What's in the eye of the beholder: The effects of pupil size and iris brightness in prosocial behavior towards non-human primates.

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Abstract

This study examines the effects of pupil dilation and iris brightness on the prosocial behavior of people and their attitudes toward primates. We hypothesize that these factors influence perceptions of primates and have an impact on monetary donations as well as ratings of attractiveness, friendliness, and cuteness. The study used a modified dictator game as the primary methodology, with 81 participants completing an online survey and meeting the criteria. Participants were randomly assigned to different iris brightness conditions, either dark or light. During the survey, participants were presented with a total of 64 image pairs, each containing facial portraits of 32 different primate species. We manipulated iris brightness and pupil size of the portraits. Analysis of the data, conducted using mixed repeated measures ANOVA, revealed that pupil dilation significantly influenced several variables. Primates with dilated pupils received higher donation amounts. Although the effects of iris brightness did not reach statistical significance, there was a notable trend indicating increased generosity toward primates with lighter irises. Interestingly, when the pupil was more visible, as shown in the light iris condition, the effects of pupil dilation tended to be more pronounced, although they did not reach the threshold for statistical significance. This research contributes to our understanding of the complex mechanisms behind prosocial behavior when exposed to specific facial features and provides insight into how humans perceive and interact with non-human species, particularly in the context of eye appearance.

Layman’s abstract

Unlocking the secrets of generosity through primate eyes.

Have you ever wondered how the size of a primate's pupils or the brightness of their eyes might affect your feelings about them? We wanted to understand how these eye features influence our generosity and our overall opinion of these magnificent creatures. For this study, 81 people took part in an online survey. We showed them pictures of different types of primates and secretly changed the size of the pupils and the brightness of the eyes in these pictures. The participants didn't know about these changes. When the primates had larger pupils, people tended to be more generous. However, the brightness of the iris didn't have a strong effect, though there was a hint

that lighter-colored eyes might make people a bit more generous when they could see the pupil better. This study helps us understand why we feel a certain way about animals just by looking at their eyes. It's like a little peek into the world of generosity and how we connect with animals, especially when we look into their eyes.

Introduction

Extensive research in psychology highlights the importance of the human face in behavior, perception, and social dynamics. It serves multiple functions in expression, communication, identity formation, and social interaction (Zebrowitz & Montepre, 2008). Studies have shown that specific facial features and their expressions influence people's judgments and predict important social outcomes toward strangers (Kleisner et al., 2013; Oosterhof & Todorov, 2008). The face is where people make their first judgments with minimal information, assessing intentions, emotions, and trustworthiness in a single glance (Todorov et al., 2009). The complexity of the face allows for a wide palette of expressions through coordinated movements, resulting in a diverse range of emotions and expressions that people can display. For example, the Duchenne smile, which involves both the upturning of the mouth and the contraction of the muscles around the eyes, is considered a genuine expression of happiness and is often associated with a more positive perception (Ekman, Davidson & Friesen, 1990). Ekman and Friesen's (1978) developed "The Facial Action Coding System" whereby in a systematic and standardized way the extensive palette of facial expressions can be analyzed and described. This system gives researchers insight into a person's emotional state or underlying emotions, even when a person tries to hide or suppress their feelings. As such, it has been widely used in research.

The perception of the face is very important in various domains of interaction. For example, research shows that facial expressions allow for emotional expression and empathy, which promotes understanding and supportive interactions (Ekman, 1992; Decety & Jackson, 2004). Nonverbal facial cues, including subtle eye movements, play a critical role in building trust and confidence in others (Frith, 2009). And the cross-cultural universality of facial expressions enhances emotional understanding across diverse backgrounds (Matsumoto & Ekman, 1989; Elfenbein & Ambady, 2003). Ekman and Friesen's (1969) research highlights the role of the face in microexpression deception detection. Furthermore, the work of Bruce and Young (1986) and

Haxby et al. (2000) underscores how facial recognition promotes social identity and recognition. In attachment studies, Bowlby (1982) and Ainsworth et al. (2015) emphasize the importance of facial interactions in early attachment and relationship formation, particularly the importance of the eyes as a window to emotion and attachment.

While the face can provide a variety of social information, the eyes have a particularly prominent role within the face. They contain distinct features, dynamic expressions, and nonverbal cues that significantly influence how we perceive others and how we are perceived. The eyes play a central role in prosocial behavior, contributing to nonverbal communication, attention, empathy, trust, cooperation, facial recognition, and social engagement (Kleinke, 1986; Emery, 2000). Research suggests that the eyes are critical for conveying emotional information, understanding the mental state of others, and forming social connections (Tomasello et al., 2007). Farroni et al. (2002) found that even within the first few days of life, newborns showed a preference for faces with direct eye contact, suggesting an early sensitivity to this social cue. These findings support the notion that the ability to perceive and respond to eye contact is an innate and fundamental aspect of human social development, emphasizing the importance of the eyes in early communication and bonding processes. Studies using eye-tracking show that humans tend to pay more attention to certain areas, particularly the eye region, than for example our primate relatives. Primates pay more attention to social stimuli, such as facial characteristics and body parts, in line with their social nature (Kano & Tomonaga, 2009).

In studying the influence of eye contact on social interactions and perception, researchers have focused on specific eye features that may influence prosocial behavior. Haley and Fessler (2005) demonstrated in their study that the presence of eye-like stimuli in the environment increased participants' generosity, suggesting the existence of automatic cognitive mechanisms for detecting social gaze and regulating social behavior. Numerous replication and field studies have confirmed the influential effects of eye images in promoting generosity and prosocial behavior (Oda et al., 2011; Ekström, 2011). However, some laboratory studies provide conflicting results. For example, Tane and Takezawa (2011) conducted a study in a dark room and concluded that the observer effect did not manifest in darkness, likely due to the lack of identification of the other person. Thus, it is important to note that procedural differences and contextual factors could contribute to the differences between these studies.

