

Exploring the Müller-Lyer Illusion in a Nonavian Reptile (*Pogona vitticeps*)

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Visual illusions have been widely used to compare visual perception among birds and mammals to assess whether animals interpret and alter visual inputs like humans, or if they detect them with little or no variability. Here, we investigated whether a nonavian reptile (*Pogona vitticeps*) perceives the Müller-Lyer illusion, an illusion that causes a misperception of the relative length of 2 line segments. We observed the animals' spontaneous tendency to choose the larger food quantity (the longer line). In test trials, animals received the same food quantity presented in a spatial arrangement eliciting the size illusion in humans; control trials presented them with 2 different-sized food portions. Bearded dragons significantly selected the larger food quantity in control trials, confirming that they maximized food intake. Group analysis revealed that in the illusory test trials, they preferentially selected the line length estimated as longer by human observers. Further control trials excluded the possibility that their choice was based on potential spatial bias related to the illusory pattern. Our study suggests that a nonavian reptile species has the capability to be sensitive to the Müller-Lyer illusion, raising the intriguing possibility that the perceptual mechanisms underlying size estimation might be similar across amniotes.

Keywords: nonavian reptiles, visual illusion, distortion illusion, comparative perception

A visual illusion is an erroneous representation of reality that makes a certain stimulus appear bigger, smaller, longer, or shorter (or different in many other characteristics), than it is in reality (Gregory, 1968). This phenomenon is due to the processing and interpretation of information from visible light to obtain a representation of the surrounding environment (Kelley & Kelley, 2014). Recent research has revealed different sensitivities to size distortion illusions in nonhuman animals (Feng, Chouinard, Howell, & Bennett, 2017). For example, chimpanzees (*Pan troglodytes*), ca-

puchin monkeys (*Cebus apella*), and bearded dragons (*Pogona vitticeps*) perceive the Delboeuf illusion (a target circle appears bigger when surrounded by a small circumference outer circle) in a similar manner to humans (Parrish & Beran, 2014; Parrish, Brosnan, & Beran, 2015; Santacà, Miletto Petrazzini, Agrillo, & Wilkinson, 2019), whereas dogs (*Canis familiaris*), rhesus macaques (*Macaca mulatta*), and red-footed tortoises (*Chelonoidis carbonaria*) appear not to experience this illusory phenomenon (Byosiere et al., 2017; Miletto Petrazzini, Bisazza, & Agrillo,

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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.

Maria Santacà collected data, carried out the statistical analyses, participated in the design of the study, and drafted the manuscript; Maria Elena Miletto Petrazzini participated in the design of the study and helped draft the manuscript; Christian Agrillo conceived of the study, designed the study, and helped draft the manuscript; Anna Wilkinson participated in the design of the study, coordinated the study, and helped draft the manuscript. All authors gave final approval for publication.

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2017; Parrish et al., 2015; Santacà, Miletto Petrazzini, Wilkinson, & Agrillo, 2020). Moreover, dolphins (*Tursiops truncatus*) and redbtail splitfin fishes (*Xenotoca eiseni*) experience the Ebbinghaus illusion (a target circle appears bigger when surrounded by small circles) in the same way as humans (Murayama, Usui, Takeda, Kato, & Maejima, 2012; Sovrano, Albertazzi, & Rosa Salva, 2015). In contrast, baboons (*Papio anubis*) and common starling (*Sturnus vulgaris*) appeared not to perceive any illusion when presented with the Ebbinghaus pattern (Benhar & Samuel, 1982; Qadri & Cook, 2019), whereas pigeons (*Columba livia*) and bantams (*Gallus gallus domesticus*) seem to experience a reversed illusion, meaning that they perceive the illusion in the opposite way to humans (Nakamura, Watanabe, & Fujita, 2008; Nakamura, Watanabe, & Fujita, 2014). The sensitivity to these illusory patterns (and the perceptual systems underlying these phenomena) are thought to reflect the different environmental pressures and ecological niche requirements of the species (Feng et al., 2017; Fujita, Nakamura, Sakai, Watanabe, & Ushitani, 2012).

The Müller-Lyer illusion results in a misperception of the relative length of two stimuli (Müller-Lyer, 1889). Figure 1 shows a classic version of the illusory pattern: Two parallel lines, one of which ends in inward pointing arrows and the other which ends with outward pointing arrows, are presented. To a human observer, the line with the inward pointing arrows appears to be significantly longer than the other. This pattern has been widely investigated in human perceptual studies (Gregory, 1997; Roberts, Harris, & Yates, 2005; Weidner, Boers, Mathiak, Dammers, & Fink, 2010), and different theories have been proposed to explain the illusion. According to Gregory's inappropriate constancy scaling theory (Gregory, 1963), the outward pointing arrows are thought to be arranged in a configuration that makes the line appear closer in depth, whereas the inward pointing arrows makes the line appear

