UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

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“Metaanálisis sobre factores biológicos y metodológicos que influyen en la respuesta a ilusiones visuales geométricas en vertebrados adultos no humanos”

TESIS

PARA OBTENER EL TÍTULO DE:

BIÓLOGO

PRESENTA:

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Índice

1. Resumen

Las ilusiones visuales se han estudiado en muchas especies de vertebrados no humanos, abarcando una amplia gama de variables biológicas y metodológicas. Mientras que las primeras revisiones han sido útiles para proveer una descripción general del campo, no han sido acompañadas de análisis cuantitativos para evaluar sistemáticamente a la contribución de factores biológicos (p.e., hábitat, posición de los ojos) y metodológicos (p.e., tipo de ilusión y método de prueba, número de ensayos durante el entrenamiento y en las pruebas, y la proporción de sexos de los individuos) en la proporción de elección sobre ilusiones. En el presente estudio meta analítico, confirmamos que las ilusiones visuales geométricas son un fenómeno general entre los vertebrados no humanos. Sin embargo, el tipo de ilusión podría alterar significativamente la magnitud de la susceptibilidad a estas. En términos de metodología, los estudios con un tamaño de muestra mayor reportan tamaños de efecto menores, mientras que los estudios más recientes muestran preferencia por pruebas espontaneas sobre pruebas con entrenamiento previo. Discutimos sobre los retos y obstáculos en esta área de estudio, los cuales, de ser tomados en cuenta, podrían llevar a mejores avances a futuro.

2. Abstract

Visual illusions have been studied in many non-human vertebrate species, spanning a wide range of biological and methodological variables. While early reviews have proved useful in providing an overview of the field, they have not been accompanied by a quantitative analysis to systematically evaluate the contribution of biological (e.g., habitat, and position of the eyes) and methodological factors (e.g., type of illusion and testing method, the number of trials during the training and testing, and the sex ratio of the subjects) on the proportion of illusory choice. In the current meta-analytical study, we confirm that geometrical visual illusion perception is a general phenomenon among non-human vertebrates. However, illusion type could significantly alter the magnitude of susceptibility. In terms of methodology, studies with larger samples report smaller effect sizes, while more recent studies prefer spontaneous choice over training. We discuss the challenges and bottlenecks in this area of study that, if addressed, could lead to more successful advances in the future.

3. Introducción

3.1 Ilusiones visuales geométricas

Se conoce como ilusión visual al fenómeno en el cual se observan inconsistencias entre la percepción visual de un observador y las características físicas del objeto observado (Gregory, 1997; Howe & Purves, 2005). Desde su descubrimiento en humanos hasta la fecha son un fenómeno de especial interés para la psicología y sus ramas interdisciplinarias con las ciencias biológicas, por ejemplo, la psicobiología. El estudio de este fenómeno en humanos se remonta desde la antigua Grecia (ver Coren et al., 1976 para una reseña histórica), hasta la actualidad. Durante este periodo, se han registrado una gran cantidad de ilusiones y con ello, se crearon de diversas categorías. Debido a su amplia variedad, las ilusiones visuales se han clasificado de forma general. Por ejemplo, en el trabajo de Gregory Richard (1997) son agrupadas en cuatro clases con base en un criterio que el autor nombró como "errores de lenguaje", puesto que relaciona el origen del lenguaje con la necesidad de clasificar los objetos y las acciones que realizan.

El término de ilusiones óptico-geométricas (actualmente: ilusiones visuales geométricas) apareció mucho antes del trabajo de Gregory Richard; en 1855 Johann Joseph Oppel publica su investigación titulada: "Sobre las ilusiones óptico–geométricas". Respecto a esta investigación Wade et al., (2017) nos menciona que Oppel hizo mucho más que nombrar una clase de distorsiones visuales-espaciales, pues examinó una variedad de figuras y fenómenos que fueron precursoras de las después llamadas ilusiones además de intentar cuantificarlas e interpretarlas. De igual forma, Oppel provee de una definición del fenómeno en los primeros párrafos de su artículo. Sin embargo, podemos encontrar una definición más corta en el trabajo de Ehm y Wackermann, (2016) la cual dice textualmente: "En las ilusiones óptico-geométricas las propiedades de un estímulo – por ejemplo, su tamaño, ángulos, área y formas – son afectadas y sistemáticamente alteradas por la presencia de otros elementos en el campo visual".

