Schalk, Hawk, Fischer, & Doosje, 2011). Asian eyes (out-group) were derived from the Japanese and Caucasian Facial Expressions of Emotion (JACFEE) database (Matsumoto & Ekman, 1989). We chose the ADFES for the in-group faces as these were taken from Dutch students and therefore closer to our participants than the Caucasian faces from the JACFEE.

Pictures were standardized in Adobe Photoshop, converted to gray scale, and cropped to reveal only the eye region. Cropping to reveal just the eye region threatens ecological validity, but enables improved measurement (Kret et al., 2014, also see Baron-Cohen, Jolliffe, Mortimore, & Robertson, 1997). After cropping each stimulus, we erased everything between the eyelashes (eye white, iris, and pupil; see Fig. 1). Next, the average luminance and contrast were calculated for each picture, and each picture was adjusted to the mean. The eyes were then filled with new eye whites and irises, and an artificial pupil was added in Adobe After Effects. The intermediate shade of the iris used in all new pictures was taken from the shade of one iris pair. To emphasize the convex shape of the eye and increase naturalness, we made the eye white around the iris brighter than the eye white in the outer edges of the eye. The exact same eye template (eye white, iris, and pupil) was used for in-group and out-group eyes, and all were in gray scale; this was done so that eye color or contrast would not play a role in our findings. Although the same template was used for all stimuli, less or more eye white was visible in particular stimuli because of individual differences in the shape of the eyes. An analysis of variance (ANOVA) on all the in-group and out-group stimuli and the number of pixels showing eye whiteness revealed no effects, which indicates that our stimulus sets did not differ in terms of eye whiteness.

Pupil dilations and constrictions occurred within the physiological range of 3 to 7 mm (always from 5 to 7 mm, from 5 to 3 mm, or from 5 to 5 mm). To increase ecological validity, we added a slightly trembling corneal reflection, and although the pupil dilation or constriction was linear, the edges were rounded off with an exponential function (natural formula implemented in After Effects) to smooth the change. Previously, we observed that the peak in mimicry occurred after 3 s (Kret et al., 2014). In the current study, we therefore based the time course of partner's pupil change on actual pupil responses from participants in our previous study, and thus the maximum or minimum of partners' pupil change was achieved after 3,000 ms, after which the pupils remained static for another 1,000 ms. Although 4,000 ms of direct eye contact may seem long, this duration is consistent with the facial-mimicry literature, in which electromyographic responses are most commonly measured over 4,000 ms (Kret, Roelofs, Stekelenburg, & de Gelder, 2013; Kret, Stekelenburg, Roelofs, & de Gelder, 2013; Niedenthal, Brauer, Halberstadt, & Innes-Ker, 2001).

Validation of in-group/out-group categorization

We verified that images of the partners reflected in-group/out-group differences. Students ($N = 29$; 7 male, 22 female) not involved in the main study evaluated the images in terms of self-other inclusion (Aron, Aron, & Smollan, 1992). Participants rated partners of Western European descent as closer to themselves and to their in-group than Asian partners, $F(1, 497) = 10.846$, $p = .001$, 95% confidence interval (CI) = [−1.627, −0.671]; $F(1, 497) = 8.510$, $p = .004$, 95% CI = [−1.722, −0.651].

Experimental procedure

Upon arrival in the laboratory, participants provided informed consent and completed medical screening. They were then seated at a 75-cm distance from the computer