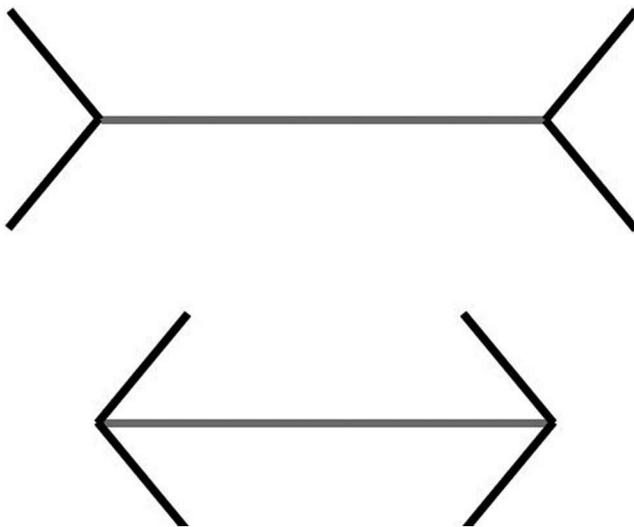


Figure 1. Müller-Lyer illusion. This illusion occurs when two same length lines are perceived to be different depending upon the surrounding context. In this example, two parallel lines, one of which ends in inward pointing arrows and the other which ends with outward pointing arrows, are presented. When observing the two lines, the one with the inward pointing arrows appears to be significantly longer than the other.

further in depth; therefore, this pattern would induce relative size-constancy scaling of the lines (Ward, Porac, Coren, & Girgus, 1977). Alternatively, according to the Howe and Purves's probabilistic theory in natural scenes (Howe & Purves, 2005), the inward pointing arrows are more likely to indicate longer lines, suggesting that the Müller-Lyer illusion could be owing to a probabilistic strategy of visual processing. In humans, neuro-imaging studies have shown that the Müller-Lyer illusion is related to top-down modulation from the posterior parietal cortex (Weidner & Fink, 2007) and the anterior cingulate cortex (Qiu, Li, Zhang, Liu, & Zhang, 2008). However, low-level explanations, which do not fully depend on these parts of the cerebral cortex, have been proposed to account for this phenomenon (Zanker & Abdullah, 2004). These suggest that the perception of the Müller-Lyer illusion could be ascribed to the filtering occurring in the early visual system. Such filtering could cause a nonprecise location of line endings (Coren & Girgus, 1978). For example, the optical blur has been proved to affect the magnitude of such illusion (Ward & Coren, 1976). With respect to this issue, animal models are particularly useful to assess the role of cortex as *sine qua non condition* for the emergence of the illusion.

The Müller-Lyer illusion has been investigated in birds (homing pigeons [Malott, Malott, & Pokrzywinski, 1967; Nakamura, Fujita, Ushitani, & Miyata, 2006; Nakamura, Watanabe, & Fujita, 2009], ringneck doves [*Turtur risorius*; Warden & Baar, 1929], African gray parrots [*Psittacus erithacus*; Pepperberg, Vicinay, & Cavanagh, 2008], and Plymouth Rock chicks [Winslow, 1933]) and mammals (capuchin monkeys [Suganuma, Pessoa, Monge-Fuentes, Castro, & Tavares, 2007], rhesus macaques [Tudusciuc & Nieder, 2010], and dogs [Keep, Zulch, & Wilkinson, 2018]). Recently, susceptibility to this illusory pattern has also been shown in a fish species (redtail splitfin; Sovrano, Da Pos, & Albertazzi, 2016). All the aforementioned species seem to perceive the Müller-Lyer illusion in a human-like way. However, one challenge of testing the Müller-Lyer illusion in nonhuman animals is that the animals cannot be easily instructed to attend to the length of the lines without including the length of the arrowheads. Thus, if animals perceive each stimulus figure (including arrowheads) as a whole then their responses would parallel those observed in humans without them actually perceiving the illusion. This effect is particularly important when the inducers (i.e., the arrowheads) are not substantially different from the target lines; for example, these are of the same color or composition. Thus, to truly test perception of the Müller-Lyer illusion it is essential to include controls that allow us to pull apart whether a choice is based on differences in the perceived line length (as would be the case if the animals perceived the illusion) or other spurious stimulus features. Despite their importance, different previous studies did not include any control that checked for the possibility that subjects' choices were exclusively based on the length of the target line and not the overall length of the stimuli (Malott et al., 1967; Nakamura et al., 2006; Tudusciuc & Nieder, 2010; Warden & Baar, 1929). This prevents any firm conclusions from being drawn about the true sensitivity for the Müller-Lyer of some of the aforementioned species, such as pigeons, doves, and rhesus macaques. In fact, thanks to presence of these controls, the dogs' apparent susceptibility to the Müller-Lyer illusion was ultimately interpreted to be a consequence of their use of the global size to solve the task (Keep et al., 2018).

Investigating a distortion illusion in nonavian reptiles (reptiles from now on) is particularly useful, as it allows assessment of the similarities and differences in the perceptual bias underlying visual perception in amniotes. In this study, we investigated whether bearded dragons, *Pogona vitticeps*, perceive the Müller-Lyer illusion. We adopted a spontaneous choice test using food portions as stimuli; a similar methodological approach has been previously used to investigate the sensitivity to another distortion illusion in different animal species, including chimpanzees (Parrish & Beran, 2014), ring-tailed lemurs (Santacà, Regaiolli, Miletto Petrazzini, Spiezio, & Agrillo, 2017), dogs (Miletto Petrazzini et al., 2017), and reptiles (Santacà et al., 2019, 2020). In control trials, the lizards were tested in their spontaneous tendency to choose the bigger food quantity. Such control trials consisted of two different-sized food portions presented in an identical context and differing by a ratio of 0.67. A similar methodology was previously used in lizards to assess quantitative skills in foraging contexts (Burghardt, 1964). Intermixed with the control trials, we presented test trials that resembled the Müller-Lyer illusion: two identical food quantities with arrowheads positioned in a pattern that elicits the illusion in humans. Animals were expected to maximize food intake by reaching for the physically larger food portion in control trials and the perceptually larger portion in test trials, if they perceive the illusion like humans.