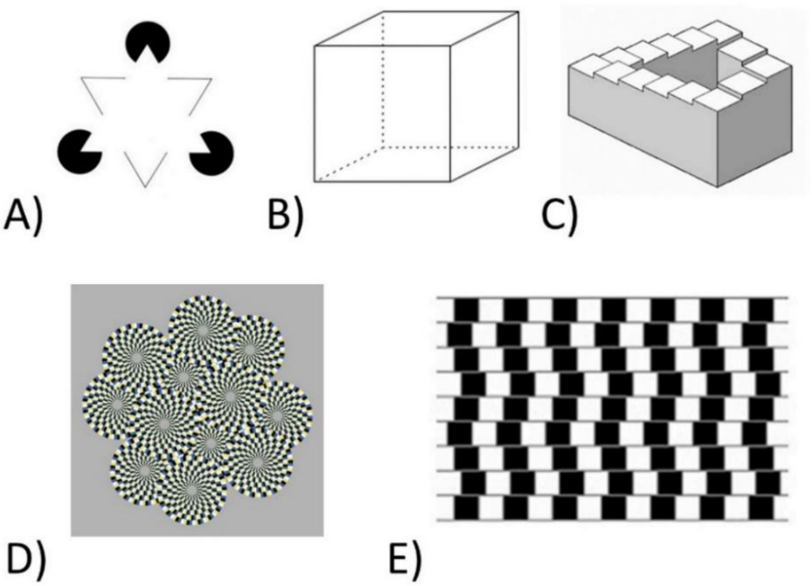

Imagen 1. Ejemplos de diferentes tipos de ilusiones visuales: A) Ilusión de Kanizsa (ilusión de contornos), B) Cubo de Necker (ilusión cognitiva ambigua), C) Escaleras de Penrose (ilusión de paradoja cognitiva), D) Ilusión de movimiento, E) La pared del Café (ilusión de distorsión cognitiva).

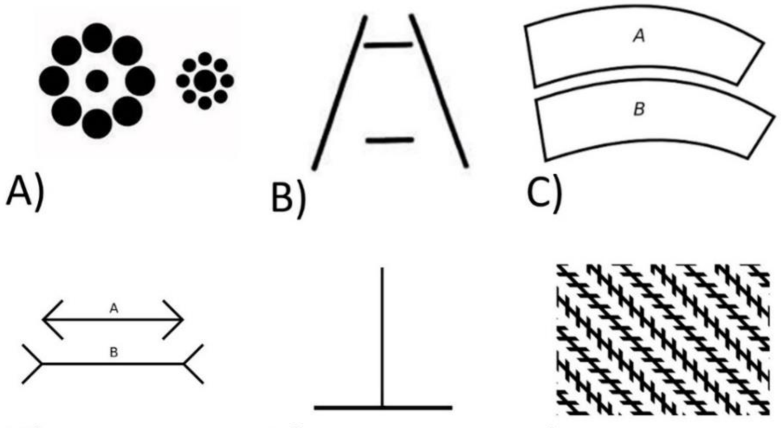

Imagen 2. Ejemplos de ilusiones visuales geométricas: A) Ilusión de Ebbinghaus., B) Ilusión de Ponzo, C) Ilusión de Jastrow, D) Ilusión de Müller-Lyer, E) Ilusión horizontal – vertical, F) Ilusión de Zöllner.

3.2 La percepción de las ilusiones visuales en los vertebrados

Una vez identificadas en seres humanos surgió la interrogante ¿Los animales (en específico los miembros del clado Craniata) son susceptibles percibir ilusiones visuales? Es un hecho que la percepción visual entre los vertebrados varía enormemente. Miembros de este subfilo tienen diversas características fisiológicas, morfología ocular y contextos ecológico también distintos; por ejemplo, algunos animales carecen de visión a color y otros cuentan con una visión disminuida o con una mayor agudeza visual en comparación con los humanos (Jacobs, 1981; Walls, 1942). Sin embargo, en décadas recientes se descubrió que hay mamíferos (no humanos) que pueden percibir estas ilusiones. Además, en trabajos más recientes, se ha revelado que las aves y peces igualmente perciben algunas ilusiones, a veces de forma opuesta a nuestra especie (Freeberg, 2019).

