Can reptiles perceive visual illusions? Delboeuf illusion in red-footed tortoise (*Chelonoidis carbonaria*) and bearded dragon (*Pogona vitticeps*)

Maria Santacà[1*], Maria Elena Miletto Petrazzini[2], Christian Agrillo[1] & Anna Wilkinson[3]

1) Department of General Psychology, University of Padova, Italy

2) School of Biological and Chemical Science, Queen Mary University of London, UK

3) School of Life Sciences, University of Lincoln, Lincoln, UK

**Corresponding author:* Maria Santacà. Department of General Psychology, Via Venezia 8, 35131 Padova (Italy). Phone: +39 0498277424, e-mail: santacamaria@gmail.com

Abstract

Optical illusions have been widely used to compare visual perception among vertebrates as they can reveal how the system is able to adapt to visual input. Sensitivity to visual illusions has never been studied in reptiles. Here we investigated whether red-footed tortoises, *Chelonoidis carbonaria*, and bearded dragons, *Pogona vitticeps*, perceive the Delboeuf illusion. This illusion involves the misperception of the size of a target circle depending upon the context in which it is presented. We adopted the same size discrimination for both species to compare their performance. Animals were presented with two different types of trial. In control trials they received two different-sized food portions on two plates of the same size. In test trials, they received two same-sized food portions but presented on two different-sized plates. If they perceived the illusion in the same way as humans, we expected them to select the food portion presented on the smaller plate. The tortoises exhibited poor performance in the control trials which prevented us from drawing any conclusions about their perception of the Delboeuf illusion. In contrast, the bearded dragons selected the larger amount of food in control trials. In test trials, they selected the portion presented on the smaller plate significantly more often than chance, suggesting a human-like sensitivity to the Delboeuf illusion. Our study provides the first evidence of the perception of a visual illusion in a reptile species, suggesting that rather than simply detecting visual input, they interpret sensory information captured by photoreceptors.

Keywords: reptile cognition; visual illusions; size illusions; Delboeuf illusion

Introduction

Animals are found in almost every habitat on earth and they have developed extraordinarily different eyes and ways of seeing the world (Lazareva, Shimizu, & Wasserman, 2012). As such, it is essential to investigate similarities and differences in perception between species. Optical illusions, subjective interpretations that differ from physical stimulation, are becoming an increasingly popular tool to investigate animal visual perception (e.g., Feng, Chouinard, Howell, & Bennett, 2017; Kelley & Kelley, 2014). This approach allows us to assess whether animals interpret visual inputs as humans do, or, whether they detect visual inputs with little or no variability (Feng et al., 2017). Investigation of species differences in susceptibility to illusions may also shed light on the impact of environmental and evolutionary pressures on visual perception (Feng et al., 2017).

The majority of the current work in this area has focused on mammals, such as chimpanzees [*Pan troglodytes* (e.g. Fujita, 1997; Parrish & Beran, 2014)], rhesus monkeys [*Macaca mulatta* (e.g. Bayne & Davis, 1983; Fujita, 1997; Agrillo, Parrish, & Beran, 2014a; Agrillo, Parrish, & Beran, 2014b)], capuchin monkeys [*Cebus apella* (e.g. Suganuma, Pessoa, Monge-Fuentes, Castro, & Tavares, 2007; Parrish, Agrillo, Perdue, & Beran, 2016; Agrillo et al., 2014b)], baboons [*Papio papio* (Parron & Fagot, 2007)], ring-tailed lemurs [*Lemur catta* (Santacà, Regaiolli, Miletto Petrazzini, Spiezio, & Agrillo, 2017)], dogs [*Canis familiaris* (e.g. Byosiere, Feng, Woodhead, Rutter, Chouinard, Howell, & Bennett, 2017; Miletto Petrazzini, Bisazza, & Agrillo, 2017; Keep, Zulch, & Wilkinson, 2018)] and bottlenose dolphins [*Tursiops truncates* (Murayama, Usui, Takeda, Kato, & Maejima, 2012)]. Only three species of birds have been investigated regarding their susceptibility to illusory patterns: grey parrot [*Psittacus erithacus* (e.g. Pepperberg & Nakayama, 2016; Pepperberg, Vicinay, & Cavanagh, 2008), domestic chicks [*Gallus gallus* (e.g. Rosa Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013; Watanabe, Nakamura, & Fujita, 2013)] and pigeons [*Columba livia* (e.g. Nakamura, Watanabe, & Fujita, 2008; Watanabe, Nakamura, & Fujita, 2011)]. In elasmobranches only bamboo sharks have been studied [*Chiloscyllium griseum* (e.g. Fuss, Bleckmann, & Schluessel, 2014; Fuss & Schlüssel, 2017)] while a larger range of teleost fishes has been studied, including zebrafish [*Danio rerio* (e.g. Gori, Agrillo, Dadda, & Bisazza, 2014)], guppies [*Poecilia reticulata* (e.g. Agrillo, Miletto Petrazzini, & Bisazza, 2016; Gori et al., 2014)], redtail splitfin fish [*Xenotoca eiseni* (e.g. Sovrano, Albertazzi, & Rosa Salva, 2015; Sovrano, & Bisazza, 2009; Sovrano, Da Pos, & Albertazzi, 2016)], goldfish [*Carassius auratus* (Wyzisk & Neumeyer, 2007)] and damselfish [*Chromis chromis* (e.g. Fuss & Schlüssel, 2017)]. Susceptibility to illusory patterns was also studied in invertebrates, such as the perception of illusory contours and contextual size illusions by honeybees [*Apis mellifera* (e.g. Horridge, Zhang, & O'Carroll, 1992; Howard, Avarguès-Weber, Garcia, Stuart-Fox, & Dyer 2017)]. Some of these species showed a human-like perception of illusory phenomena, while others exhibited a reversed illusion, meaning that animals perceived a sort of illusion but in the opposite way to human observers [e.g., pigeons (Nakamura et al., 2008; Watanabe et al., 2011) and bantams (Watanabe et al., 2013)]. Furthermore, some species did not appear to perceive the illusion [e.g., rhesus monkeys (Agrillo et al., 2014b); bamboo sharks (Fuss et al., 2014)]. However, in some cases there is evidence that different methods of investigating illusion sensitivity can lead to different results in the same species. One remarkable example is the case of bantam chickens and the Ebbinghaus illusion, a relative size perception illusion. Rosa Salva et al. (2013) demonstrated that four-day-old chicks perceived the illusion in a human-like direction, while Nakamura, Watanabe, and Fujita (2014) concluded the opposite testing 6-month-old chickens.

At this stage, no firm conclusions can be made regarding the universality of perceptual mechanisms, as many species are yet to be studied. One specific class, the Reptilia, has not been investigated. Reptiles were long considered to be sluggish and unintelligent, however, when tested under appropriate experimental conditions, they exhibit an impressive array of cognitive abilities [e.g. red-footed tortoise, *Chelonoidis carbonaria*, and bearded dragon, *Pogona vitticeps*, (Kis, Huber, & Wilkinson, 2015; Mueller-Paul, Wilkinson, Aust, Steurer, Hall, & Huber, 2014; Reviewed by Matsubara, Deeming, & Wilkinson, 2017; Wilkinson & Glass, in press)]. Work has recently shown that these two species are able to perceive similarities between pictures and the objects that they represent (Wilkinson, Mueller-Paul & Huber, 2013), respond to video stimuli (Wilkinson, Sebanz, Mandl, & Huber, 2011; Siviter, Deeming, van Giezen, & Wilkinson, 2018) and, crucially for this experiment, discriminate between different quantities of food reward (and remember this association for 18 months; Soldati, Burman, John, Pike, & Wilkinson, 2017). This ability was also found in another reptile species, the Italian wall lizard, *Podarcis sicula* (Miletto Petrazzini, Fraccaroli, Gariboldi, Agrillo, Bisazza, Bertolucci, & Foà, 2017).