Senju and Johnson (2009) investigated in their critical review how eye contact influences various aspects of social interactions and perception. With their findings, they suggested that eye contact has a profound influence on various aspects of social interaction, attention engagement, emotional perception, and social cognition. They state that eye contact can enhance the perception of trustworthiness, facilitate emotion recognition, and foster a sense of connection and engagement with others.

A particularly intriguing aspect of the eyes is the role of pupil size in the human eye's appearance, which is beyond conscious control. Pupil diameter not only adjusts according to light intensity but also correlates with various affective and cognitive states (Laeng et al., 2012). Studies have revealed that individuals with larger pupils tend to be perceived as more positive and attractive, while those with smaller pupils are often seen as distant and cold (Kret et al., 2015). Furthermore, people with dilated pupils are generally considered to be more trustworthy (Amemiya & Ohtomo, 2012; Kret and De Dreu, 2017, 2019). These findings add to the growing body of literature that emphasizes the intricate relationship between the eye and prosocial behavior, highlighting how specific features of the eye, such as pupil size, can influence social perception and engagement.

The mechanism of the pupil comes hand-in-hand with the iris. The iris is the colored, ring-shaped part of the eye that surrounds the pupil. The iris contains muscles that contract or relax, thereby altering the size of the pupil and regulating the amount of light that reaches the retina. Research on the autonomic nervous system links pupil dilation, controlled by the iris, to social and emotional responses. Pupil size reflects emotional arousal and attention, and during prosocial behavior, such as empathy or generosity, pupils tend to dilate. The iris response may be associated with the emotional and cognitive processes involved in prosocial behavior. Furthermore, the connection between the iris and oxytocin, a hormone involved in social bonding, suggests a potential link between the iris response and prosocial behavior influenced by oxytocin (Kret and De Dreu, 2017).

Although the pupil and iris have been identified as a critical part of the eye for eliciting prosocial effects, no studies have specifically examined the role of iris brightness in this context. As the pupil is the opening of the iris, changes in iris brightness may influence the visibility of changes in pupil size (Perea-García et al., 2021). In a study by Perea-García et al. (2022), primates were found to have a wide variety of eye colors, including variation in iris coloration and

brightness. This suggests the intriguing possibility that certain iris colorations may facilitate the perception of pupil dilation due to the contrast between the iris and the pupil. The study by West (2011) focuses on the perceived differences in gaze direction between individuals with dark and light irises. They found that monocular gaze (single eye) is often perceived as deviating outward from its true direction, more so in people with light irises, especially when the pupils are absent or centered. Binocular gaze (both eyes) is generally perceived as centered, but pupil centration within light irises significantly influences perceived gaze direction, possibly due to the interaction of brightness contrast between the iris and the surrounding eye area. In short, while existing evidence suggests that the brightness of the iris affects the perception of the pupil, no studies address whether this could affect processes of social perception.

Humans worldwide have a large palette of iris coloration and brightness. Despite the significant variation in iris color in humans compared to other species (Negro et al., 2017), research has not found evidence that these differences affect perceived attractiveness (Gründl et al., 2012). However, Hecht and Horowitz (2015) examined human preferences for various physical attributes of dogs, including eye-related features. Their results showed that participants preferred human-like features, such as colored irises over complete darkened eyes. These findings suggest that dogs elicit positive emotional responses and increase their perceived attractiveness or "cuteness" to humans, potentially leading to more altruistic behavior toward animals with lighter irises. It is thus conceivable that changes in iridal brightness affect processes of social perception by themselves, in addition to how these changes affect the visibility of the pupil.

Given that iris brightness could influence the perception of pupil size, differences in iris brightness could influence the role of pupil dilation in prosocial behavior. Furthermore, it is possible that the perception of brighter irises directly influences prosocial behavior, independent of its effect on the perception of changes in pupil size.

In this study, we manipulate two aspects of external eye appearance, namely pupil size and iris brightness, to investigate their potential influence on prosocial behavior. As primates exhibit a vast array of external eye morphologies, our stimuli appear naturalistic while allowing for manipulation. By using images of other species, such as primates, we can experiment with altering pupil size and iris brightness without making the stimuli appear unnatural to our participants.

Our primary objective is to test whether exposing participants to images of primates with dilated pupils motivates them to make greater donations compared to exposure to images of

primates with constricted pupils. We aim to determine if similar effects to those observed in humans (Kret et al., 2015), where pupil size is linked to various affective and cognitive states, can be observed in the context of prosocial behavior towards members of other species. Additionally, we explore the influence iris brightness on prosocial behavior. The manipulation of iris brightness is another crucial aspect of our study, where we investigate whether the effect of pupil size on prosocial behavior is more pronounced when the images of primates represent brighter irises as opposed to darker ones (Perea-García et al., 2021). By examining these aspects of external eye appearance and their impact on prosocial behavior, we hope to gain a deeper understanding of the role that eye features play in influencing human interactions and behavior.

Based on existing evidence from prior studies and previous literature, we have formulated the following hypotheses:

H1: Humans have more positive attitudes towards primates with dilated pupil size compared to constricted pupils. This positive attitude is expected to influence the amount of monetary donation and the ratings of attractiveness, friendliness, and cuteness. This hypothesis is supported by the findings of Amemiya &Ohtomo (2012), Kret, et al. (2015) and Kret & De Dreu (2019), where faces with larger pupils were perceived as more attractive, friendly, and trustworthy.

H2: Humans have more positive attitudes towards primates with a brighter iris. Grundl et al. (2012) found no difference in attractiveness based on different iris colorations in humans. However, Hecht and Horowitz (2015) found in their study that dogs with visible iris color were preferred over dogs with completely black irises, suggesting a potential preference for visible iris color in humans.

H3: The effect of pupil dilation is greater when combined with lighter irises compared to darker irises. This hypothesis is based on the proposal that the contrast between lighter irises and the pupil facilitates the perception of changes in pupil size (Perea-García et al., 2021; West, 2011).