Materials and Method

Subjects, Stimuli, and Apparatus

Twelve bearded dragons (*Pogona vitticeps*), eight females and four males, participated in this study (see Table 1). They were all adults, and none was participating in any other experiment while taking part in this study. The bearded dragons had previously participated in a study regarding their sensitivity to another size illusion, the Delboeuf illusion (Santacà et al., 2019). The reptiles were housed individually or in pairs in a heated room. All bearded dragons had permanent access to fresh water, shelter, UV light, and heat lamps. They were not food deprived during the experiment but were fed their main meal after experiments were finished for the day.

The stimuli consisted of vegetable extract (kale, cucumber, and mint) jelly, which was used as it is a highly preferred food for bearded dragons. The jellies were prepared each day and cut with a knife to get a straight line. Then, each jelly stimulus was placed in the middle of a 7.5- × 8.5-cm white plastic card. Two different portion sizes were presented to the reptiles: The longer food portion was 3 cm in length, whereas the shorter food portion was 2 cm in length. The food portions were 0.5 cm in width and 0.5 cm in height. The inducers consisted of black arrowheads and were printed on the cards; they were not covered in any part by the jelly. Each card was presented on a presentation table that consisted of an L-shaped steel bracket (7.5 × 8.5 × 4 cm) to ensure that the lizards could readily see the stimuli.

The experiment was run in an arena measuring 100 × 100 cm (see Figure 2) located in a dedicated test room without any external cues on the wall. The test room was maintained at 28°C (± 3°C). The inner part of the arena was covered with black plastic sheets to minimize the experimental variability and to allow proper cleaning to reduce the possibility of following olfactory trails (Wilkinson, Chan, & Hall, 2007). To ensure the animals had a perpendicular view of the stimuli before making a choice, they were placed at the top of a ramp (inclination angle of 36.02 degrees); they then descended the ramp to make their choice. From the arena, the only object that a subject could view other than the experimental set up was a video recorder, which was placed outside the arena itself and was centered above the midpoint of the arena and pointed straight down. After placing a subject in the arena (the exact position was marked to ensure it was central), the experimenter remained out of the subject's sight until it had made a choice. The experimenter was able to hear when the bearded dragon descended the ramp to reach a food portion; therefore, the subject had made a choice and could remove the unselected food portion from the arena.

Procedure

No familiarization phase was necessary, as the animals were already habituated to the apparatus from the previous experiment (Santacà et al., 2019). Each bearded dragon received 48 trials over

Table 1
Information of the Bearded Dragons Participating in the First Investigation and Individual Analyses

Subject	Different length control (<i>p</i>)	Inducer control (<i>p</i>)	Müller-Lyer illusion (<i>p</i>)
Shuriken	13/16 (.021)*	12/16 (.079)	14/16 (.004)*
Malie	12/16 (.079)	14/16 (.004)*	14/16 (.004)*
Nimoy	13/16 (.021)*	16/16 (.0001)*	7/16 (.804)
Quadra	15/16 (.0005)*	11/16 (.210)	16/16 (.0001)*
Norbert	11/16 (.210)	14/16 (.004)*	10/16 (.455)
Dr. Tom Pike	14/16 (.004)*	12/16 (.079)	11/16 (.210)
Alberta	11/16 (.210)	13/16 (.021)*	13/16 (.021)*
Heinz	12/16 (.079)	13/16 (.021)*	12/16 (.079)
Cecilia	13/16 (.021)*	14/16 (.004)*	11/16 (.210)
Oscar	14/16 (.004)*	15/16 (.0005)*	14/16 (.004)*
Mushu	13/16 (.021)*	13/16 (.021)*	14/16 (.004)*
Haku	15/16 (.0004)*	13/16 (.021)*	13/16 (.012)*

Note. Different Length Control and Inducer Control = frequency of choices for the longer food portion; Müller-Lyer illusion = frequency of choices for the food portion ending with inward pointing arrow.

* A significant departure from chance at binomial test ($p < .05$).

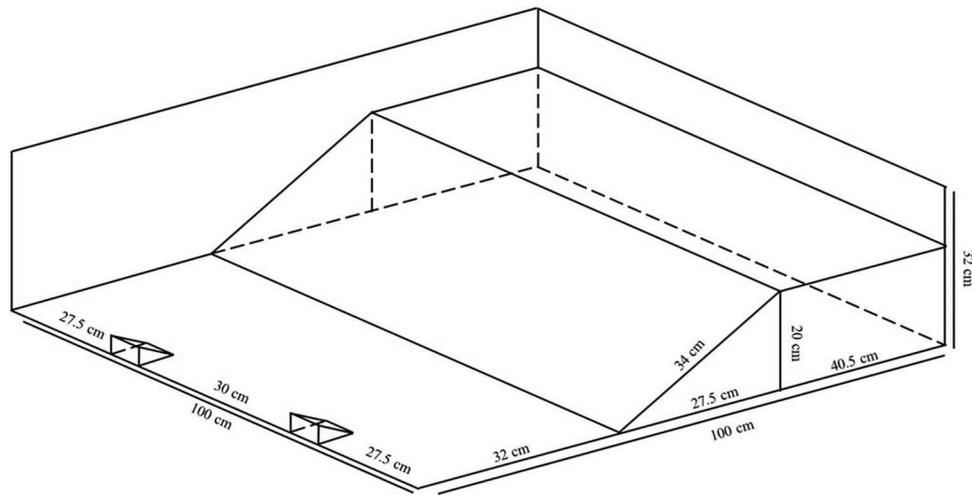


Figure 2. Experimental setup. The experiment was run in a square area. The bearded dragons could view the food portions, presented on white plastic card, from the top of a ramp. As the dependent variable we recorded the first stimulus approached and touched by the subject in each trial.