This study therefore investigated how two reptile species, the red-footed tortoise (*Chelonoidis carbonaria*) and the bearded dragon (*Pogona vitticeps*), perceive one of the most famous geometrical illusions, the Delboeuf illusion. In the most familiar version of this illusion, two identical circles are near each other. One is encircled by a circle with a small circumference while the other in encircled by a circle with a large circumference (Figure 1). Humans tend to perceive the former as larger than the latter despite them being the same size (Pressey, 1977). Similarly, capuchin monkeys (Parrish, Brosnan, Beran, 2015) have been shown to overestimate the size of a circle when surrounded by a circle with a small circumference. In another version of the illusion, used with chimpanzees, the target circles were replaced by food portions. Chimpanzees (Parrish & Beran, 2014) tended to overestimate the dimension of a food portion included in the smaller array while they tended to underestimate the dimension of the same food portion when it was presented in the larger array. Interestingly it has been demonstrated that humans' perception of food portion is influenced by the Delboeuf pattern. Humans overestimate food sizes when food is presented on small plates (e.g., Davis, Payne, & Bui, 2016; Van Ittersum & Wansink, 2007; Wansink & Cheney, 2005). In humans, the illusion seems to be a combination of both assimilation and contrast effects (King, 1988). The food portion presented on the smaller plate is thought to assimilate to the contour of the plate, leading to it being perceived as larger than it is; whereas the food portion presented on the larger plate is thought to contrast to the contour of the plate, leading to an underestimation of the food portion size. In order to reduce the methodological variability and make a reliable comparison between the different species, we adapted the same spontaneous choice procedure adopted in the studies of chimpanzees (Parrish & Beran, 2014), lemurs (Santacà et al., 2017) and dogs (Miletto Petrazzini, Bisazza, et al., 2017) to investigate this question in reptiles. In spontaneous choice tests, animals are thought to exhibit their natural behaviour and their performance is likely to reflect the cognitive and perceptual functions they would activate in nature. On the contrary, intensive training procedures might lead to extraordinary performances through experience and the recruitment of other neural networks to accommodate for the extensive requirements of a specific cognitive task (Agrillo & Bisazza, 2014).

Reptiles were observed spontaneously selecting one of two arrays containing food portions. We arranged two different control trials, to verify the tendency of the subjects to maximize the food intake in our experimental context, and test trials with the illusory pattern. In the control trials, we presented two different-sized food portions [(with a ratio of 0.67 between them, a ratio commonly used in spontaneous discrimination tasks with animals, including reptiles (e.g. Banszegi, Urrutia, Szenczi, & Hudson, 2016; Miletto Petrazzini & Wynne, 2016; Miletto

Petrazzini, Fraccaroli, et al., 2017)] on two same-sized arrays. In test trials, we presented two identical food portions but on two different-sized arrays, one small and one large. If red-footed tortoises and bearded-dragons perceived the Delboeuf illusion in a human-like way, they were expected to choose the portion presented on the smaller array.

Materials and methods

Subjects

Eight red-footed tortoises (*Chelonoidis carbonaria*; 5 females and 3 males), and twelve bearded-dragons (*Pogona vitticeps*; 8 females and 4 males), participated in this study (Table 1 and 2). The reptiles were maintained at the School of Life Sciences, University of Lincoln. The tortoises were housed all together in a heated (28ºC) and humidified room while the bearded dragons were housed individually or in pairs in vivaria in an adjacent room. All animals had permanent access to fresh water, shelter, UV light, and heat lamps. No subject was food deprived during the experiment but they received a favored food reward during the experiment. All animals were handled by humans on a daily basis. None of the subjects were experimentally naïve (e.g. Siviter, Deeming, Rosenberger, Burman, Moszuti, & Wilkinson, 2017; Siviter et al., 2018; Soldati et al., 2017; Moszuti, Wilkinson, & Burman, 2017), but they had not previously taken part in tests to investigate the susceptibility to visual illusions. Each subject was tested individually.

Stimuli and apparatus

The stimuli consisted of mango jelly for the tortoises and vegetable extract (kale, cucumber and mint) jelly for the bearded dragons, highly preferred food for both species. The jellies were prepared each day and cut with a circular cutter to get a consistent round form. Then, each jelly was placed in the middle of a 7.5 x 8.5 cm black plastic card. In each card one central white circle represented the plate. Two different sizes of plates were used: the larger plates had a diameter of 4.92 cm while the smaller plates had a diameter of 1.83 cm. Two different portion sizes were presented to the reptiles: the larger food portion was 1.5 cm in diameter (area = 1.77 cm^2), whereas the smaller food portion was 1.23 cm in diameter (area = 1.19 cm^2). Each card was presented on a Lshaped steel bracket (7.5 x 8.5 x 4 cm) in order to improve the visibility of the arrays from subjects' points of view.

The experiments were run in an arena measuring 100 × 100 cm (Figure 2) located in a room maintained at 28ºC (+/- 3ºC). To ensure the animals could see the entire array, they were positioned at the top of a ramp inclined by a 36.02 degree angle with both food plates at the bottom. The same apparatus was used for both species with two differences. For the tortoises, the inner part of the arena was all covered with grip and dark bark only in the choice area, while for the bearded dragons it was entirely covered with black plastic. The arena was also covered with a wire mesh for the bearded dragons to avoid the possibility of escaping from the apparatus. To reduce the possibility of subjects using olfactory cues, the apparatus was cleaned after each trial.

Procedure

Before starting the test phase, each animal received a short familiarization phase. During the familiarization phase, subjects were presented with a single card containing some pieces of jelly in the center of the choice area. This procedure allowed us to habituate the animals to the cards, and to ensure they ate the jelly in the choice area. All animals did this readily and therefore this phase lasted for only one day; each animal receive a total of 8 trials. The test phase began as soon as the familiarization phase was complete. For the illusory investigation, reptiles received 12 sessions, each consisting of four trials, receiving a total of 48 trials. They received two sessions each day with at least a one-hour interval between sessions. Both control and test trials were presented to the subjects (Figure 3), control trials were used to assess their motivation to choose the larger food portion. In half of the control trials (Control A), the two different-sized portions of jelly were both on small plates, whilst in the other half (Control B), they were presented on large plates. In these trials, the physical difference between the two portions was equal to 0.67 (Banszegi et al., 2016; Luxon-Xiccato, Miletto Petrazzini, Agrillo, & Bisazza, 2015; Miletto Petrazzini & Wynne, 2016; Miletto Petrazzini, Fraccaroli, et al., 2017). In contrast, in the test trials, the subjects were presented with two same-sized jelly portions, one on a large plate and the other on a small plate. The ratio between the area of the jelly and the smaller plate was equal to 0.67, a ratio commonly used in human research to elicit the Delboeuf illusion (Piaget, 1957). In total, each subject was presented with 16 trials for each condition.