These hypotheses serve as the foundation for investigating the influence of pupil size and iris brightness on human attitudes and behavior towards primates. By testing these hypotheses, we aim to expand our understanding of the factors that shape human perceptions and responses to non-human species, particularly in the context of variation in pupil size and iris brightness.

Method

Participants

The recruitment was carried out via SONA, a management tool used by the University of Leiden. To raise awareness of this particular study, online flyers were additionally circulated through selected groups on social media. The main characteristics of the research sample were (psychology) students, both male and female, ranging in age from 18 to 40.-A total of 133 students from Leiden University were recruited to participate in this study. Due to experimenter error or incomplete data, we decided to exclude 12 participants prior to hypothesis testing. The final sample of this study consisted of 121 participants between the ages of eighteen and thirty-eight (109 females, 11 males, and 1 other, M_{age} = 19.88, SD_{age} = 2.92). We further used two manipulation checks – one to remove participants who noticed that the pictures had been manipulated, and one more that specifically asked which part of the primate had been manipulated (n=40), resulting in a total of n=81 (male=5) eventually included in the analysis. The participant sample shows a gender disproportion, which will require additional attention. This disproportion is discussed in both the results and discussion sections of this paper.

The University of Leiden Ethics Board approved the experimental content and procedures of this study (EC No. 2020-12-18-J. TAN-V1-2833). The participants provided informed consent prior to the experiment. After completing the study, they received a debriefing and a pay-out of two credits, as well as a chance to win up to €20 through a lottery.

Procedure and experimental task

The implementation of this study was an online survey through Qualtrics®, where the participants were tested individually. Participants were informed in advance that participating on a mobile device was not permitted and that the survey had to be conducted using a computer. Additionally, participants were asked to complete the survey in a quiet room and in isolation to minimize external influences.

Before starting the survey, participants were given information about participating in a study on the social perception of non-human primates (Appendix A1). They were also notified of the option to enter a lottery, where one out of ten participants could win up to €20, depending on the randomly selected trial's allocation of money. After signing the informed consent (Appendix

B) and being notified of the possibility to withdraw from the survey at any time, the actual experiment could begin.

Prior to the trial, participants were randomly divided into two different conditions, the light iris color condition and the dark iris color condition. Then, participants were given a practice trial, followed by two blocks of 32 trials each, totaling 64 trials. The order of trials was randomized within these blocks, with a short pause provided between the two blocks. Each trial started with an image of the primate displayed on the screen for 4000 milliseconds, ensuring that all participants had sufficient time to view the image. Immediately after, participants were asked how much money they would donate to charity to preserve the primate, ranging from 1 to 20 Euros. This question was based on the modified dictator game (Camerer, 2011) for this study. Participants were informed in advance that the potential money would be donated to charity due to the absence of a real partner in this setting. The assumption was made that participants would not retain the total amount.

Following that, participants were asked three additional questions about the grade they would assign to the primate for kindness, cuteness, and attractiveness, on a scale of 1-10. These questions were put in a different order on each new trial to minimize the chance of random answers. The image of the primate remained visible during all the questions to ensure participants could still look at the primate.

After the final trial, participants were presented with several closing questions. These questions checked the manipulation and controlled the belief regarding the donation of the money (Appendix C). Participants in this study were then debriefed through an explanation letter about the study's content and received gratitude for their participation (Appendix D). Additionally, participants were provided with contact details for any possible questions or comments.

Stimuli

This study used a questionnaire containing two sets of 64 stimuli from 32 source images. These images show portraits of 32 different primate species. The images had to meet a number of requirements in order to be used in this study. First, only one species must be seen in the image. Second, the image must show a portrait of the primate’s head and is full faced. The face and eye gaze must be directed towards the participant (facing forward). Third, the distinction of the pupil and iris area of the primate’s eyes, must be relatively clear to make manipulation of the pupil size

possible. Fourth, the primates used in these images should be representative of the whole primate radiation, which is composed of the following clades; 1) the prosimians, 2) new world monkeys, 3) old world monkeys, 4) hominids. The number of primates per clade was evenly distributed and therefore each clade was represented by 8 different species.

This study is based on a 2 (lightened vs. darkened iris) x 2 (dilated vs. constricted pupil) design. For the creation of the testing stimuli, each source image was edited into the four testing stimuli with the program Adobe Photoshop®. All images show the face completely and are 600 X 600 pixels. By using the "Screen" blending mode in Photoshop®, the iridal area was lightened 75%, to create the lightened iris stimuli (fig 1&2). By using the "Multiply" blending mode in Photoshop®, the iridal area was darkened 75%, to create the darkened stimuli (fig. 3 & 4). To shape both the pupil stimuli, 75% of the iris size was used for pupil enlargement to create the dilated stimuli (fig 2 & 4), and 25% of the iris size to create pupil constriction (fig. 1 & 3).

Figure 1. Constricted pupil, brightened iris

Figure 2. Dilated pupil, brightened iris

Figure 3. Constricted pupil, darkened iris

Figure 4. Dilated pupil, darkened iris

Dictator Game

One of the questions in this study's questionnaire was based on the Dictator Game (DG), an experimental paradigm that is widely used in social psychology. The "classic" dictator game involves two participants: the dictator and the recipient. It is designed to study altruistic behavior, fairness, and decision-making in a controlled laboratory setting (Bolton et al., 1998). In the dictator game, the dictator is given a fixed amount of money and has the exclusive authority to decide how to divide it between himself and the receiver, without regard to the receiver's preferences or input. The dictator's decision reflects his willingness to be altruistic or self-interested toward the receiver. The receiver can accept or reject this offer, but remains unchanged (Bolton et al., 1998).