12 sessions; each day all subjects received two sessions (a total of eight trials per day) with at least a 1-hr interval between sessions. To avoid any social influences, each subject was tested individually. Sessions were composed of both control and test trials (see Figure 3). The control trials consisted of the presentation of two linear jelly portions of different lengths and presented as isolated stimuli (“Different Length Control”) or with inducers (two black oblique lines) positioned above and below the target stimuli (“Inducer Control”). These visual patterns resembled those used in a previous experiment on Müller-Lyer illusion in pigeons (Nakamura et al., 2006) and were also used in a training study of fish (Sovrano et al., 2016). In the Inducer Control, the arrowheads were not attached to the food portions. Such a configuration was used to familiarize the subjects to the presence of arrowheads to avoid the emergence of any kind of neophobic reactions in illusory trials. Subjects could see the arrowheads when choosing between the two different-sized food portions; however, as the arrowheads’ positions were identical for both stimuli, subjects could not rely on the arrowheads to solve the discrimination task. The food portions presented in control trials differed by a ratio of 0.67, a ratio commonly discriminated by different species (Bánszegi, Urrutia, Szenczi, & Hudson, 2016; Lucon-Xiccato, Santacà, Miletto Petrazzini, Agrillo, & Dadda, 2019; Miletto Petrazzini et al., 2017). In test trials, two linear food portions of identical length (3 cm) were presented, one ending with inward pointing arrows (inclination angle of 45 degrees in respect to the target food portion) and the other with outward pointing arrows (inclination angle of 135 degrees in respect to target food portion). Each bearded dragon performed 16 trials per condition.

Animals were allowed one choice; a choice was considered as approaching and touching a stimulus. After making a choice, the animals were allowed to consume the jelly stimulus and were removed from the arena after doing so. Trials were presented in a pseudorandom sequence in which bearded dragons were never presented with two test trials consecutively and the

sessions never started with a test trial. The position (left/right) of the longer food portion was counterbalanced over trials just like the presentation of the two configurations of the test trials. All sessions were video recorded for later analysis.

To control for the possibility that, in the presence of the illusory pattern, the animals used physical differences that existed between the two arrays as the discriminative cue (the array with the arrowheads pointing inward inevitably occupied an overall larger space than the other), we presented supplementary control trials to a subsample of subjects (nine out of 12). Unfortunately, it was not possible to test all the 12 subjects, as three subjects died of natural causes before the collection of these supplementary data. The setup was identical to the previous trials with the exception of stimuli. We presented the same control trials (eight of each), but these were intermixed with two additional control conditions (16 trials of each). In “Overall Length Control,” two different length portions were presented to the subjects. One stimulus was the same as the original inward arrows; this was paired with a stimulus of the same overall length but that was made up of only the isolated food portion (see Figure 4). In these control trials, bearded dragons were expected to select the longer isolated food portion if the size judgments in test trials of the previous experiment were based on the length of the food portion and not the overall length of the stimuli (Food Portion + Arrowheads). However, it was possible that the animals chose the longer line because it was the one without arrowheads. To assess whether bearded dragons simply exhibited a spontaneous preference for selecting food portion without arrowheads, we presented another type of control trial. In “Presence of Arrowhead Control,” two equal food portions were presented, one with the original outward arrow paired with an overall equal length isolated food portion (see Figure 4). In these control trials, bearded dragons were expected to randomly choose between the two food portions if they did not have any bias in favor of food items without arrowheads.

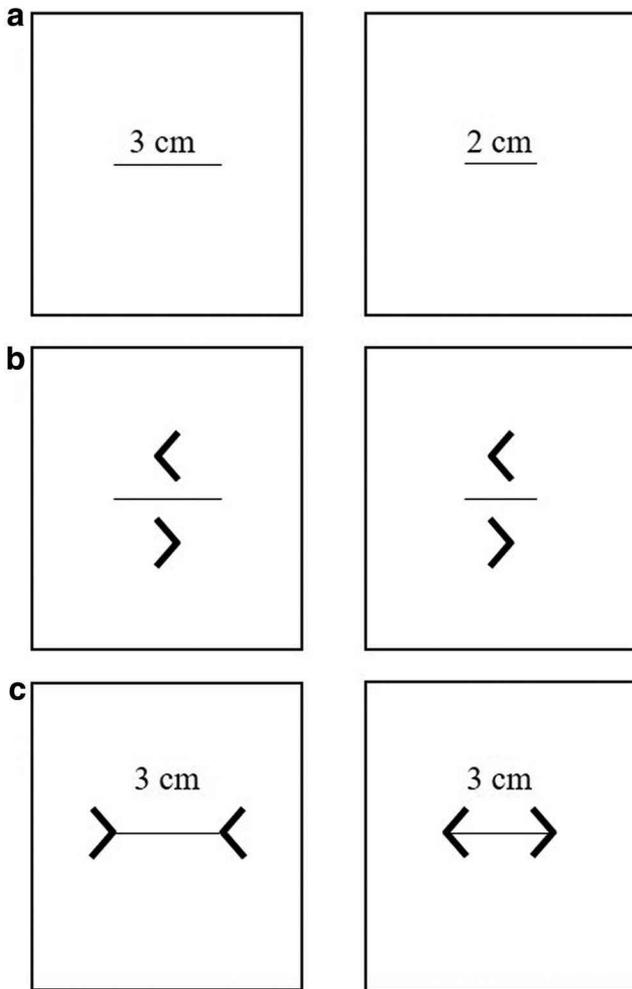


Figure 3. Experimental stimuli. Two arrays containing different or equal-length linear jelly portions were presented: (a) Different Length Control with different length portions presented as isolated stimuli; (b) Inducer Control with different length portions presented with inducers positioned above and below; and (c) test trials with equal-length food portions, one ending with inward pointing arrows and the other ending with outward pointing arrow.