The sequence of presentation of the trials was pseudo-randomized with the restriction that the test trial was never presented more than twice in a row and a session never began with a test trial. The position (left/right) of the larger food portion in the control trials and of the plate size (large/small) in the test trials was counterbalanced across trials. Each session was recorded and the videos were analysed to note the reptiles' choices (defined as the first jelly touched by the animal and in the meantime the other jelly was removed). One third of the videos of both species were analyzed by an additional observer and inter-rater reliability was excellent (Pearson's correlation $r = 1.0$, $p < 0.0001$).

The results of this study left open the possibility that the bearded dragons learned to avoid as much white as possible. Indeed, in control trials, the larger portion of food was intrinsically encircled by a smaller portion of white plate; in test trials, the choice for the smaller plate was also characterized by the fact that a smaller portion of the plate was visible in the chosen-array compared to the other option. To assess whether the subjects had learnt the rule to choose the configuration with less white, we arranged an additional type of control trials (Control C), presenting the two different-sized food portions in identical backgrounds without plates. (Figure 3.c). We tested 9 out of 12 bearded dragons (two had died of natural causes and one was unwell at the time of testing) adopting the same procedure of the previous tests with the exception of receiving only one type of trials: they received two sessions each day, each consisting of four trials, receiving a total of 16 trials of Control C. Therefore, the 9 bearded dragons received a total of 64 trials divided in 16 trials for each condition. The sequence of presentation of the trials was randomized with the restriction that the larger food portion was never presented more than twice in a row in the same position (left/right).

Data analysis

Statistical analyses were performed using SPSS 24.0. Individual analyses were performed on the frequency of choices of the larger food portion in the control trials and of the food portion presented on the smaller plate (the apparently larger portion from a human perspective) in the test trials. Two-tailed chi-square tests ($\alpha = 0.05$) were performed. Data were also analysed at population level. Not all data were normally distributed, hence we used parametric statistics for the data normally distributed (Shapiro-Wilk test, $p > 0.05$) and non-parametric statistics for the data that were not normally distributed (Shapiro-Wilk test, $p < 0.05$). One sample t-tests (chance level = 0.5) were performed to assess the discrimination of the two food portions in control trials and whether reptiles selected the apparently larger food portion (to humans) more than chance in test trials. The performances in the two types of control trials were compared using paired t-tests. To investigate a possible change in performance in all types of trials over sessions, we performed an ANOVA.

Results

Pogona vitticeps

Individual analyses (chi-square tests) on the frequency of choices for the larger food portion showed that 9 bearded dragons out of 12 in Control A and 5 subjects in Control B significantly selected the larger food portion (Table 1). Group analysis showed a significant discrimination of the larger quantity in both Control A (mean: 0.750, 95% CI [0.662, 0.838], one-sample Wilcoxon Signed Rank test $p = 0.003$) and Control B (mean: 0.703, 95% CI [0.655, 0.703], $t(11) = 9.275$, $p < 0.001$). No difference was found between the two control trials (Related-sample Wilcoxon Signed Rank test $p = 0.162$).

In the test trials, individual analyses showed that 7 out of the 12 bearded dragons significantly selected the food portion presented on the smaller plate (the one apparently larger to humans; Table 1). Group analyses also showed a significant preference for the food portion presented on the smaller plate (mean: 0.703, 95% CI [0.640, 0.765], $t(11) = 7.294$, $p < 0.001$, Figure 4.a).

The ANOVA revealed a non significant difference in the bearded dragons' performance as a function of time in all types of trials ($F_{(11, 12)} = 2.478$, $p = 0.0671$) indicating a lack of learning effect during the experiment.

In control C trials, individual analyses (chi-square tests) on the frequency of choices for the larger food portion showed that 6 out of 9 bearded dragons significantly selected the larger food portion (Table 1). Group analysis showed a significant discrimination of the larger quantity (mean: 0.757, 95% CI [0.696, 0.818], $t(8) = 9.7167$, $p < 0.01$, Figure 4.a). To further exclude the possibility that they simply learned to avoid as much white as possible, we analyzed the performance in the first trial of control C: 8 out of 9 bearded dragons selected the bigger food portion the first time they were presented with such trial. This result thus shows that bearded dragons were not driven by a tendency to avoid as much white as possible, but instead they focused on the biologically-relevant stimuli presented in the arrays, the food portions.

Chelonoidis carbonaria

Chi-square tests showed that only two tortoises significantly selected the larger food portion in Control A and only one in Control B (Table 2). Contrary to expectations, one subject significantly selected the smaller portion in Control A. Group analyses revealed the lack of significant preference for any portion size in either type of control trial: Control A (mean: 0.547, 95% Confidence Interval CI [0.340, 0.694]; one-sample t-test $t(7) = 0.753$, $p = 0.476$) and Control B (mean: 0.539, 95% CI [0.447, 0.631], $t(7)= 1.000$, $p = 0.351$). A paired t-test revealed the absence of any differences between the two control trials ($t(7)= 0.099$, $p = 0.924$).

In the test trials, individual analyses revealed that tortoises did not significantly select one food portion more than the other (Table 2). This result is confirmed by group analyses (mean: 0.516, 95% CI [0.449, 0.583], one-sample Wilcoxon Signed Rank test p = 0.705, Figure 4.b).

Discussion

The present study represents the first attempt to investigate whether reptiles perceive visual illusions. To achieve this goal, we tested two species, *Chelonoidis carbonaria* and *Pogona vitticeps*, with one of the most popular size illusions from the human literature, the Delboeuf illusion. The findings revealed that the bearded dragons were susceptible to the illusion and appeared to perceive it in a similar manner to humans and some other species [e.g. chimpanzees (Parrish & Beran, 2014) and capuchin monkeys (Parrish et al., 2015)]; however, the tortoises did not select the larger food portion when they differed in reality or when the difference was (potentially) illusory.

In control trials, 10 out of 12 bearded dragons significantly selected the larger food portion in Control A and 5 out of 12 in Control B. Bearded dragons' group analysis confirmed the discrimination of the larger quantity with no difference in the two control trials. When presented with the test trials, individual (7 subjects out of 12) and group analysis showed that bearded dragons selected the food portion included in the smaller plate suggesting a human-like perception of the Delboeuf illusion. The results of Control C trials, where there were no white plates, clearly demonstrated that subjects were not basing their choice on the basis of the quantity of white visible.