Previous studies have introduced variations of the DG (Nettle et. al., 2013; Kret et al., 2017). In this particular study, the recipient (referred to as the primate) had no role in accepting or rejecting the money offered by the dictator. Instead, the amount a participant was willing to give to protect the primate in a given stimulus served as a measure of prosocial behavior toward the primate. The absence of a real partner in this setting was acknowledged, and participants were informed that the potential money would be donated to charity, with the expectation that the participant would keep only a portion of the amount. In the traditional DG, the potential payment is divided into two equal amounts. As a research tool, the DG provides valuable insights into human preferences for fairness, cooperation, and social norms.

Statistical analysis

For the pre-processing of the data in this study, we utilized the data analysis software R®. Since our dependent variable is continuous (including the amount of donated money, attractiveness, cuteness, and friendliness), while our independent variables are categorical, we opted to perform a repeated-measure ANOVA. Additionally, our independent variables, pupil dilation, has two levels within subjects (large vs. small pupil), while the other independent variable, iridal coloration, has two levels between-subject factors (light iris vs. dark iris). This led us to conclude that a mixed repeated-measure ANOVA was the most appropriate choice. Assumptions for sphericity and homoscedasticity of the residuals were met.

Results

Tabel 1.

Summary of demographics:

Variable	Statistics	Explanation
Age	M = 19,75, SD = 2.562 Min = 18, Max = 32 18 = 38,3% 19 = 24,7% 20 = 16,0% 21 = 7,4% 22 = 3,7% 24 = 2,5% 25 = 3,7% 26 = 1,2% 29 = 1,2% 32 = 1,2%	Most participants were between the 18 and 19 years
Gender	Female = 92,6%, Male = 6,2%, Other =1,2%	More than 9/10 were female
Iris condition	Dark = 44,4 % Light = 55,6	Light-Iris condition was slightly more represented

Research question 1

We tested all our hypotheses by running a repeated multi-level ANOVA that mixes one between-subjects variable and one within-subjects variable. The between subjects' factor is iris brightness. The within-subjects factor is pupil size. To test the first hypothesis - that humans hold more positive attitudes towards primates with dilated pupil sizes compared to constricted pupils - , we examined the amount of money donated by participants in the DG (ranging from 0 to 20). Descriptive statistics (Table 2) revealed that, on average, our participants donated greater amounts in the dilated pupil condition (M = 12.824, SD = 6.619) than in the constricted pupil condition (M = 11.824, SD = 6.689). The main effects of dilated pupil size compared to constricted pupils, $F(1, 9) = 20.38$, $p < .001$, was highly significant which indicated that participants donated more money to the primates with dilating pupils compared to those with constricting pupils (Figure 5). These results were in line with the previous findings of Amemiya and Ohtomo (2012) and Kret, and De Dreu (2019), where faces with larger pupils were perceived as more attractive, friendly, and trustworthy.

Table 2

Differences in donation means in the two conditions of pupil dilation
Descriptive Statistics

	Mean	Std. Deviation	N
Donation in dilated condition	12.089	6.619	2592
Donation in constricted condition	11.824	6.689	2592

Research question 2

To test the second hypothesis where we state that humans have more positive attitudes towards primates with a brighter iris, we examined the amount of donated money by the DG (ranging from 0 to 20) based on the between-subjects factor of iris brightness. Descriptive statistics (Table 3) revealed that, on average, our participants donated greater amounts in the light iris condition (M = 12.812, SD = 6.839) than in the dark iris condition (M = 10.889, SD = 6.257), which was in line with Hecht and Horowitz's (2015) research where they found a greater preference in colored irises over completely darkened eyes. Figure 5 shows this trend, however, the effect size was not significant, $F(1, 6039) = 1.6853$, $p = .1981$).

Table 3

Differences in donation means in the two conditions of iris brightness
Descriptive Statistics

	Mean	Std. Deviation	N
Donation in light condition	12.812	6.839	2880
Donation in dark condition	10.889	6.257.	2304

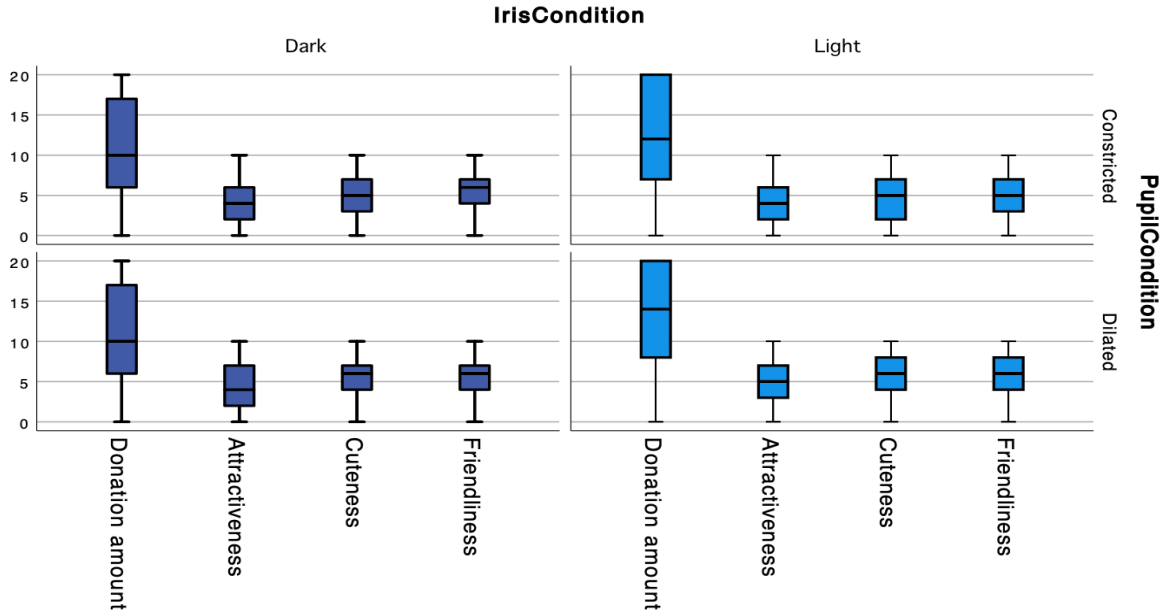

Figure 5. Boxplot of the two factorial independent conditions; Pupil size and Iris brightness and their effect on the four dependent variables; dictator game, attractiveness, cuteness and friendliness.