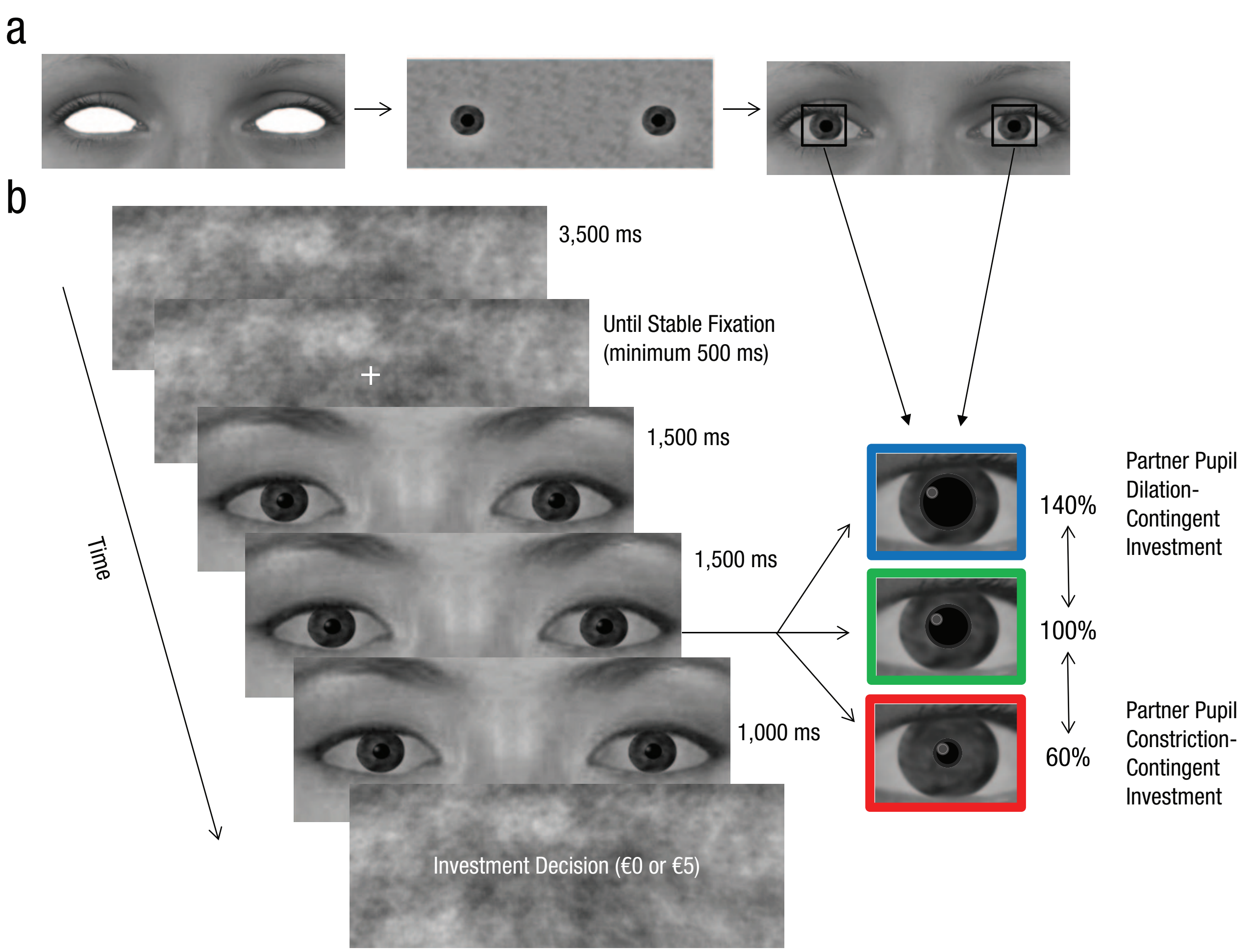

Fig. 1. Stimulus characteristics (a) and sample trial sequence (b). To create partner stimuli, we removed the eyes from pictures of the eye regions of faces and then added the same eye white, iris, and pupil to each stimulus (independent of partner's group or emotion). In each trial, a scrambled image of a stimulus was presented for 4,000 ms. The scrambled image was then replaced by the stimulus itself. In all conditions, the stimulus remained static for the first 1,500 ms, but in the dilation and constriction conditions, the pupils gradually changed in size over the following 1,500 ms and then remained at that size during the final 1,000 ms (in the static condition, shown here, pupils remained at the same size throughout the trial). Finally, a screen appeared asking participants to decide to transfer €0 or €5 to their partner. We examined the relation between changes in partner pupil size and the amount that participants invested.

screen (ViewSonic monitor, VX2268WM, 1,680 × 1,050 pixels, 120-Hz refresh rate). At this distance, eye tracking products are designed to work most optimally (Harrison et al., 2009; Harrison et al., 2006; Lavin et al., 2014). Such distance reflects a personal space that includes close relationships and informal contact but typically excludes formal business-type interactions (Hall, 1966). Partner pupils were 9 cm apart on the computer screen, which makes a horizontal visual angle of 6.867.