Our study provides the first evidence that a reptile species, *Pogona vitticeps*, perceives a visual illusion. This indicates that, like some mammals, birds and fish, some reptiles can interpret and alter visual input related to object size, rather than detecting visual inputs with little or no variability. The fact that bearded dragons perceive this illusion suggests the existence of assimilation and contrast phenomena in reptiles, raising the intriguing possibility that these perceptive mechanisms could be widely shared in the animal world. Also, the illusory phenomenon requires the overall perception of the array (food portion and the surrounding array). However, only few studies investigated the global and local precedence in animals. Chimpanzees and redtail splitfin fish, such humans, display a rather robust global-to-local precedence (e.g., Fujita & Matsuzawa, 1990; Hopkins, 1997; Hopkins, & Washburn, 2002; Kimchi, 1992; Navon, 1977; Truppa, Sovrano, Spinozzi, & Bisazza, 2010) and they both demonstrated perception of respectively the Delboeuf and the Ebbinghaus illusion as human observers. In contrast, local-to-global precedence was found in other species (e.g., capuchin monkeys, De Lillo, Palumbo, Spinozzi, & Giustino, 2001; pigeons: Cavoto & Cook, 2001) that do not display susceptibility to the Delboeuf Illusion. In this context, dogs (Miletto Petrazzini et al., 2017), showed a larger inter-individual variability than humans and non-significant trend for global precedence (Pitteri, Mongillo, Carnier, & Marinelli, 2014). Given the lack of studies investigating this phenomenon, no firm conclusion can be drawn regarding the relationship between the global/local precedence and the perception of the Delboeuf illusion. What can be claimed is that the global-to-local precedence is a prerequisite but not a predictor of the illusory sensitivity. Although no study has investigated whether reptiles show global-to-local precedence , the results of our study suggest the existence of a global-to-local precedence in bearded dragons.

In contrast, this procedure proved to be less successful for studying the perception of the Delboeuf illusion in red-footed tortoises. In control trials, only two tortoises (Savina and Charles Darwin) significantly selected the larger food portion in control A and only one (Gerard) in control B; in control A one tortoise (Ranieri) selected the smaller one instead. This performance was confirmed by group analyses that indicated no significant choice for any food portion in both types of control trials. These results suggest that, within this context, the tortoises did not maximize their food intake; therefore, we cannot draw any conclusion about their perception of the Delboeuf illusion. Why did tortoises exhibit such a poor performance? This species has been shown to optimize food intake previously and will work harder for both larger and favoured food rewards, further, they are able to retain information about stimuli associated with a greater food reward for at least 18 months (Soldati et al., 2017). It is possible that because both portion sizes used in this experiment were large (and were substantially larger than those used by Soldati et al., 2017) that they either did not need to maximize their intake or they were trying to maximize food intake but the physical difference between the food portions presented in control trials (ratio of 0.67) was too subtle to be detected. There is currently no literature regarding the discrimination ratios in this species. If the red-footed tortoises did not discriminate a 0.67 ratio, it is likely that they would not perceive a subjective difference between the two food portions in the Delboeuf pattern. The position of the stimuli in the experimental arena could be another factor influencing their performance. Although the ramp was designed to maximize the animals' view of the entire array, perhaps this was not optimal for the tortoises.

Finally, we acknowledge our limited sample size of tortoises (N = 8) – although similar to the sample size used in the previous studies that investigated the spontaneous emergence of the Delboeuf illusion in other species (Beran & Parrish, 2014; Miletto Petrazzini et al., 2017). Despite the limitations of a small sample, we suggest that the null results observed in tortoises could easily reflect an unidentified feature of our methodology. After determining red-footed tortoises' size discrimination abilities, one could, adopting different methodologies (e.g. training procedures or different size/position of the stimuli), investigate again their perception of the Delboeuf illusion.

The importance of reducing methodological variability is a well-known and highly debated issue in scientific community, especially in the investigation of cognitive abilities of vertebrates (e.g. Agrillo & Bisazza, 2014; Feng et al., 2017). However as emerged in this study, the use of the same procedure and setting may prevent a reliable comparison. The use of multiple methodological approaches (e.g., free choice tests vs. operant conditioning procedure, use of food vs. two-dimensional figures as stimuli) is necessary to compare the subjective world of different species.

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Ethical Note

This research was approved by the ethics committee of the School of Life Sciences, University of Lincoln (CoSREC364). Applicable national guidelines for the care and use of animals were followed.

References

Agrillo, C., & Bisazza, A. (2014). Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. *Journal of Neuroscience Methods*, *234*, 82 – 91.

Agrillo, C., Miletto Petrazzini, M. E., & Bisazza, A. (2016). Brightness illusion in the guppy (*Poecilia reticulata*). *Journal of Comparative Psychology*, *130*(1), 55.

Agrillo, C., Parrish, A. E., & Beran, M. J. (2014). Do rhesus monkeys (*Macaca mulatta*) perceive the Zöllner illusion?. *Psychonomic Bulletin & Review, 21*(4), 986-994.

Agrillo, C., Parrish, A. E., & Beran, M. J. (2014b). Do primates see the solitaire illusion differently? A comparative assessment of humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *128*, 402 – 413.

Banszegi, O., Urrutia, A., Szenczi, P., & Hudson, R. (2016). More or less: Spontaneous quantity discrimination in the domestic cat. *Animal Cognition*, *19,* 879 – 888.

Bayne, K. L., & Davis, R. (1983). Susceptibility of rhesus monkeys (*Macaca mulatta*) to the Ponzo illusion. *Bulletin of the Psychonomic Society*, *21*, 476 – 478.

Byosiere, S. E., Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). Visual perception in domestic dogs: susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Animal Cognition, 20*(3), 435-448.

Cavoto, K. K., & Cook, R. G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*, 3-16.

Davis, B., Payne, C. R., & Bui, M. (2016). Making small food units seem regular: How larger table size reduces calories to be consumed. *Journal of the Association of Consumer Research*, *1*, 115 – 124.

De Lillo, C., Spinozzi, G., Palumbo, M., & Giustino, G. (2011). Attention allocation modulates the processing of hierarchical visual patterns: A comparative analysis of capuchin monkeys (*Cebus apella*) and humans. *Journal of Experimental Psychology: Animal Behavior Processes*, *37*(3), 341.

Faul, F., & Erdfelder, E. (1992). GPOWER: A priori, post-hoc, and compromise power analyses for MS-DOS [Computer software]. *Bonn, Germany: Bonn University, Department of Psychology*.

Feng L. C., Chouinard P. A., Howell T. J., & Bennett P. C. (2017). Why do animals differ in their susceptibility to geometrical illusions? *Psychonomic Bulletin & Review*, *24*, 262 – 276.

Fujita, K. (1997). Perception of the Ponzo illusion by rhesus monkeys, chimpanzees, and humans: Similarity and difference in the three primate species. *Perception & Psychophysics*, *59*, 284 – 292.

Fujita, K., & Matsuzawa, T. (1990). Delayed figure reconstruction by a chimpanzee (Pan troglodytes) and humans (Homo sapiens). *Journal of Comparative Psychology*, *104*(4), 345-351.

Fuss, T., & Schlüssel, V. (2017). The Ebbinghaus illusion in the gray bamboo shark (*Chiloscyllium griseum*) in comparison to the teleost damselfish (*Chromis chromis*). *Zoology*, *123*, 16-29.

Fuss, T., Bleckmann, H., & Schluessel, V. (2014). The brain creates illusions not just for us: Sharks (*Chiloscyllium griseum*) can "see the magic" as well. *Frontiers in Neural Circuits, 8,* 24.

Gori, S., Agrillo, C., Dadda, M., & Bisazza, A. (2014). Do fish perceive illusory motion? *Scientific Reports*, *4*.

Hopkins, W. D. (1997). Hemispheric specialization for local and global processing of hierarchical visual stimuli in chimpanzees (*Pan troglodytes*). *Neuropsychologia*, *35*(3), 343-348.