Research question 3

To test the third hypothesis, which states that the effect of pupil dilation is greater when combined with brighter irises compared to darker irises, we examined the interaction effect of two factors: pupil size (within-subjects) and iris brightness (between-subjects). We found no significant interaction effect between pupil and iris conditions $F(1, 9) = 1.3783$, $p = .2440$; however, the plot showed a slight trend towards a bigger difference in the dilated condition (Figure 6). This trend aligns with the proposal of Perea-García et al. (2021) and West (2011) that the brightness of the iris importantly affects the perception of the pupil.

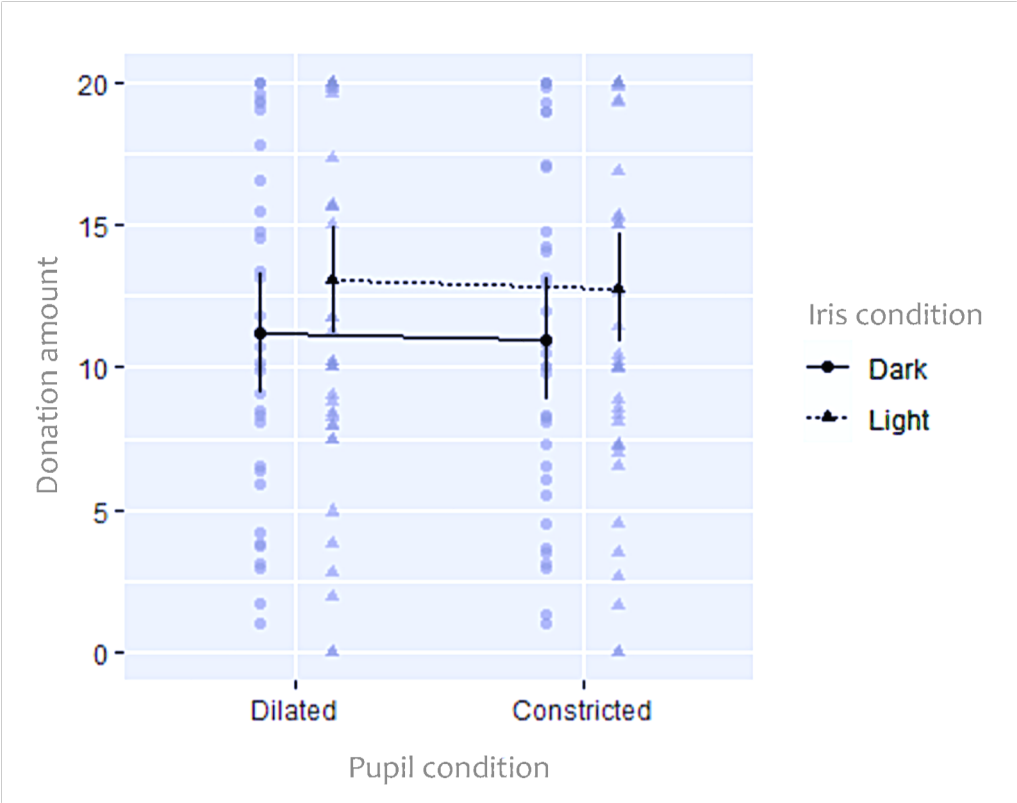

Figure 6. The four conditions; dark – and light iris; dilated- and constricted pupil size on the donation amount (ranging from 0 to 20).

General discussion and conclusion

In this study, we examined the effects of two external factors of eye appearance - pupil size and iris brightness - on prosocial behavior. We aimed to address inconsistencies in previous research by investigating how both pupil size and pupil visibility influence prosocial behavior by making people feel generous when they look at the eyes. The use of naturalistic stimuli, including images of primates, allows for manipulation while maintaining realism. Our primary goal was to determine whether exposure to images of primates with dilated pupils leads participants to make larger donations compared to primates with constricted pupils. We sought to uncover whether similar effects observed in humans, linking pupil size to emotional and cognitive states, apply to prosocial behavior towards nonhuman primates. In addition, we investigated whether iris brightness influences prosocial actions. We also manipulated iris brightness and investigate whether the effect of pupil size on prosocial behavior is enhanced with brighter irises.

Our study revealed that participants donated more money to primates with dilated pupils compared to those with constricted pupils. This finding aligns with previous research suggesting that individuals with larger pupils are often perceived as more positive, attractive, friendly, and trustworthy (Amemiya & Ohtomo, 2012; Kret & De Dreu 2019; Kret et al., 2015). These positive perceptions may have motivated participants to engage in more prosocial behavior, as evidenced by their increased donations. This result supports our first hypothesis (H1), suggesting that humans hold more positive attitudes toward individuals with dilated pupil sizes, which, in turn, influences their willingness to engage in prosocial actions.

In regard to our second hypothesis (H2), we did not find a significant effect of iris brightness on prosocial behavior. Participants' donations did not significantly differ between primates with light and dark irises. This result aligns with the findings of Grundl et al. (2012), who also found no difference in attractiveness based on different iris colors in humans. Therefore, while iris brightness may influence other aspects of perception, such as preferences for human-like features, such as colored irises over completely darkened eyes (Hech & Horowitz, 2015), it does not appear to directly impact prosocial behavior in the context of our study. The lack of significance in this outcome could be attributed to several factors, with the most apparent being the issue of statistical power, particularly after we had to exclude one-third of the participants following the manipulation checks. This issue of statistical power will be further addressed in the limitations section.