Data Analysis

All trials were coded from video recordings. A choice was considered as the first food portion touched by the animal. To assess the interrater reliability, one third of the trials of each subject were coded by a blind observer; an excellent concordance was found (Pearson's correlation, $r = 1.0$, $p < .001$).

Statistical analyses were performed in R Version 3.5.3 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>). Initially, we performed a generalized mixed-effects model with binomial response distributions (GLMMs, "glmer" function of the "lme4" R package) using the data on the choice of the longer food portion in the control trials and on the choice of the food portion perceived as longer by humans in the illusory trials. The effect of day was also included in the model to ensure that bearded dragons' performance was stable. Then, we used binomial

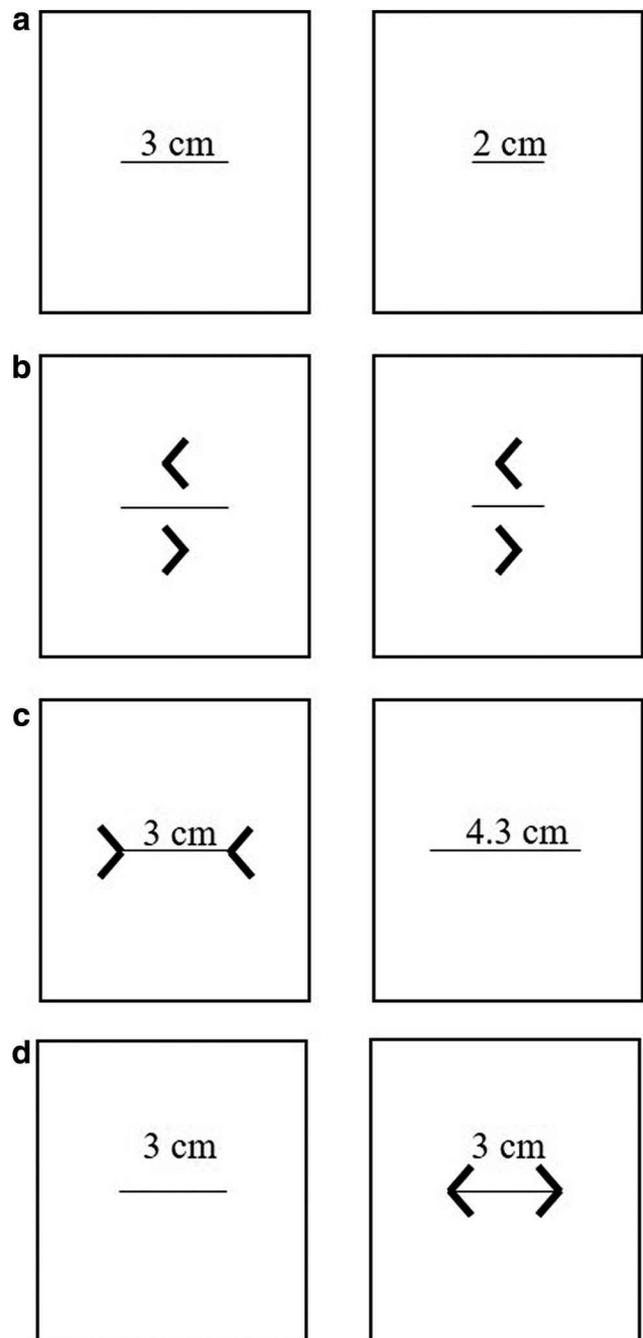


Figure 4. Additional controls. Two arrays containing different or equal-length linear jelly portions were presented: (a) Different Length Control with different length portions presented as isolated stimuli; (b) Inducer Control with different length portions presented with inducers positioned above and below; (c) Overall Length Control with different length food portions, one with original inward arrows paired with an overall equal length isolated food portion; and (d) Presence of Arrowhead Control with equal food portions, one with original outward arrows paired with an overall equal length isolated food portion.

tests (“binom.test” function) to compare the choice of the longer food portion in the control trials, and the choice of the food portion perceived as longer in illusory trials, with chance level set at 0.50, both at the individual and at the group level. To assess differences between subjects, we performed another generalized mixed-effects model considering the subjects’ ID as a fixed factor. Post hoc power analyses on binomial tests were performed using the statistical software G*Power (Faul & Erdfelder, 1992) that calculated the statistical power achieved based on the observed effect size. To calculate the achieved power with G*Power, we ran *t* tests involving a sample’s difference from a constant, which in our case is the chance level (0.5). We set two-tailed tests, α error probability of 0.05, a total sample size of 12 for the first investigation and of nine for the second one, and a calculated effect size. The effect size was calculated from the mean and standard deviation obtained for each type of trial. Post hoc power analyses on GLMMs were performed using the “SIMR” R package that calculate the power analysis based on Monte Carlo simulations (Green & MacLeod, 2016). Partial eta-squared (η_p^2 ; “eta_sq” function of the “sjstats” package) were used as effect size statistics for GLMM.