Hopkins, W. D., & Washburn, D. A. (2002). Matching visual stimuli on the basis of global and local features by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *Animal Cognition*, *5*, 27–31.

Horridge, G. A., Zhang, S. W., & O'Carroll, D. (1992). Insect perception of illusory contours. *Philosophical Transactions of the Royal Society of London B*, *337*(1279), 59-64.

Howard, S. R., Avarguès-Weber, A., Garcia, J. E., Stuart-Fox, D., & Dyer, A. G. (2017). Perception of contextual size illusions by honeybees in restricted and unrestricted viewing conditions. *Proceedings of the Royal Society B*, *284*(1867), 20172278.

Keep, B., Zulch, H. E., & Wilkinson, A. (2018). Truth is in the eye of the beholder: Perception of the Müller-Lyer illusion in dogs. *Learning & Behavior*, *46*(4), 501-512.

Kelley, L. A., & Kelley, J. L. (2014). Animal visual illusion and confusion: the importance of a perceptual perspective. *Behavioral Ecology*, *25*(3), 450-463.

Kimchi, R. (1992). Primacy of wholistic processing and global/local paradigm: A critical review. *Psychological Bulletin*, *112*(1), 24.

King, D. L. (1988). Assimilation is due to one perceived whole and contrast is due to two perceived wholes. *New Ideas in Psychology*, *6*(3), 277-288.

Kis, A., Huber, L., & Wilkinson, A. (2015). Social learning by imitation in a reptile (*Pogona vitticeps*). *Animal Cognition*, *18*(1), 325-331.

Lazareva, O. F., Shimizu, T., & Wasserman, E. A. (Eds.). (2012). How animals see the world: Comparative behavior, biology, and evolution of vision. *Oxford University Press*.

Lucon-Xiccato, T., Miletto Petrazzini, M. E., Agrillo, C., & Bisazza, A. (2015). Guppies discriminate between two quantities of food items but prioritize item size over total amount. *Animal Behaviour*, *107*, 183 – 191.

Matsubara, S., Deeming, D. C., & Wilkinson, A. (2017). Cold-blooded cognition: new directions in reptile cognition. *Current Opinion in Behavioral Sciences*, 16, 126-130.

Miletto Petrazzini, M. E., & Wynne, C. D. (2016). What counts for dogs (*Canis lupus familiaris*) in a quantity discrimination task? *Behavioural Processes*, *122*, 90 – 97.

Miletto Petrazzini, M. E., Bisazza, A., & Agrillo, C. (2017). Do domestic dogs (*Canis lupus familiaris*) perceive the Delboeuf illusion? *Animal Cognition*, *20*(3), 427-434.

Miletto Petrazzini, M. E., Fraccaroli, I., Gariboldi, F., Agrillo, C., Bisazza, A., Bertolucci, C., & Foà, A. (2017). Quantitative abilities in a reptile (*Podarcis sicula*). *Biology Letters*, *13*, 20160899.

Moszuti, S. A., Wilkinson, A., & Burman, O. H. (2017). Response to novelty as an indicator of reptile welfare. *Applied Animal Behaviour Science*, *193*, 98-103.

Mueller-Paul, J., Wilkinson, A., Aust, U., Steurer, M., Hall, G., & Huber, L. (2014). Touchscreen performance and knowledge transfer in the red-footed tortoise (*Chelonoidis carbonaria*). *Behavioural Processes*, *106*, 187-192.

Murayama, T., Usui, A., Takeda, E., Kato, K., & Maejima, K. (2012). Relative size discrimination and perception of the Ebbinghaus illusion in a bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals*, *38*(4), 333.

Nakamura, N., Watanabe, S., & Fujita, K. (2008). Pigeons perceive the Ebbinghaus-Titchener circles as an assimilation illusion. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 375 – 387.

Nakamura, N., Watanabe, S., & Fujita, K. (2014). A reversed Ebbinghaus–Titchener illusion in bantams (*Gallus gallus domesticus*). *Animal Cognition*, *17*(2), 471-481.

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, *9*(3), 353-383.

Parrish, A. E., & Beran, M. J. (2014). When less is more: like humans, chimpanzees (*Pan troglodytes*) misperceive food amounts based on plate size. *Animal Cognition*, *17*(2), 427-434.

Parrish, A. E., Agrillo, C., Perdue, B. M., & Beran, M. J. (2016). The elusive illusion: Do children (*Homo sapiens*) and capuchin monkeys (*Cebus apella*) see the Solitaire illusion? *Journal of Experimental Child Psychology*, *142*, 83 – 95.

Parrish, A. E., Brosnan, S. F., & Beran, M. J. (2015). Do you see what I see? A comparative investigation of the Delboeuf illusion in humans (*Homo sapiens*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Learning and Cognition, 41*, 395 – 405.

Parron, C., & Fagot, J. (2007). Comparison of grouping abilities in humans (*Homo sapiens*) and baboons (*Papio papio*) with the Ebbinghaus illusion. *Journal of Comparative Psychology*, *121*(4), 405.

Pepperberg, I. M., & Nakayama, K. (2016). Robust representation of shape in a Grey parrot (*Psittacus erithacus*). *Cognition*, *153*, 146-160.

Pepperberg, I. M., Vicinay, J., & Cavanagh, P. (2008). Processing of the Müller-Lyer illusion by a grey parrot (*Psittacus erithacus*). *Perception, 37*, 765 – 781.

Piaget, J. (1957). *Les Mécanismes Perceptifs*. Paris: Presses Universitaires de France.

Pitteri, E., Mongillo, P., Carnier, P., & Marinelli, L. (2014). Hierarchical stimulus processing by dogs (*Canis familiaris*). *Animal Cognition*, *17*(4), 869-877.

Pressey, A. W. (1977). Measuring the Titchener circles and Delboeuf illusions with the method of adjustment. *Bulletin of the Psychonomic Society*, *10*(2), 118-120.

Rosa Salva, O., Rugani, R., Cavazzana, A., Regolin, L., & Vallortigara, G. (2013). Perception of the Ebbinghaus illusion in four-day-old domestic chicks (*Gallus gallus*). *Animal Cognition, 16*, 895 – 906.

Santacà, M., Regaiolli, B., Miletto Petrazzini, M. E., Spiezio, C., & Agrillo, C. (2017). Preliminary study to investigate the Delboeuf illusion in ring-tailed lemurs (*Lemur catta*): Methodological challenges. *Animal Behavior and Cognition*, *4*(3), 365-377.

Siviter, H., Deeming, D. C., Rosenberger, J., Burman, O. H. P., Moszuti, S. A., & Wilkinson, A. (2017). The impact of egg incubation temperature on the personality of oviparous reptiles. *Animal Cognition*, *20*(1), 109–116. http://doi.org/10.1007/s10071-016-1030-1

Siviter, H., Deeming, D. C., van Giezen, M. F. T. & Wilkinson, A. (2018). Incubation environment impacts the social cognition of adult lizards. *Royal Society Open Science*

Soldati, F., Burman, O. H. P., John, E. A., Pike, T. W., & Wilkinson, A. (2017). Long-term memory of relative reward values. *Biology Letters*, *13*(2), 20160853. http://doi.org/10.1098/rsbl.2016.0853

Sovrano, V. A., & Bisazza, A. (2009). Perception of subjective contours in fish. *Perception*, *38*(4), 579-590.