Regarding our third hypothesis (H3), which proposed that the impact of pupil dilation might be more pronounced when combined with brighter irises, our study did not find a significant interaction effect between pupil size and iris brightness on prosocial behavior. Although we observed a noticeable trend indicating a larger difference between the two iris conditions, particularly in the case of pupil dilation, this trend did not reach statistical significance. This trend observation aligns with prior research suggesting that the contrast between iris brightness and the pupil could aid in perceiving the pupil (Perea-García et al., 2021; West, 2011). While our findings suggest that iris brightness may not significantly influence the effect of pupil size on prosocial behavior within the scope of our study, a more substantial sample size may reveal a notable effect. Further research is needed to thoroughly investigate this potential interaction.

An alternative explanation for our findings may lie in the importance of specific eye features in inducing positive emotional responses. This concept is related to the baby schema

proposed by Lorenz (1943). According to the baby schema theory, facial characteristics that resemble those of infants, such as bulging cheeks and large eyes, tend to trigger nurturing responses in adults. It is worth noting that children generally have larger pupils than adults, a natural phenomenon attributed to the decrease in pupil size with age (Birren et al., 1950). The tendency toward more positive behavior in response to infant-like features is not limited to human infants; it extends to animals with similar features, such as cats and dogs. Previous research has shown that faces with infant-like features are often perceived as cuter than faces with more adult-like features (Archer & Monton, 2011; Little, 2012). In a study conducted by Hecht and Horowitz (2015), participants showed a preference for eye features associated with the infant schema, specifically large and wide eyes. In addition, participants showed a preference for features similar to those found in humans, such as colored irises. These combined findings suggest that certain eye characteristics in animals, including the adult primate faces in our study, can be interpreted as an infantilization of their appearance. This, in turn, may lead to positive emotional responses that increases their perceived attractiveness or cuteness to humans. Ultimately, this may contribute to more altruistic behavior toward animals, especially those with lighter irises. Our research contributes to the growing literature on the role of facial features, particularly the eyes, in shaping human social interactions. The finding that dilated pupils led to increased prosocial behavior highlights the importance of pupil size as a nonverbal cue that influences interpersonal perceptions.

In the broader context of human social interactions, it is worth noting a study conducted by Lior Zeevi et. al. (2022). Their research explored the co-regulation of behavior and physiology during romantic interactions. While our study focused primarily on specific facial features, Zeevi's research explored how physiological and behavioral responses synchronize during social encounters, particularly in the context of romantic attraction. Zeevi's findings show the importance of co-regulation in promoting attraction between individuals. This suggests that physiological synchrony functions as a mechanism that supports bonding and prosocial behavior. Our findings complement Zeevi's work by highlighting the specific role of pupil size as a nonverbal cue in this process. Although our studies differ in subject matter, both contribute to our understanding of how humans perceive and respond to various visual cues, physiological factors, and behavioral dynamics in social interactions. Altogether, they provide valuable insights into the intricate mechanisms that underlie human social behavior and decision making. These insights can have far-reaching implications, extending from the area of romantic relationships to their relevance in

cultivating trust in a wide range of social and professional settings. Indeed, the practical implications of our findings are noteworthy, particularly in areas where trust and prosocial behavior play a central role. For example, in business negotiations, the ability to build trust can significantly influence negotiation outcomes (Lewicki et al., 1997). Our results suggest that individuals who wish to foster trust and prosocial behavior might consider using the subtle yet powerful cue of dilated pupils during negotiations. Additionally, in interpersonal relationships, knowing how certain cues, such as dilated pupils, can influence perceptions and behaviors can help individuals navigate social interactions more effectively. This knowledge can also be beneficial in the commercial sector, where displaying people or animals with dilated eyes could potentially enhance the generosity of individuals, such as in charity campaigns or advertisements. Therefore, individuals seeking to foster trust and prosocial behavior may be able to use the subtle yet powerful cue of dilated pupils to their advantage.

Moreover, this study underscores the complexity of human perception and the multifaceted nature of prosocial behavior. While pupil size had a clear and significant effect on giving, iris brightness did not have a similarly clear effect. This suggests that people's judgments and behaviors are influenced by a combination of facial cues, and the influence of each cue may vary in different social contexts. Future research could explore how these cues interact and whether the influence of iris brightness on prosocial behavior is more pronounced in certain situations or with different stimulus materials.

Looking ahead, our study opens avenues for future research to explore how different facial cues, including pupil size and iris brightness, interact in different social contexts and with different stimulus materials. Investigations of the combined effects of these facial features, synchrony, and their contextual dependencies could provide deeper insights into the mechanisms underlying human social interactions and prosocial behavior. Cross-cultural studies could also contribute to a broader understanding of how these cues and synchrony operate in different societies, shedding light on cultural variations in human social behavior.

Limitations

Despite the valuable insights provided by our study, several limitations should be considered when interpreting the results. One notable limitation is the gender disproportion in our participant sample, with a majority of females. This imbalance may introduce bias into the

findings, as gender can influence social perceptions and behaviors (Eagly & Steffen, 1986). Future studies should strive for more balanced gender representation to ensure the generalizability of our results to a broader population. Additionally, the age range of our sample was limited to 18 – 32, with most participants being younger than 22. This raises questions about whether young people generally donate more than older individuals or if there are age-related differences in prosocial behavior. Previous research has shown that young people are less likely to donate money than older individuals. Furthermore, men were less likely to donate than women (Lee & Chang, 2007). These demographic factors may have influenced our results and limit the generalizability of our findings to a wider age and gender range.

Another possible impact on the observed effects could be the background of our participants. All participants were students in the faculty of social sciences, with a majority studying psychology. These students are already part of the WEIRD demographic (western, educated, industrialized, rich, and democratic), which comprises the majority of participants in scientific research (Henrich et al., 2010). The overrepresentation of WEIRD participants may not accurately represent the general population's attitudes and behaviors. Moreover, it can be assumed that these participants, being social science students, are already interested in social matters due to their choice of study. This predisposition may have made them more willing to donate in the first place, potentially influencing the observed prosocial behavior. To address this limitation, future studies should aim to replicate this experiment with a more diverse participant pool that includes individuals from different educational backgrounds and demographic groups.