The experimenter referred to the trust game as an "investment task" and told participants the following. In a series of 96 investment trials, they would decide to invest €0 or €5 in another player, their virtual partner. Investments would be tripled and matched to the decision of their partner (return nothing, some specific amount, or everything). Participants were told that they would not receive feedback regarding partner decisions during the experiment, but that investments and partner choices would be matched at the end of the experiment. Decisions were binary in order to ensure that participants' fixations would not alternate between the computer screen and response box, and to reduce mental effort, which can have confounding effects on participants' pupil size. Three practice questions were used to verify that participants understood the game and the consequences of their decisions.

Partner payments were based on back-transfer decisions (i.e., decisions about the amount they would transfer back to their partners) made by 15 students (2 males, 13 females) in the role of trustee, who were given a form with 10 investment decisions of others (€0–€10) and asked how much they would reciprocate given a certain investment. These back-transfer decisions were randomly chosen and paired to those made by participants in the main experiment, to calculate actual earnings from the trust decisions. For each trial, we randomly drew a decision to calculate participants' earnings after the experiment was over (i.e., no feedback between trials was given). We informed participants that we had recordings of their partners and that prior to making decisions, they would be shown short clips of these recordings. Participants pressed a button to begin with a nine-point calibration of the eye tracker, followed by the start of the first trial. To minimize pupil constriction following new information presented on the screen, we optimally controlled the luminance throughout all trials. Each trial started with the presentation of a stimulus-unique phase-scrambled image for 4,000 ms, on which a small gray fixation cross was presented during the final 500 ms. The fixation cross was followed by an image of the interaction partner's eyes for 4,000 ms. The eyes were static for the first 1,500 ms, and then the pupils dilated, remained static, or constricted over the next 1,500 ms. For the final 1,000 ms, the pupils remained at the same diameter as at the end of the preceding interval. Next, a text screen appeared asking participants to decide to transfer €5 or nothing at all to their partner.

The experiment used a randomized block design. Participants were randomly assigned to start with the in-group or out-group block (48 trials each), and within these two blocks, emotion (anger and happiness) and partner pupil (dilating, static, and constricting) was fully randomized. In addition to the investment decisions, we measured heart rate, skin conductance responses (not analyzed because of a lack of skin conductance responses), and changes in participant's pupils while they watched the recording of their exchange partner. After the experiment, participants filled out some exit questions so we could check whether they had any ideas about the purpose of the experiment.

Data preparation

Participants' pupil size was continuously sampled every 16 ms and down-sampled to 100-ms time slots. Pupil data were collected with FaceLAB equipment (Seeing Machines, Tucson, AZ). We interpolated gaps smaller than 250 ms. Trials were excluded only if more than 50% of the data within that trial were missing (e.g., because the eye tracker lost the pupil). We smoothed the data with a 10th-order low-pass Butterworth filter. The average pupil size 500 ms prior to the start of changes in a partner's pupils (computed per participant, eye, and trial) served as a baseline (i.e., 1,000–1,500 ms after stimulus onset) and was subtracted from each sample during the remaining stimulus presentation (1,500–4,000 ms). Heart rate was measured with three 3M Red Dot disposable electrocardiogram electrodes placed around the heart and down-sampled to 500-ms time points.