Sovrano, V. A., Albertazzi, L., & Salva, O. R. (2015). The Ebbinghaus illusion in a fish (*Xenotoca eiseni*). *Animal Cognition*, *18*(2), 533-542.

Sovrano, V. A., Da Pos, O., & Albertazzi, L. (2016). The Müller-Lyer illusion in the teleost fish *Xenotoca eiseni*. *Animal Cognition*, *19*(1), 123-132.

Suganuma, E., Pessoa, V. F., Monge-Fuentes, V., Castro, B. M., & Tavares, M. C. H. (2007). Perception of the Müller–Lyer illusion in capuchin monkeys (*Cebus apella*). *Behavioural Brain Research, 182*, 67 – 72.

Truppa, V., Sovrano, V. A., Spinozzi, G., & Bisazza, A. (2010). Processing of visual hierarchical stimuli by fish (*Xenotoca eiseni*). *Behavioural Brain Research*, *207*(1), 51-60.

Van Ittersum, K., & Wansink, B. (2007). Do children really prefer large portions? Visual illusions bias their estimates and intake. *Journal of the American Dietetic Association, 107*, 1107 – 1110.

Wansink, B., & Cheney, M. M. (2005). Super bowls: Serving bowl size and food consumption. *The Journal of the American Medical Association*, *293*, 1727 – 1728.

Watanabe, S., Nakamura, N., & Fujita, K. (2011). Pigeons perceive a reversed Zöllner illusion. *Cognition*, *119*, 137 – 141.

Watanabe, S., Nakamura, N., & Fujita, K. (2013). Bantams (*Gallus gallus domesticus*) also perceive a reversed Zöllner illusion. *Animal Cognition*, *16*, 109 – 115.

Wilkinson, A., & Glass, E. (in press). Cold-blooded Cognition: How to get a tortoise out of its shell. Field and Laboratory Methods in Animal Cognition. *Cambridge University Press*, UK.

Wilkinson, A., & Huber, L. (2012). Cold-blooded cognition: reptilian cognitive abilities. *The Oxford Handbook of Comparative Evolutionary Psychology*. *Oxford University Press*, *New Jersey*, 129-143.

Wilkinson, A., Mueller-Paul, J., & Huber, L. (2013). Picture–object recognition in the tortoise *Chelonoidis carbonaria*. *Animal Cognition*, *16*(1), 99-107.

Wilkinson, A., Sebanz, N., Mandl, I., & Huber, L. (2011). No evidence of contagious yawning in the red-footed tortoise *Geochelone carbonaria*. *Current Zoology*, *57*(4), 477-484.

Wyzisk, K., & Neumeyer, C. (2007). Perception of illusory surfaces and contours in goldfish. *Visual Neuroscience*, *24*(3), 291-298.

Figure captions

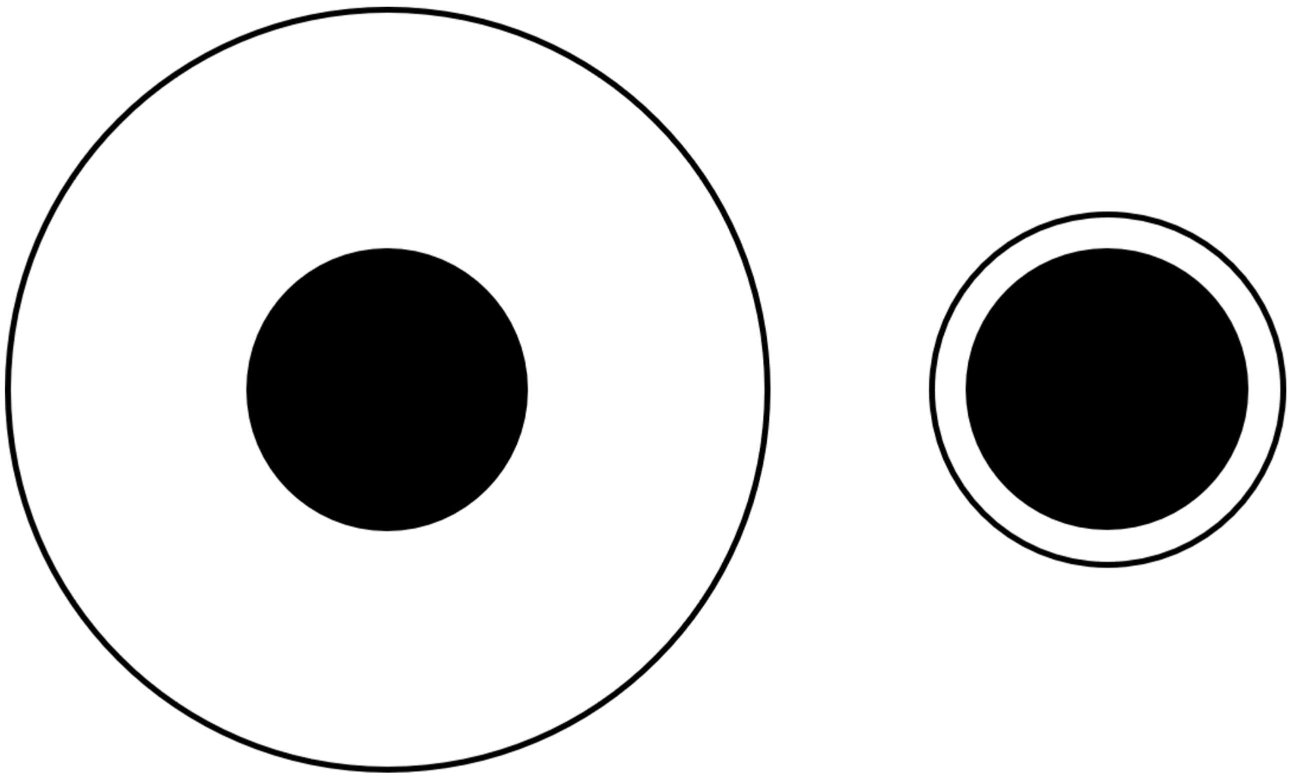

Figure 1. Delboeuf illusion. This illusion occurs when two same-sized circles are perceived to be different depending on the context in which they are presented. In the classical version the central target circles are physically identical, but human observers typically underestimate the size of the one included in the larger ring and tend to overestimate the size of the one encompassed by the smaller ring.