3.3 Investigación sobre la percepción a ilusiones visuales geométricas en animales

En el caso de los animales, la primera descripción de este fenómeno apareció a inicios del siglo XX. Thayer (1909) fue el primero en referirse a los efectos visuales creados por algunos animales, por ejemplo, las rayas sobre la piel de las cebras o las marcas sobre las alas de algunas mariposas, como "ilusiones". Ahora, se refiere a estos patrones como coloración disruptiva o camuflaje.

En 1924, Géza Révész realizó la primera investigación sobre ilusiones visuales geométricas en animales no humanos, específicamente en una gallina domestica (*Gallus gallus*) la cual expuso a la ilusión de Jastrow (**Imagen 2C,**) después de haber realizado sesiones de entrenamiento con el fin de que aprendiera a discriminar las figuras por tamaños. Géza Révész se preguntaba si los animales son susceptibles a las mismas ilusiones ópticas que los humanos. Esta pregunta le era interesante en dos formas. La primera es que él deseaba saber si este fenómeno óptico, que no se podía explicar sin la colaboración de factores psicológicos centrales, podría ser descubierta también en animales. Segunda, ¿Es posible realizar un experimento que lleve a resultados confiables con animales? Estas cuestiones lo llevaron a desarrollar un método que varios investigadores utilizan hasta la fecha.

Aun con las complicaciones o desventajas de su investigación, Révész y su experimento fueron excepcionales. A pesar de ello, la comunidad científica no se incorporó realmente a la investigación sobre percepción de ilusiones visuales en animales, los cuales siguieron siendo considerados por varias décadas como máquinas que percibían replicas exactas de los estímulos que se les daba. Aun con algunas excepciones, esta visión no cambio mucho hasta años recientes cuando la investigación reveló que probablemente algunos animales son muy similares a los humanos en la forma en que sus cerebros alteran sus estímulos visuales, además de que varias especies manipulan su ambiente para crear ilusiones visuales. Respecto a esto, Mascalzoni y Regolin, (2011) propusieron una hipótesis sobre la percepción de los animales a contornos ilusorios (ilusión visual donde una figura carece de trazos para completar su contorno, pero el sistema visual procesa la imagen como si se encontraran ahí), esto nos dice que el valor adaptativo de esta habilidad podría estar en que le podría permitir a las especies el poder detectar objetos bajo condiciones de baja iluminación, identificar camuflajes, etc.

En las últimas dos décadas los estudios comparativos entre humanos y otras especies de mamíferos sobre percepción a ilusiones visuales se han incrementado en cantidad y reconocimiento por ser una herramienta no invasiva para entender mejor la percepción visual, sus mecanismos subyacentes y evolución.

En años recientes, se han hecho también algunos trabajos intentando resumir la literatura sobre el tema con el objetivo de obtener un mejor panorama general y atraer la atención a posibles deficiencias además de revelar nuevas áreas y oportunidades de investigación. Hasta la fecha, la mayoría de las revisiones sistemáticas en el tema se enfocan únicamente en una especie o grupo. Por ejemplo, en el trabajo de Agrillo et al. (2013), se enfocaron únicamente en estudios con peces y diferentes tipos de ilusiones visuales enfatizando en las diferencias entre los sistemas visuales de peces con otros vertebrados y su complejidad; recientemente Agrillo et al. (2020), realizaron nuevamente una revisión en peces con el fin de destacar las interrogantes evolutivas y comparativas del estudio entre especies acuáticas y de ambientes terrestres. Byosiere et al. (2020) se enfocaron específicamente en la literatura sobre perros, si estos son susceptibles a ilusiones visuales, si las perciben igual que los humanos o de forma diferente y si los resultados son consistentes entre todos los estudios, y a su vez describieron cuáles son los dos principales métodos utilizados en la investigación sobre ilusiones visuales, estos son las pruebas espontaneas y los procedimientos con entrenamiento.