Results

The GLMM showed that the performance of bearded dragons was stable across the 6 days ($\chi_3^2 = 4.727$, $p = .450$, $\eta_p^2 = 0.009$, power = 0.976) and did not vary as a function of the type of trials ($\chi_2^2 = 1.682$, $p = .431$, $\eta_p^2 = 0.003$, power = 0.987). The Day \times Type of Trial interaction was not significant ($\chi_{10}^2 = 13.139$, $p = .213$, $\eta_p^2 = 0.024$, power = 0.999). Group analyses revealed that the lizards were able to discriminate between the two portion sizes, selecting the longer one to maximize the food intake in both versions of the control trials: Different Length Control (M : 0.813, 95% confidence interval [CI; 0.759, 0.866], $p < .001$; power = 1.000; Figure 5a) and Inducer Control (M : 0.834, 95% CI [0.779, 0.888], $p < .001$; power = 1.000). Individual analyses (binomial tests) on the frequency of choices of the longer food portion showed that seven bearded dragons out of 12 in the Different Length Control and nine subjects in the Inducer Control significantly selected the longer food portion (see Table 1). In the visual illusion test trials, group analyses revealed a significant preference for the portion within the inward pointing arrows (M : 0.776, 95% CI [0.681, 0.871], $p < .001$; power = 0.999; Figure 5a). Individual analyses showed that seven out of the 12 bearded dragons significantly selected the food portion ending with inward pointing arrows in illusory trials (the one apparently longer to humans; Table 1). This suggests that the lizards were sensitive to the Müller-Lyer illusion. However, to demonstrate this conclusively, it was necessary to investigate whether they were using the overall stimulus size rather than portion size to make their decisions. The GLMM revealed that the 12 subjects did not statistically differ from each other ($\chi_{11}^2 = 8.851$, $p = .636$, $\eta_p^2 = 0.022$, power = 0.934) and no significant interaction between the Subject \times Type of Trial ($\chi_{22}^2 = 16.525$, $p = .789$, $\eta_p^2 = 0.031$, power = 0.926).

Similar patterns of performance on the length control trials were observed in the second part of the experiment that was performed with nine out of 12 subjects. The GLMM showed that the performance of bearded dragons was stable across the 6 days ($\chi_3^2 = 0.598$, $p = .988$, $\eta_p^2 = 0.001$, power = 0.998). Their performance varied according to the type of trial ($\chi_3^2 = 28.447$, $p < .001$, $\eta_p^2 =$

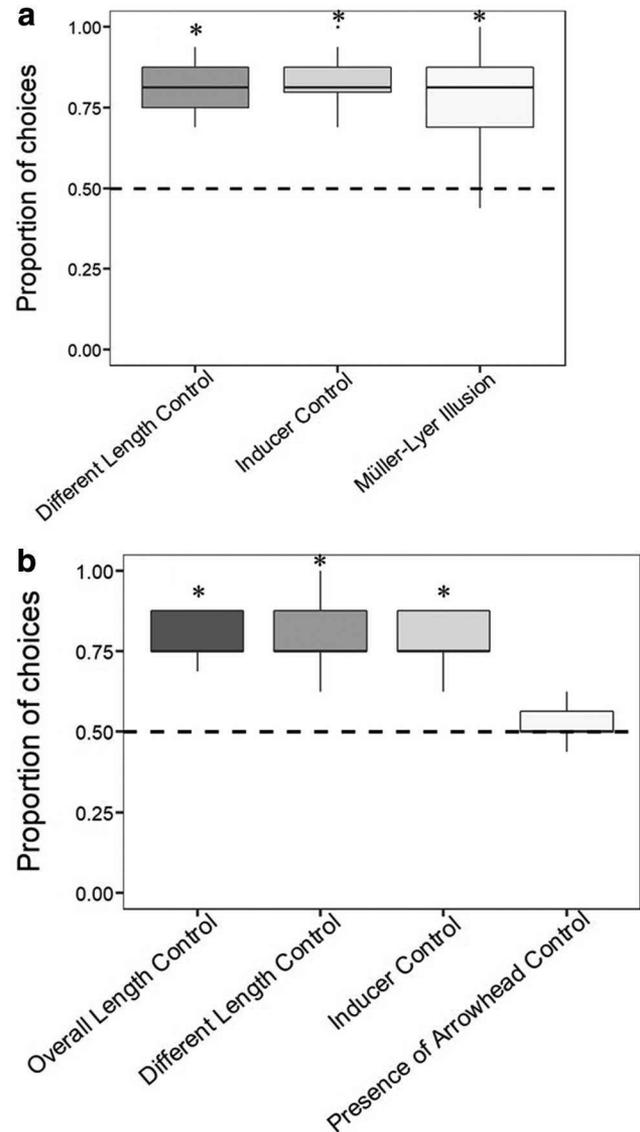


Figure 5. Results. Boxplot representing median, first quartile, third quartile, ranges, and outliers (data points 1.5 interquartile ranges smaller than the first quartile or greater than the third quartile). (a) Test results. The Y-axis refers to the proportion of choices for the longer food portion in Different Length Control (different length portions presented as isolated stimuli) and Inducer Control (different length portions presented with inducers positioned above and below), and the proportion of choices for the food portion ending with outward pointing arrow in test trials. (b) Results of additional controls. The Y-axis refers to the proportion of choices for the longer food portion in the Different Length Control (different length portions presented as isolated stimuli), Inducer Control (different length portions presented with inducers positioned above and below), Overall Length Control (different length portions, one with inward arrows paired with an overall equal length isolated stimulus), and the proportion of choices for the food portion ending with outward pointing arrow in Presence of Arrowhead Control (two equal food portions, one with outward arrows paired with an overall equal length isolated stimulus). The asterisk (*) denotes a significant departure from chance level (dashed line).