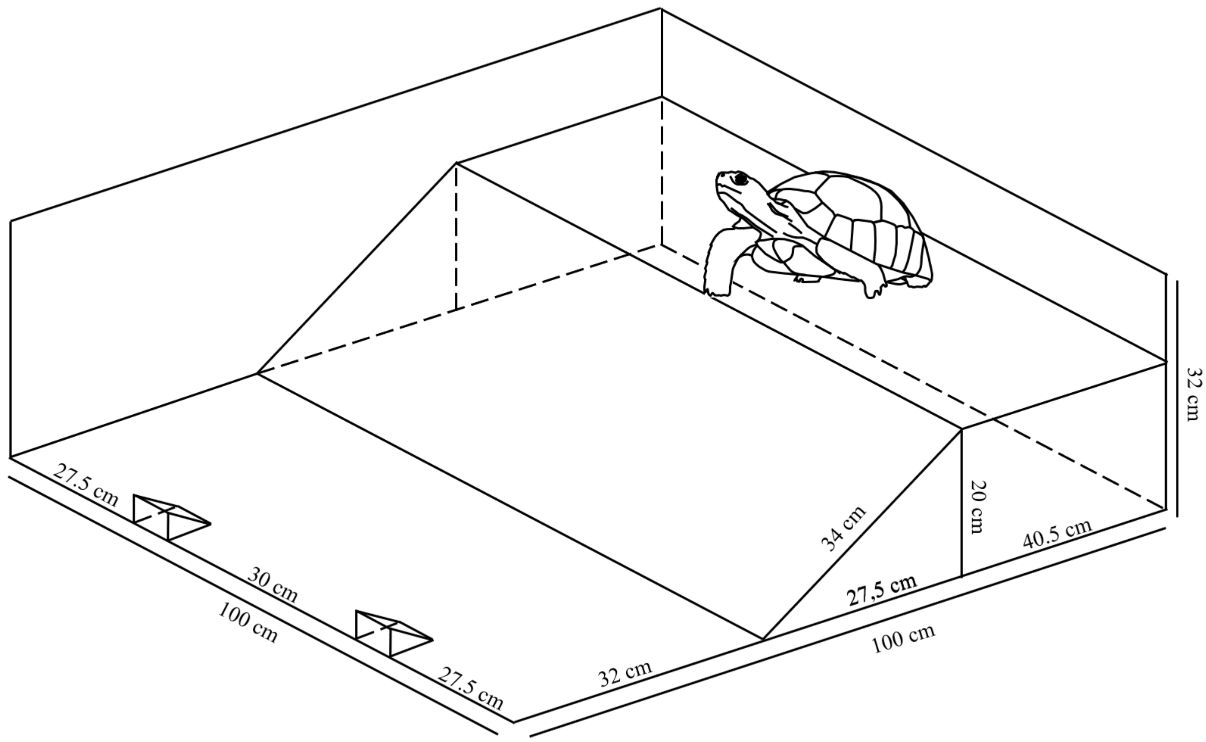

Figure 2. Experimental setup. Three-dimensional representation of the experimental apparatus. Subjects had to descend a ramp in order to reach the plates containing the jellies. As dependent variable we recorded the first food portion touched by the animal in each trial.

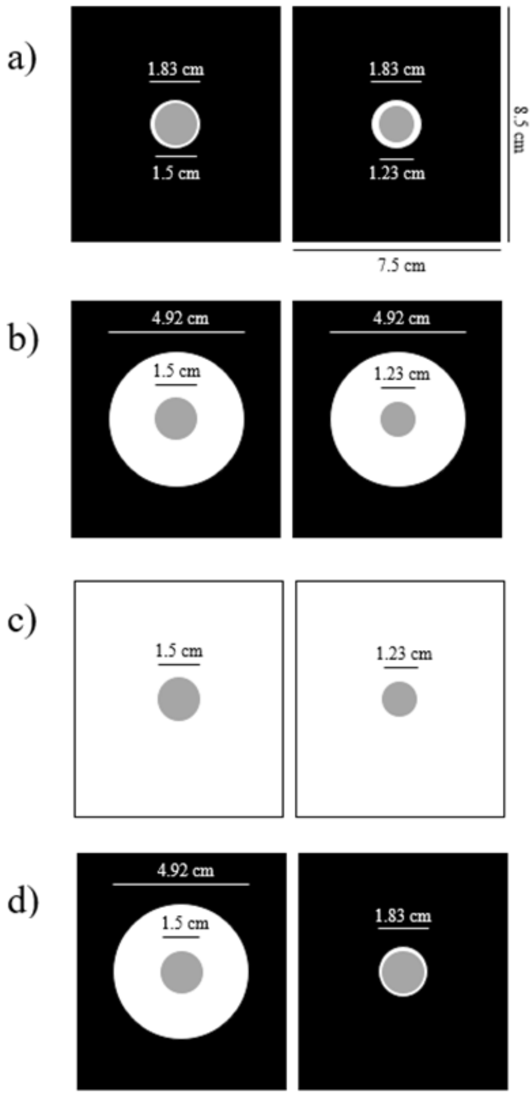

Figure 3. Stimuli. Different or equal-sized food portions were presented on white plates: (a) control A (different food portions in two identical small plates); (b) control B (different food portions in two identical large plates); (c) control C (different food portions in identical neutral backgrounds); (d) test trials (equal-sized food portions in two different-sized plates).