Statistical analysis

There are multiple ways to analyze pupil size. While the most common way is to average pupil size over stimulus-presentation time, an alternative is to analyze the peak amplitude. Both indices are informative, but effects on the slope of the pupil response cannot be detected when pupil size is averaged over time or when just one time point is selected. Fortunately, there is a more complete and precise analysis method that allows us to model the intercept and the steepness and curvature of the slope of participants' pupil size over time. For that purpose, multilevel models have been suggested as the most appropriate analytical tool for any type of psychophysiological study, including pupillometry (Bagiella, Sloan, & Heitjan, 2000). Another advantage is the possibility of including all sampled data points in the analysis without the necessity of averaging over trials, time points, or even the two eyes, and all variance in the data is maintained while still accounting for independence in the data. With the possibility of including fixed and random factors, the statistical model can be set up in such a way that it most optimally explains this variance. Thus, all data were analyzed using multilevel modelling. Partners' pupil size was coded as −1 (constricting), 0 (static), and 1 (dilating), emotion expression was coded as −1 (anger) and 1 (happy), and group membership was coded as −1 (out-group) and 1 (in-group). Analyses of pupil-related measures included those 48 participants who had less than 50% signal loss during less than half of the trials (also see Harrison et al., 2006).

For the investment decisions, the multilevel structure was defined by the different trials, nested within participants. To test for pupil mimicry, we used a four-level model. The multilevel structure was defined by the repeated measures, that is, time (Level 1) nested in trials (Level 2) nested in eyes (Level 3) nested in participants (Level 4). Time (twenty-five 100-ms slots) was included as a repeated factor with a first-order autoregressive covariance structure to control for autocorrelation. Fixed effects were partner pupil size, partner emotion, Partner Pupil Size × Partner Emotion, partner group, Partner Pupil Size × Partner Group, and Partner Pupil Size × Partner Emotion × Partner Group. To model the curvilinear relationship between participants' pupil size and time, we included linear, quadratic, and cubic terms and interactions with the previously mentioned factors. As is common, nonsignificant factors were dropped one by one, starting with the higher-order interactions. Via log-likelihood tests, we determined whether dropping a nonsignificant factor improved model fit or significantly worsened it, in which case the nonsignificant factor was kept. After specifying the fixed effects, model building proceeded with statistical tests of the variances of the random effects. All models described here included a

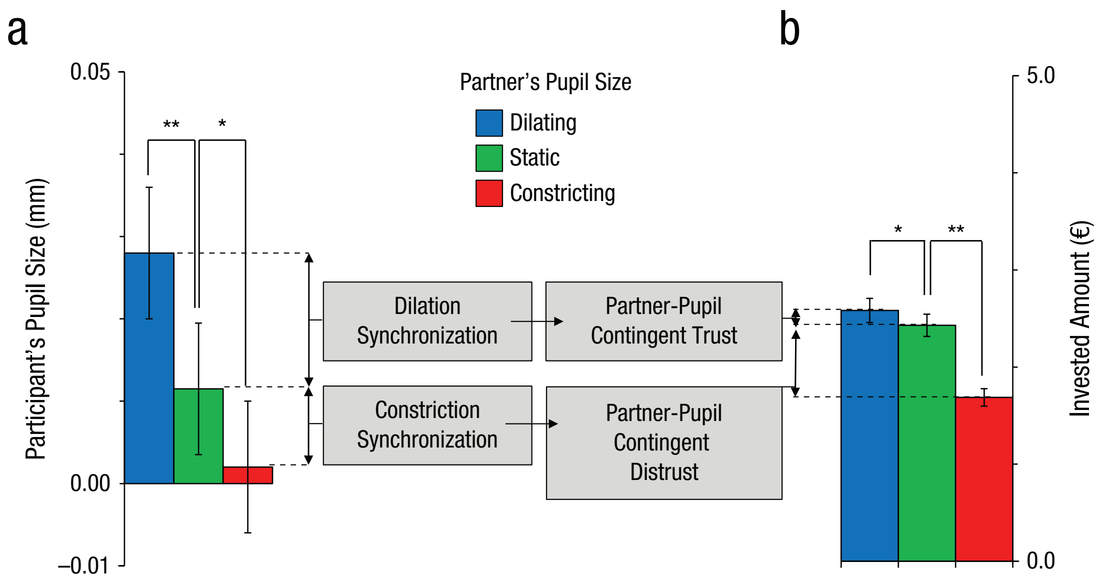

Fig. 2. Participants' mean pupil size (a) and the mean amount that participants invested in their partner (b) as a function of their partners' pupil size. The dashed lines highlight the ranges providing evidence for the hypothesized mechanisms underlying the link between participants' pupil size and participants' investment decisions. Asterisks indicate significant differences between groups (*$p < .05$, **$p < .001$). Error bars indicate ±1 *SE*.