In addition to these demographic considerations, one limitation of our study is the sample size, which affected our statistical power to detect effects. We employed a within-subjects design for pupil size and a between-subjects design for iridal brightness. Within-subjects designs tend to be more statistically powerful because they reduce individual variability. In contrast, between-subjects designs often require a larger sample size, sometimes double or more, to achieve the same level of power. As a result, we observed a significant effect in pupil size but not in iridal brightness, partially due to differences in statistical power between the two designs.

Furthermore, our study employed a controlled online survey setting, which, while providing experimental control, may not fully capture the complexities of real-world prosocial behavior. Participants possible awareness of their donations not directly benefiting the primates, could have influenced their decisions. Real-world prosocial behavior is influenced by a broad scale

of factors, including empathy, social norms, and the perceived impact of one's actions, which were not measured in our study. To enhance external validity, future research could explore prosocial behavior in more ecologically valid settings to better understand how our findings apply to real-world contexts.

Lastly, this study did not consider potential cross-cultural variations in the perception of facial cues and prosocial behavior. Cultural differences can significantly impact social norms and behaviors (Markus & Kitayama, 1991). Given that our participant pool was predominantly from Western societies, the extent to which our findings generalize to other cultural contexts remains uncertain. Future research should investigate whether our results hold true in diverse cultural settings, which could provide valuable insights into the universality or cultural specificity of the observed effects.

Conclusion

Our study revealed that larger pupils elicited higher donation amounts, and this effect was more pronounced when the iris was brighter. However, while our research offers valuable insights into the impact of pupil size and iris brightness on prosocial behavior, it is essential to consider several limitations when interpreting the results. These limitations primarily concern sample characteristics, external validity, and the potential influence of cross-cultural variations. Addressing these limitations by involving more diverse and larger participant groups and exploring various experimental settings will enhance our understanding of the extent to which our findings can be applied to different situations and populations.

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Appendices

Appendix A - Information letter

Information letter

Aim of the study
The aim of the study is to investigate the social perception of nonhuman animals.

Design of the study
In addition to the course credits you receive for participation, you can enter a lottery to win an extra €20 at the end of the research project.

This study requires that you be seated in front of a computer monitor, in a slightly darkened room to avoid glare on the computer monitor. Please complete this study by yourself.

You will be asked to pay attention to the images presented on the screen during the experimental trials. In each trial, you will first view an image displaying a primate species. Then you will be asked to decide how to divide €20 – the maximal prize money from the lottery. You can allocate the €20 between yourself and a non-profit cause to protect this primate species from extinction (the Conservation Fund of the International Primatological Society, and **the money you have allocated will actually be given to them**). Then you will be asked to answer three questions about this species. The experiment will begin with a practice session, followed by a total of 64 test trials and several exit questions at the end. The entire experiment will take approximately 1 hour to complete.

After all data collection has been completed, 10% of the participants will be randomly selected to win the lottery. The winners will receive up to €20 based on how they have allocated the money during the trials.

Specifically, for each winner, we will then randomly select one of the 64 experimental trials he/she has completed. The amount the winner has allocated to the primate in that particular trial will be the amount given to the non-profit cause for the conservation of the primate species; the rest will be given to the winner him/herself.

Drawbacks and benefits for the participant
Participating in this study will take approximately one hour and you will receive 2 credits, plus a potential monetary payoff of up to €20 if you win the lottery.

If and only if you win this lottery, we will reach out to you through email by the end of the fall semester, 2020 regarding the payout of participant compensation. We will then collect additional personal data (Address, IBAN bank account number and registered name for this bank account). These personal data will be saved separately from the research data and will be shared with the financial administration of Leiden University, who will pass this information on to the Tax Department. The University is legally obliged to report the participant compensation to the Tax Department. Whether or not the Tax Department will make you pay taxes on these cash payments, will depend on your personal situation.

Voluntary participation
Your participation is voluntary. Even after you give consent to participate in this study, you will always be able to withdraw that decision at any point of the experiment. You will not owe the researcher any explanation, and you will still receive the corresponding credits for participating in the study (i.e. 1 credit per 30 minutes).

Confidentiality of data
You can be assured that all information and data that is acquired during this study is treated confidentially. All data will be coded with a number for identification. Only the researchers have access to the names that match the numbers. The outcomes of this study may be used for scientific publications, but your individual data will not be recognizable. All digital data will be transferred securely to a university-owned server (with access restricted to researchers involved in data analysis) after each day of testing where they will be stored for a maximum duration of five years, after which they will be discarded.

Requirements for this study
To participate in the study, you must be 18 or older.

Contact for privacy related matters
University Data Protection officer
email: privacy@bb.leidenuniv.nl

-
Principal investigator:
Dr. Jingzhi Tan
e-mail: jztan.pku@gmail.com

Appendix B - Consent form

Consent form

For participation in the scientific study:

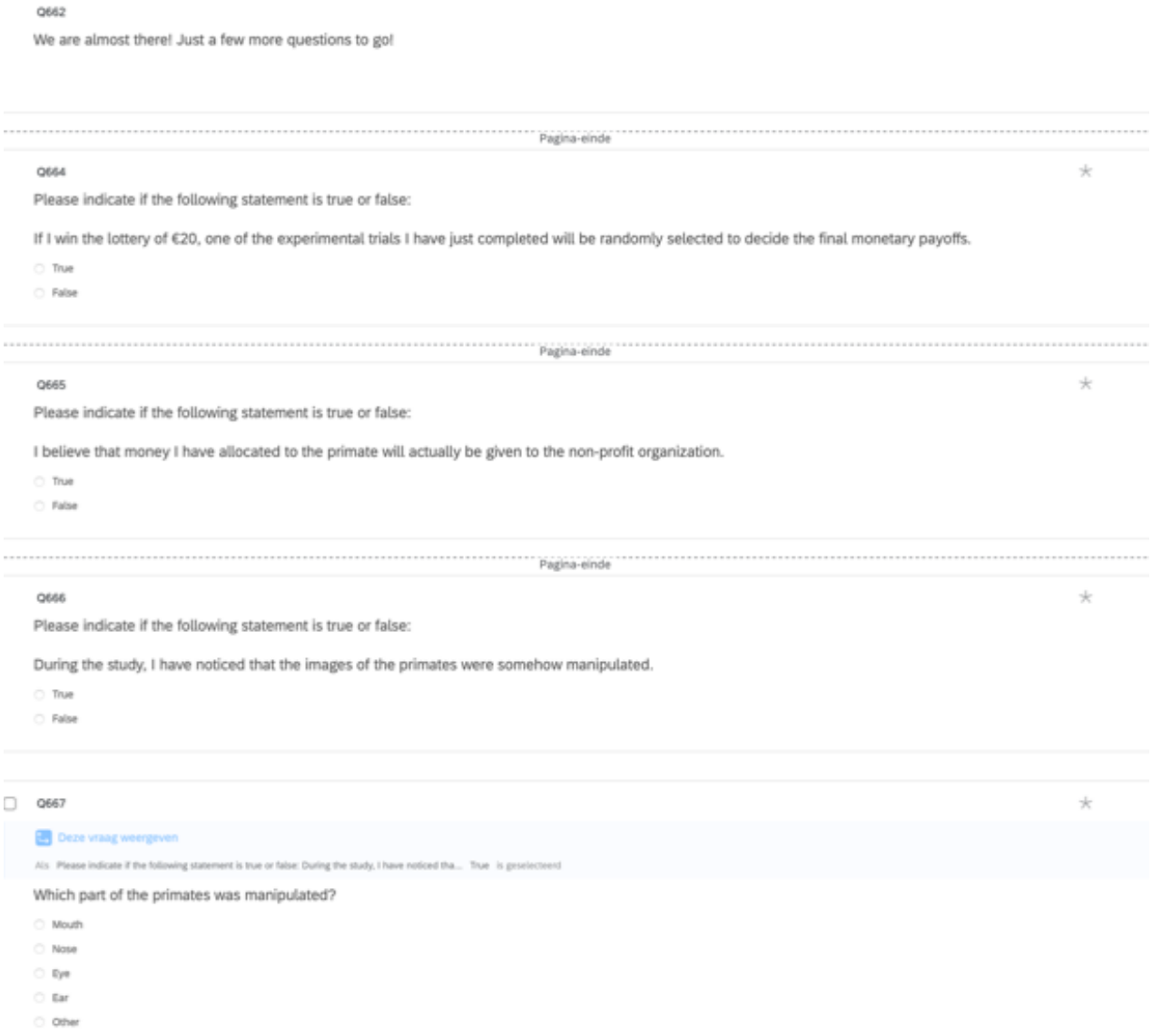
"social perception of nonhuman animals"

I have read and understand the explanation and information provided to me. I have had all my questions answered to my satisfaction. I was given enough time to think about my decision to participate and I know I have the right to withdraw my consent at any time, without providing a reason for this.

I answered the above questions truthfully and I voluntarily agree to participate in this study.

- ○ Yes, I consent
- ○ No, I do not consent

Appendix C – Manipulations checks



Appendix D – Debriefing form

Debriefing

Thank you for participating. More information on the study will follow.

Debriefing

Thank you for participating in this study. More information on the study will follow.

Goals of the study

The human eyes are believed to play a special role in cooperation. Pupil size conveys meaningful information about potential cooperative partners. Faces with larger pupils are perceived to be more attractive, friendly and trustworthy (e.g. Amemiya and Ohtomo 2012; Kret and De Dreu 2019). Pupil dilation has been shown to promote interpersonal trust (Kret et al. 2015; Kret and De Dreu 2017, 2019), prosociality (van Breen et al. 2018) and affiliation (Brambilla et al. 2019). In our Study 1, we found that pupil dilation even promotes cooperation towards another species – images of nonhuman primate (henceafter primate) species with larger pupil elicited stronger positive attitudes and more monetary donations to the protection of these species.

Another aspect of the cooperative eye lies in the coloration of sclera and iris. Iridic coloration is closely linked to the visibility of the pupil and hence might affect the role of pupil dilation on cooperation. Most research used stimuli of Caucasian populations. Evidence that pupil dilation in brown eyes can facilitate cooperation remains elusive (e.g. Kret et al. 2015). There is also evidence that the thickness of the dark edge of the iris (a.k.a. the limbal ring) is an indicator of desirable features such as young age and attractiveness (Peshek et al. 2011). Finally, in the context of cooperation towards nonhuman species, nonhuman eyes often do not have large exposed sclerae like humans do. Lighter iridic coloration might "hijack" human's predisposition for white sclerae. For example, images of dogs with artificially blackened irises are considered undesirable (Hecht and Horowitz 2015).

The current study aims to answer these questions:

1) Does pupil dilation lead to more cooperation (i.e. pro-conservation attitudes and behaviors towards endangered primates)?
2) Does lighter/darker iridic coloration of primates elicit/inhibit cooperation?
3) lighter/darker iridic coloration enhance/mitigate the effect of pupil size on cooperation?

Our hypotheses are that primates with dilated pupils will 1) be rated more positively in attractiveness, friendliness and cuteness, and 2) will receive more donations to protect them from extinction. This effect will be particularly strong when the irises have been brightened.

If you should win the lottery, the amount you have given to protect the primate species will indeed be donated to the Conservation Fund of the International Primatological Society.

We kindly ask you to keep this information to yourself, as other people might also want to participate in the study.

Thank you again for participating. If you have any other questions or complaints, please contact the experiment leader or the principle investigator.

Principal investigator:
Dr. Jingzhi Tan
e-mail: jrtan.pku@gmail.com

Reference:

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