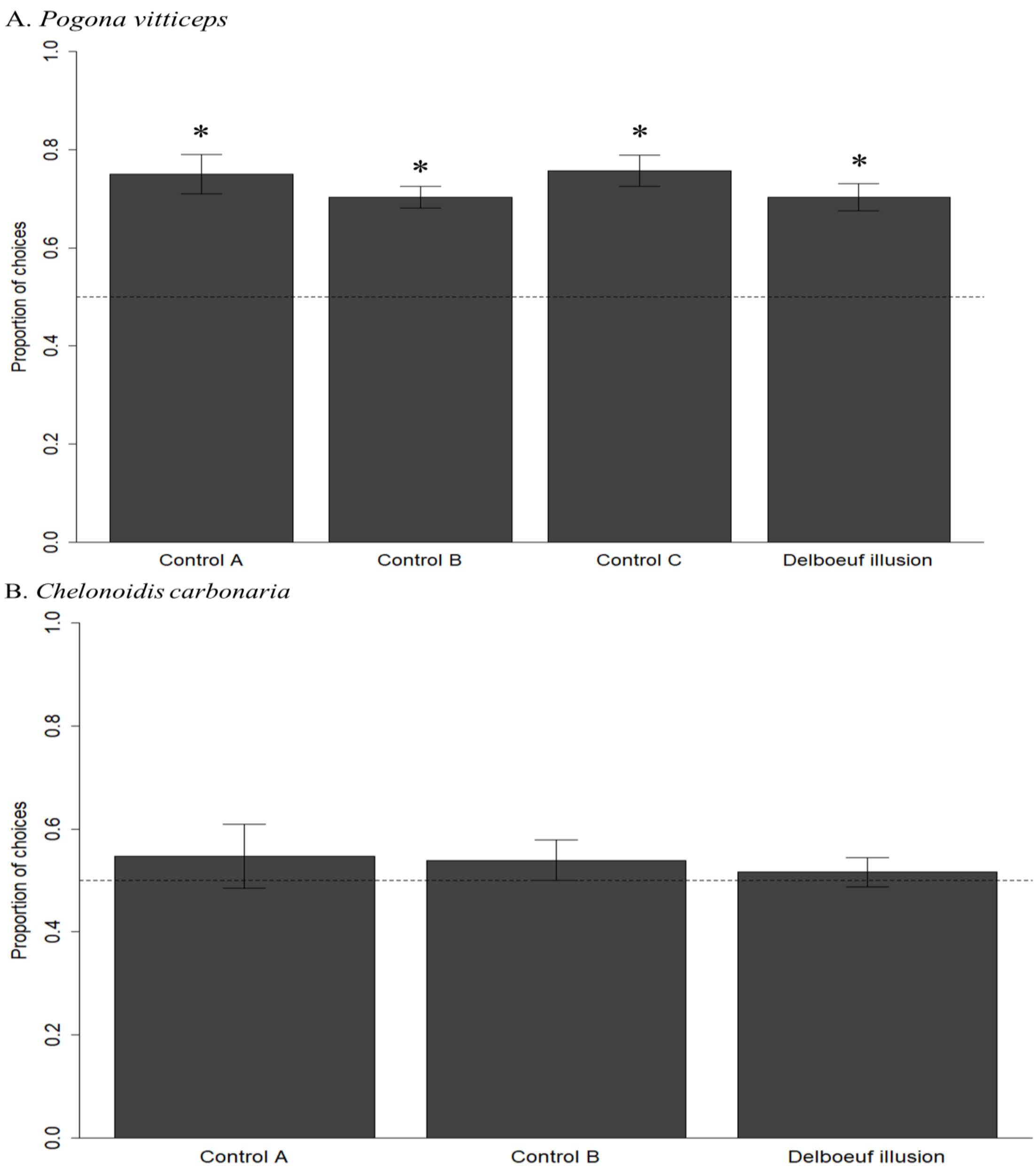

Figure 4. Results. The Y-axis refers to the proportion of choices for the larger food portion in the control trials and the proportion of choices for the food portion presented on the small plate in the test trials. Bearded dragons (a), but not tortoises (b), selected the larger food portion in all control trials. Tortoises did not show a preference for any portion in test trials (b) while bearded dragons significantly chose more than chance the food portion included in the small plate suggesting a human-like perception of the Delboeuf illusion (a). Bars represent the standard error. The asterisk (*) denotes a significant departure from chance level.

Table 1. Information of the Bearded Dragons Participating in the Study and Individual Performance.

SUBJECT	Control A	Control B	Control C	Test trials
Shuriken	12/16, $\chi^2 = 4.000$, $p = 0.047$ *	12/16, $\chi^2 = 4.000$, $p = 0.047$ *	12/16, $\chi^2 = 4.000$, $p = 0.047$ *	12/16, $\chi^2 = 4.000$, $p = 0.047$ *
Malie	11/16, $\chi^2 = 2.250$, $p = 0.134$	12/16, $\chi^2 = 4.000$, $p = 0.047$ *	11/16, $\chi^2 = 2.250$, $p = 0.134$	12/16, $\chi^2 = 4.000$, $p = 0.047$ *
Nimoy	6/16, $\chi^2 = 1.000$, $p = 0.317$	9/16, $\chi^2 = 0.250$, $p = 0.617$	11/16, $\chi^2 = 2.250$, $p = 0.134$	11/16, $\chi^2 = 2.250$, $p = 0.134$
Quadra	12/16, $\chi^2 = 4.000$, $p = 0.047$ *	10/16, $\chi^2 = 1.000$, $p = 0.317$	14/16, $\chi^2 = 9.000$, $p = 0.003$ *	8/16, $\chi^2 = 0.000$, $p = 1.000$
Norbert	12/16, $\chi^2 = 4.000$, $p = 0.047$ *	10/16, $\chi^2 = 1.000$, $p = 0.317$	13/16, $\chi^2 = 6.250$, $p = 0.012$ *	13/16, $\chi^2 = 6.250$, $p = 0.012$ *
Dr. Tom Pike	11/16, $\chi^2 = 2.250$, $p = 0.134$	12/16, $\chi^2 = 4.000$, $p = 0.047$ *	13/16, $\chi^2 = 6.250$, $p = 0.012$ *	12/16, $\chi^2 = 4.000$, $p = 0.047$ *
Alberta	13/16, $\chi^2 = 6.250$, $p = 0.012$ *	11/16, $\chi^2 = 2.250$, $p = 0.134$	12/16, $\chi^2 = 4.000$, $p = 0.047$ *	11/16, $\chi^2 = 2.250$, $p = 0.134$
Heinz	14/16, $\chi^2 = 9.000$, $p = 0.003$ *	11/16, $\chi^2 = 2.250$, $p = 0.134$	N/A	13/16, $\chi^2 = 6.250$, $p = 0.012$ *
Cecilia	12/16, $\chi^2 = 4.000$, $p = 0.047$ *	11/16, $\chi^2 = 2.250$, $p = 0.134$	N/A	10/16, $\chi^2 = 1.000$, $p = 0.317$
Oscar	15/16, $\chi^2 = 12.250$, $p = 0.0004$ *	13/16, $\chi^2 = 6.250$, $p = 0.012$ *	13/16, $\chi^2 = 6.250$, $p = 0.012$ *	12/16, $\chi^2 = 4.000$, $p = 0.047$ *
Mushu	13/16, $\chi^2 = 6.250$, $p = 0.012$ *	11/16, $\chi^2 = 2.250$, $p = 0.134$	10/16, $\chi^2 = 1.000$, $p = 0.317$	9/16, $\chi^2 = 0.250$, $p = 0.617$
Haku	13/16, $\chi^2 = 6.250$, $p = 0.012$ *	13/16, $\chi^2 = 6.250$, $p = 0.012$ *	N/A	12/16, $\chi^2 = 4.000$, $p = 0.047$ *

Note: Control trials = frequency of choices for the larger quantity; Test trials = frequency of choices for the portion of food on the smaller plate

*denotes a significant departure from chance at chi-square test ($p < 0.05$).

Table 2. Information of the Red-footed Tortoises Participating in the Study and Individual Performance.

SUBJECT	Control A	Control B	Test trials
6 (Savina)	12/16, χ^2 = 4.000, *p* = 0.047 *	8/16, χ^2 = 0.000, *p* = 1.000	8/16, χ^2 = 0.000, *p* = 1.000
7 (Patty)	8/16, χ^2 = 0.000, *p* = 1.000	9/16, χ^2 = 0.250, *p* = 0.617	7/16, χ^2 = 0.250, *p* = 0.617
8 (Charles)	12/16, χ^2 = 4.000, *p* = 0.047 *	6/16, χ^2 = 1.000, *p* = 0.317	11/16, χ^2 = 2.250, *p* = 0.134
9 (Mozart)	9/16, χ^2 = 0.250, *p* = 0.617	8/16, χ^2 = 0.000, *p* = 1.000	8/16, χ^2 = 0.000, *p* = 1.000
10 (Seisue)	8/16, χ^2 = 0.000, *p* = 1.000	8/16, χ^2 = 0.000, *p* = 1.000	7/16, χ^2 = 0.250, *p* = 0.617
19 (T19)	9/16, χ^2 = 0.250, *p* = 0.617	10/16, χ^2 = 1.000, *p* = 0.317	8/16, χ^2 = 0.000, *p* = 1.000
24 (Ranieri)	3/16, χ^2 = 6.250, *p* = 0.012 *	8/16, χ^2 = 0.000, *p* = 1.000	8/16, χ^2 = 0.000, *p* = 1.000
300 (Gerard)	9/16, χ^2 = 0.250, *p* = 0.617	12/16, χ^2 = 4.000, *p* = 0.047 *	9/16, χ^2 = 0.250, *p* = 0.617

Note: Control trials = frequency of choices for the larger quantity; Test trials = frequency of choices for the portion of food on the smaller plate

*denotes a significant departure from chance at chi-square test ($p < 0.05$).