random intercept. Random effects of trial and linear, quadratic, and cubic terms were also examined. Also, when we tested the link between mimicry and trust, we averaged as few data points as possible and therefore kept the following data structure, that is, different individual partners (Level 1) nested in participants (Level 2).

Although traditional repeated measures ANOVAs yielded similar significant results, the advantages of the current approach were that (a) intraindividual variance was maintained; (b) it allowed the analysis of participants' pupil size over time, as we could correct for autocorrelation; and (c) the most appropriate distribution function could be selected (linear for participants' pupil size or binary for their investment decisions), which rendered it a more precise method of analysis. If the linear distribution is selected, the generalized mixed model generates exactly the same *F* and *p* values as the general linear mixed model. Both are implemented in SPSS Version 20. (In the Supplemental Material available online, the full model of investments is shown in Table S1, of pupil mimicry in Tables S2–S4, and of the link between these two in Table S5.) Here, we summarize results relevant to our key predictions.

Results

Trust decisions

Results showed that happy partners were trusted more than angry partners, $F(1, 5.850) = 893.81$, $p < .001$, 95% CI = [0.870, 0.992]. The effects of partner pupil size, $F(1, 5.850) = 134.96$, $p < .001$, 95% CI = [0.362, 0.510], and a Partner Emotion × Partner Pupil Size interaction, $F(1, 5.850) = 6.242$, $p = .013$, 95% CI = [0.020, 0.167] were significant. Dilation of the partner's pupils induced trust, as reflected in a significant effect of partner pupil dilating versus constricting, $F(1, 5.850) = 4.360$, $p = .037$, 95% CI = [0.005, 0.150], and of partner pupil constricting versus remaining static, $F(1, 5.850) = 91.277$, $p < .001$, 95% CI = [0.294, 0.446]—especially when the eyes displayed happiness (Fig. 2a; also see Table S1).[1]

Pupil mimicry

The concept of pupil mimicry implies that a participant's pupil size should be larger when viewing dilating pupils than when viewing static pupils but larger when viewing static than when viewing constricting pupils. In addition, pupil mimicry might be reflected in the Linear Trend × Partner Pupil Size interaction and the Quadratic Trend × Partner Pupil Size interaction, with the former showing the steepest increase in pupil size when participants viewed partners whose pupils dilated, and the latter showing the greatest peak in pupil size when participants viewed partners whose pupils dilated. Results revealed convincing evidence of pupil mimicry with an effect of partner pupil size, $F(1, 9779.935) = 37.80$, $p < .001$, 95% CI = [0.009, 0.017] (Fig. 2b and Table S2) and a Partner Pupil Size × Linear Trend interaction, $F(1, 68296.822) = 63.60$, $p < .001$, 95% CI = [0.031, 0.052], which shows that participants' pupils were largest and increased fastest over stimulus-presentation time when partners' pupils dilated. In contrast, participants' pupils were smallest and constricted fastest when observing partners with constricting pupils. To get more insight into pupil mimicry, we decomposed this pupil-mimicry model to examine dilation mimicry, the synchronization with a positive sign, and constriction mimicry, the synchronization with a negative signal, separately.