0.055, power = 0.896). Tukey's post hoc tests revealed no significant difference between Different Length Control, Inducer Control, and Overall Length Control (all p values > 0.878). A significant difference was found between the Presence of Arrowhead Control and all the other three types of trial (all p values < 0.001). The Day \times Type of Trial interaction was not significant ($\chi^2_{10} = 10.146$, $p = .428$, $\eta^2_p = 0.020$, power = 0.893). Given that there was no difference between Different Length Control and Inducer Control, we pooled data together. Group analysis confirmed bearded dragons' tendency to maximize the food intake in Different Length Control plus Inducer Control ($M: 0.792$, 95% CI [0.728, 0.856], $p < .001$; power = 1.000). Crucially, in the additional control trials we found that lizards chose the longer food portion in the Overall Length Control trials ($M: 0.792$, 95% CI [0.728, 0.855], $p < .001$; power = 1.000; Figure 5b). Individual analyses (binomial tests) on the frequency of choices for the longer food portion showed that five bearded dragons out of nine in the Different Length Control plus the Inducer Control and four subjects in the Overall Length Control significantly selected the longer food portion (see Table 2). In the Presence of Arrowhead Control, none of the lizards selected one portion significantly more than would be expected by chance ($M: 0.514$, 95% CI [0.467, 0.561], $p = .803$; power = 0.090; Figure 5b), suggesting that subjects were not using overall stimulus size or other spurious cues (e.g., presence/absence of arrowheads) to make the discrimination. The GLMM revealed that the nine subjects did not statistically differ from each other ($\chi^2_8 = 5.800$, $p = .670$, $\eta^2_p = 0.004$, power = 0.911) and no significant interaction between the Subject \times Type of Trial ($\chi^2_{24} = 6.794$, $p = 1.000$, $\eta^2_p = 0.014$, power = 0.998).

Discussion

Visual illusions allow us to assess whether animals interpret and alter visual inputs rather than detecting them with little or no variation from reality. Thus, investigation of illusion susceptibility can inform us about the impact of environmental and evolutionary pressures on visual perception. However, until recently reptiles have been missing from this work. Investigations with this group are essential to understand the evolution of this ability but also

because of their differences in eye and brain structure to other vertebrates. Here we demonstrate, for the first time, that a reptile species is sensitive to the Müller-Lyer illusion, indicating a similarity in perceptual systems between mammals, birds, reptiles, and fish.

In the presence of illusory patterns, the lizards selected the food portion with the inward pointing arrows, the same stimulus that humans evaluate as longer. Control trials revealed that the bearded dragons did this, not on the basis of global size of the stimulus, but rather as a result of the illusion. Comparing our results with those of the other species tested can shed light on the perceptual bias underlying visual perception of distortion illusions, such as the Müller-Lyer illusion. Despite having eyes that differ compared with other amniotes, the perceptual principles underlying the elaboration of visual inputs appear to be similar. As has been observed in humans and some other animals, bearded dragons are active interpreters of reality and not passive decoders of the visual stimuli.

The bearded dragons demonstrated a preference in illusory trials indicating that they perceived the illusion and attended to the arrowheads. It might be argued that the performances exhibited by the subjects in the Overall Length Control and the Presence of Arrowheads suggest that they ignored the arrowheads. However, in the Overall Length Control, the two food portions physically differed by more than 30%. Even if the illusion had an effect in the size judgments in the Overall Length Control, it is too small to interfere with the real difference between the two food portions. Hence, the fact that they chose the longer food portion does not contradict the performance in illusory trials but instead suggests that the food is more salient than the mere presence of arrowheads and that subjects were not estimating the overall length of food by combining the length of the food and the length of the arrowheads. This second conclusion is fundamental to demonstrate that they were actually perceiving the Müller-Lyer, as in illusory trials the stimuli differed in length, considering both the food portion and the arrowheads.

The group analysis showed a strong illusory effect in the bearded dragons; however, we did not observe such substantial effect at an individual level (only three out of 12 bearded dragons

Table 2
Information of the Bearded Dragons Participating in the Second Investigation and Individual Analyses

Subject	Different length control plus inducer control (p)	Overall length control (p)	Presence of Arrowhead Control (p)
Shuriken	13/16 (.021)*	12/16 (.079)	8/16 (1.000)
Malie	15/16 (.0005)*	14/16 (.004)*	10/16 (.455)
Nimoy	11/16 (.210)	11/16 (.210)	8/16 (1.000)
Quadra	12/16 (.079)	11/16 (.210)	8/16 (1.000)
Norbert	14/16 (.004)*	14/16 (.004)*	7/16 (.804)
Dr. Tom Pike	12/16 (.079)	14/16 (.004)*	7/16 (.804)
Alberta	13/16 (.021)*	12/16 (.079)	9/16 (.804)
Oscar	13/16 (.021)*	14/16 (.004)*	8/16 (1.000)
Mushu	11/16 (.210)	11/16 (.210)	9/16 (.804)

Note. Different Length Control plus Inducer Control and Overall Length Control = frequency of choices for the longer food portion; Presence of Arrowhead Control = proportion of choices for the food portion ending with outward pointing arrow.