Dilation mimicry

Dilation mimicry was revealed in effects of partner pupil size, $F(1, 6454.070) = 14.04$, $p < .001$, 95% CI = [0.004, 0.012]; a Partner Pupil Size × Linear Trend interaction, $F(1, 45734.245) = 27.97$, $p < .001$, 95% CI = [0.017, 0.038]; and a Partner Pupil Size × Quadratic Trend interaction, $F(1, 118021.618) = 4.47$, $p = .034$, 95% CI = [−0.011, −0.000]. Participants' pupils were larger, dilated faster, and showed a greater peak when participants observed partners with dilating versus static pupils. Figure 3a shows that dilation mimicry was stronger with in-group than with out-group partners, as indicated by a Partner Pupil Size × Partner Group interaction, $F(1, 6121.753) = 12.81$, $p < .001$, 95% CI = [−0.011, −0.003], and a Partner Pupil Size × Partner Group × Linear Trend interaction, $F(1, 41543.060) = 11.18$, $p = .001$, 95% CI = [−0.025, −0.007] (see Table S3).

Constriction mimicry

Constriction mimicry was shown by an effect of partner pupil size, $F(1, 6508.795) = 5.48$, $p = .019$, 95% CI = [0.001, 0.009]; a Partner Pupil Size × Linear Trend interaction, $F(1, 40893.682) = 6.10$, $p = .014$, 95% CI = [0.002, 0.021]; and a Partner Pupil Size × Quadratic Trend interaction, $F(1, 117740.802) = 4.17$, $p = .041$, 95% CI = [0.000, 0.011]. Participants' pupils were smaller, constricted faster, and showed a smaller peak when they observed partners with constricting versus static pupils. Figure 3b shows that constriction mimicry was stronger with out-group partners, as indicated by a Partner Pupil Size × Partner Group × Linear Trend interaction, $F(1, 40896.151) = 7.39$, $p = .007$, 95% CI = [0.004, 0.022] (see Table S4).

Dilation mimicry and trust

To test whether trust due to the partner's pupil change correlates with dilation mimicry and is modulated by partner's group membership, we computed a dilation-mimicry score (participant's pupil size when partner's pupils dilated minus when partner's pupils were static) and partner-pupil contingent trust (investments in partners with dilating pupils minus investments in partners with static pupils). The statistical model included the factors partner group, dilation mimicry, and Partner Group × Dilation Mimicry. The dependent variable was partner-pupil contingent trust. Results showed no main effects, but an interaction between partner group and participant's dilation mimicry, $F(1, 513) = 6.502$, $p = .011$, 95% CI = [−2.922, −0.379]. A follow-up test of this interaction within the two partner groups showed that dilation mimicry predicted trust in the in-group partners, $F(1, 513) = 4.238$, $p = .045$, 95% CI = [−2.788, −0.063], but not in the out-group partners ($p = .072$, a trend in the opposite direction; see Fig. 3c and Table S5).

Constriction mimicry and distrust

To test whether withholding trust due to a decrease in a partner's pupil size correlated with constriction mimicry and partner's group membership, we computed a constriction-mimicry score (participant's pupil size when partner's pupils constricted minus participant's pupil size when partner's pupils were static) and partner-pupil contingent distrust (investments by partners with constricting pupils minus investments by partners with static pupils). We observed that constriction mimicry did not correlate with partner-pupil contingent distrust.

Conclusions and Discussion

In social interactions, humans spend a lot of time looking into each other's eyes. The eye region in general is very expressive and, as the current study shows, the pupils especially so. This is the first study to test the relationship between pupil mimicry and behavior related to trust. As shown here, attending to other people's pupils and synchronizing with their changes helps to quickly assess trustworthiness. Possibly, when humans unconsciously mimic the dilations of another's pupil, they come to feel reflections of that person's inner state, which signals mutual interest and liking. This process could facilitate calibrated and fast decisions in interactions with strangers, especially when such decisions are not without personal risk yet are potentially beneficial to both decision makers and the larger group within which they operate.

Changes in other people's pupils have a communicative function and are contagious (Harrison et al., 2009; Harrison et al., 2006; E. H. Hess, 1975; Kret et al., 2014). Resonating with work showing that mimicry of nonverbal signals from one's in-group is modulated by contextual cues, such as competition, and can be seen as a social regulator (U. Hess & Fischer, 2013), our study suggests that the mimicry of pupil size is related to in-group but not to out-group trust. The link between dilation mimicry and partner-pupil-contingent trust was shown for in-group partners and not for out-group partners, which fits the idea that decisions

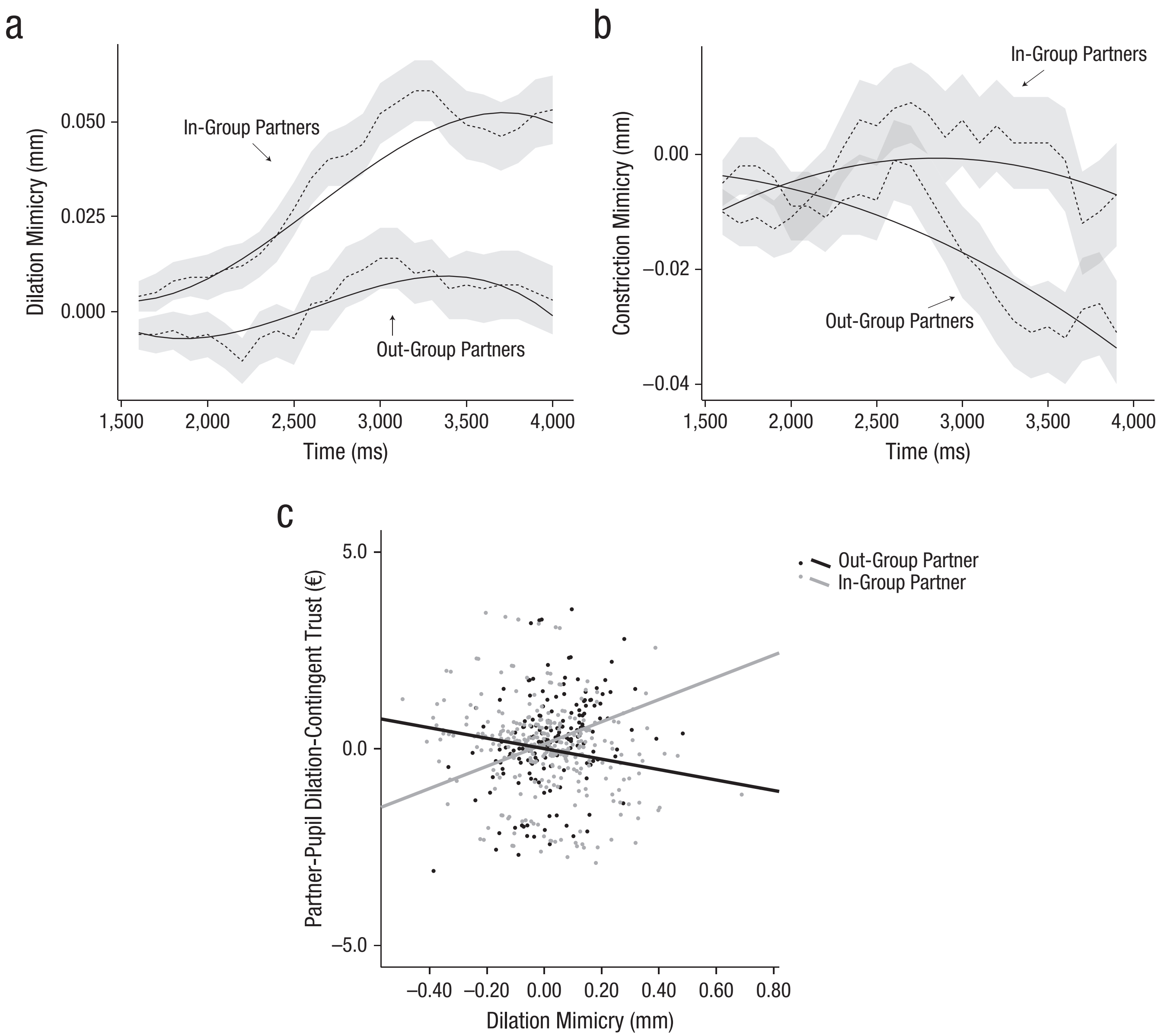

Fig. 3. Dilation mimicry, constriction mimicry, and partner-pupil-dilation-contingent trust. Mean (a) dilation mimicry and (b) constriction mimicry in response to partners' pupils are shown as a function of time. Dilation and constriction mimicry were measured by subtracting participants' pupil diameter when partners' pupils were static from the mean amount that participants' pupils expanded or constricted, respectively, in response to similar changes in the partners' pupils. The shaded bands indicate 1 *SE*, the solid lines show predicted data, and the dashed lines show observed data. The scatter plot (c) shows the relation between participants' investment decisions (investments in partners with dilating pupils minus investments in partners with static pupils) and the amount of participants' pupil dilation (dilated pupil size minus static pupil size). Data points and best-fitting regression lines are shown for in-group and out-group partners' pupils.

rest on different mechanisms when targets are in-group members versus out-group members (Cikara & Van Bavel, 2014), and resonates with the idea that human cooperation and trust are in-group bounded (Balliet et al., 2014; De Dreu, Balliet, & Halevy, 2014). We assume that whereas in-group partners' dilating pupils signal safety, enabling autonomic tendencies, such as dilation mimicry to affect decisions, partners' constricting pupils are immediately interpreted as threatening, which recruits vigilance and therefore counteracts autonomic tendencies, such as constriction mimicry, to impact on trust. Although the heart rate measures showed that pupil mimicry is more than the synchronization on the level of arousal and could not account for the effect of partners' pupils on the investment decisions, studying the neural pathways is a next step to get more insight into the underlying mechanisms. Previous research has shown that observed pupillary changes recruit activation in the amygdala (Amemiya & Ohtomo, 2012; Demos et al., 2008; Harrison et al., 2009). The ability to quickly respond to such salient cues has been attributed to an evolutionarily old subcortical route for processing of emotional information, strong enough to induce the mimicry of facial expressions (Tamietto et al., 2009). It is possible that pupil mimicry works via this route and via interactions between the amygdala and brain-stem areas that control the pupil. The effect of partner group and the implications for trust decisions suggest an interaction of this subcortical network with the empathy and theory-of-mind networks in the brain.