* A significant departure from chance at binomial test ($p < .05$).

demonstrated human-like perception of the Müller-Lyer illusion). The subjects that did not reach the significance threshold had a nonsignificant preference for the physically (control trials) or subjectively (illusory trials) longer food portion that led to the robust and significant group analyses. This result could be explained by a weaker illusory effect in bearded dragons compared with humans; however, it is more likely to be owing to the small number of trials that were conducted with each individual. Unfortunately, presenting a higher number of trials was not possible owing to the nature of the methodological approach of the spontaneous choice test. Nonetheless, it would be interesting to investigate this further using a training paradigm.

A fundamental, and little understood, issue in the field of behavioral biology is how animals integrate the information captured by the retina in the brain. Animals might first analyze the details of a scene, using local features, or instead prioritize a global perception of the elements, something typically referred to as seeing “the forest before the trees” (Navon, 1977). The perception of distortion illusions may potentially require the overall perception of the stimulus and the surrounding context (in the Müller-Lyer illusion, the arrowheads). In our experiment, if an animal has a local-to-global precedence, it was expected to focus only on the food portion and ignore the arrowheads, resulting in a lack of preference for any food portion in illusory trials. In contrast, if an animal has a global-to-local precedence, it would be expected to be influenced by the presence of the arrowheads when shown with the illusory pattern. That said, the relationship between the global-to-local precedence and the perception of the Müller-Lyer illusion is not so predictable. In fact, not all species that demonstrated the perception of this illusory pattern demonstrated a global-to-local precedence. A global-to-local precedence has been demonstrated in redbait splitfin fishes (Truppa, Sovrano, Spinozzi, & Bisazza, 2010) and humans (Fujita & Matsuzawa, 1990; Kimchi, 1992). Instead, the opposite condition—local-to-global precedence, with local analysis predominating over global one—has been found in pigeons (Cavoto & Cook, 2001) and capuchin monkeys (De Lillo, Spinozzi, Palumbo, & Giustino, 2011). This issue has been never directly investigated in reptiles. To draw firm conclusions about the global or local processing of bearded dragons, future studies should test this species in a traditional fashion using hierarchical visual stimuli in which the local and the global aspects of the stimuli can be manipulated.

In this work, we also observed lizards in their spontaneous tendency to choose the larger portion of food. All the control tests in which we presented a physical difference between the two portions indicates that bearded dragons may discriminate the larger portion of food with a 0.67 ratio. As bearded dragons showed the ability to discriminate a ratio successfully discriminated by other amniotes (Bánszegi et al., 2016), it is, therefore, possible that this species displays quantificational systems similar to those commonly described in mammals, birds, and fish (for a review, see Agrillo & Bisazza, 2018), a hypothesis that should be tested in the future.

It is interesting to note that the Presence of Arrowhead Control—initially set up to assess whether subjects exhibited a spontaneous preference for arrays without arrows—represented an incomplete version of the illusion. As a consequence, the possibility existed that subjects underestimated the size of food associated with the arrowheads pointing outward. The lack of preference

observed here indicates that the presence of inward pointing arrowheads is fundamental for the emergence of the illusion in reptiles. Alternatively, it is possible that both in the Presence of Arrowhead Control and in the Overall Length Control, the bearded dragons could be simply ignoring the arrowheads and paying attention only to the length of the food stimuli. This is unlikely, given their performance on the illusory trials. However, to tackle this issue, future studies should test bearded dragons with sets of stimuli composed of arrows in the same directions with both same and different length target lines as done in previous studies (Nakamura et al., 2006; Warden & Baar, 1929). Further work in which trained stimuli are used, ideally without humans present to ensure avoidance of a Clever Hans effect, would allow greater exploration of this area.

Much work is still needed to further explore the nature of visual illusions in this species, reptiles, and nonhuman animals in general. It would be interesting to explore the reverse Müller-Lyer illusion that occurs when the arrowheads do not touch the target line; such a configuration causes the opposite illusion in humans and no illusory effect in pigeons (Nakamura et al., 2006). Visual illusions are much better understood in humans than nonhuman animals, and this opens up many new questions that could be investigated. For example, presenting the two illusory stimuli separately instead of a simultaneous presentation would allow both illusory stimuli to be independently compared with the same neutral stimulus without any inducer. In humans, this type of investigation suggests that the entity of the illusory effect is the same for both outward and inward arrowheads when compared with a line without any arrowhead (Gilster & Kuitz-Buschbeck, 2010). However, when human observers can directly compare the two illusory stimuli, the magnitude of the illusory effect is higher; this phenomenon is known as superadditivity (Foster & Franz, 2014). This would allow greater understanding of the perceptual processes at work.

Nonavian reptiles are characterized by a great taxonomic diversity, and they inhabit very different ecological niches all over the world. In fact, evolutionary pressures are thought to be a key factor driving species' differentiation in visual and neural anatomy (Butler & Hodos, 2005); therefore, variations in evolutionary pressures could have also resulted in species differences in perceptual mechanisms. Given their great taxonomic diversity and the diversity of their ecological niches, studying the sensitivity to distortion illusions in different reptile species may shed light on the evolution of the amniotes visual system, providing information on the perceptual principles and the neural mechanism underlying visual perception in species belonging to different taxa.

This work has revealed evidence that at least one reptile species may be sensitive to the Müller-Lyer illusion. Together with recent evidence in fish (Sovrano et al., 2016), our study challenges the idea that higher level, cortical mechanisms are strictly necessary to elicit illusory size misperception. We suggest the intriguing possibility that the perceptual systems underlying size length estimation described in humans are ancient, predating the emergence of cortex and dating back ~350–450 million years ago (Hevner, 2016). Such perceptual systems might have been conserved in the mammalian lineage even after different visual functions became localized in the cortex. Future studies using animal models are now necessary to understand the neural bases of size perception.

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