Recent work (Stirrat & Perrett, 2010) uncovered that men with greater facial width, as opposed to men with lesser facial width, are seen as relatively untrustworthy and are actually more likely to exploit the trust of others. A key question awaiting new research is whether pupil dilation during a social interaction is related to actual trustworthiness and therefore is adaptive. Another issue is whether the in-group/out group effect observed here can be attributed to differences in the shapes of Asian and Caucasian eyes. We emphasize that eye white, irises, and pupils were identical across in- and out-group stimuli, but we cannot exclude the possibility that effects are limited to Caucasian participants and do not generalize to Asian participants. We do know, however, that participants of Asian descent also show pupil mimicry (Kret et al., 2014).

In the current study, we observed, first, that humans extend more trust to happy partners than to angry partners, especially when these partners showed pupil dilation rather than pupil constriction. Second, we found pupil-constriction mimicry to be strongest with out-group partners and pupil-dilation mimicry to be enhanced with in-group partners. Third, pupil-dilation mimicry with in-group partners was linked to trust.

Across history, humans have been particularly focused on others' eyes and pupils. This concern with the eyes can be illustrated by the fact that the most anxiety-provoking creatures produced in films are those without or with very small pupils. In contrast, contemporary industries thrive on products that make the human eye region more visible, pronounced, and salient. The results of the current study further confirm the important role for the human eye in what people love and fear. More specifically, pupil mimicry is useful in social interactions in which extending trust and detecting untrustworthiness in others go hand in hand, and it benefits in-group interactions, survival, and prosperity.

Author Contributions

M. E. Kret, A. H. Fischer, and C. K. W. De Dreu designed the study; M. E. Kret collected and analyzed the data; M. E. Kret and C. K. W. De Dreu wrote the manuscript, and A. H. Fischer commented on a previous version.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information can be found at http://pss.sagepub.com/content/by/supplemental-data

Note

1. For this analysis and the pupil-mimicry analyses, when we added heart rate to the statistical models to control for arousal, the significance of the effects was maintained, which permitted the same conclusions.

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