Algunas revisiones sistemáticas se enfocan únicamente en la aproximación metodológica como el artículo de Santacà et al. (2021) donde concluyen que el uso de métodos tan diferentes podría ser una de las causas principales de que se obtengan resultados contradictorios en las investigaciones.

Pecunioso et al. (2020) realizaron una revisión sobre especies con un tamaño pequeño de sus cerebros (relativo al tamaño del cuerpo), esto en comparación con vertebrados de tamaños medianos o grandes, siendo en su mayoría trabajos en peces y unos pocos en anfibios y reptiles. Los autores encontraron que el tamaño relativo del cerebro poco tiene que ver con su capacidad de ver ilusiones visuales en forma similar a un humano, por lo que existe la posibilidad de que tengan mecanismos de percepción similares a la especie *Homo sapiens* con sus respectivas diferencias. Sin embargo, hasta la fecha, en ninguna de las revisiones que se han publicado se ha propuesto algún análisis cuantitativo.

4. Objetivos

El objetivo principal del presente trabajo fue identificar los factores principales detrás de la variabilidad en los resultados de los estudios sobre susceptibilidad de los animales a ilusiones visuales mediante una aproximación metaanalítica. El presente trabajo se enfocó en las ilusiones visuales geométricas, puesto que la mayoría de los trabajos son sobre este tipo de ilusiones visuales, debido a que los métodos usados en el estudio se encuentran ampliamente consolidados (los ya antes mencionados métodos espontáneos y con entrenamiento) y las investigaciones han abarcado la gran mayoría de grupos de vertebrados.

Puesto que nuestra hipótesis propone que varios factores biológicos y metodológicos tienen influencia en la dirección y magnitud de la percepción a las ilusiones, hemos limitado nuestro análisis a una lista de moderadores principales, por lo que esperamos que cada uno de estos factores tenga una influencia significativa en la variabilidad presente en los resultados que encontremos entre todos los estudios. (El término “moderadores” se usa como sinónimo de variables en el método de metaanálisis)

5. Sobretiro del articulo

Response to geometrical visual illusions in non-human vertebrates: a meta-analysis

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5.1 Title page

Response to geometrical visual illusions in non-human vertebrates: a meta-analysis

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5.2 ABSTRACT

BÁNSZEGI, O., M. Rosetti, U. J. Olivares and P. Szenczi. Response to geometrical visual illusions in vertebrates: a meta-analysis...NEUROSCI BIOBEHAV REV 21(1) XXX-XXX, 1998.- Visual illusions have been studied in many non-human vertebrate species, spanning a wide range of biological and methodological variables. While early reviews have proved useful in providing an overview of the field, they have not been accompanied by a quantitative analysis to systematically evaluate the contribution of biological (taxonomy, habitat, and position of the eyes) and methodological factors (type of illusion and testing method, the number of trials during the training and testing, and the sex ratio of the subjects) on the proportion of illusory choice. In the present meta-analytical study, we confirm that geometrical visual illusion perception is a general phenomenon among non-human vertebrates. However, illusion type significantly alters the magnitude of susceptibility. In terms of methodology, studies with larger samples report smaller effect sizes, while more recent studies prefer spontaneous choice over training. We discuss the challenges and bottlenecks in this area of study that, if addressed, could lead to more successful advances in the future.

KEYWORDS Geometrical visual illusion, Vertebrates, Spontaneous testing, Training, Individual differences, Perception, Ebbinghaus illusion, Motivation

HIGHLIGHTS

Data from 32 studies suggests that vertebrates are susceptible to visual illusions.

Illusion type significantly influences the magnitude of susceptibility.

Studies with larger sample sizes report smaller effect sizes.

Recently more studies opted for spontaneous choice, rather than training methods.

5.3 Introduction

There has been long-standing theoretical and practical interest in how animals (including humans) see the world; in particular, how they perceive basic elements of objects, e.g., colour, shape, size, motion. The topic has been even more alluring since we know that the perception of the physical world may sometimes be distorted, with inconsistencies appearing between an observer's visual percept and a stimulus' physical characteristics. Such distortions are known as visual illusions (Gregory 1997; Howe and Purves 2005) and they are present in everyday life where they exploit our misguided senses, for example, in restaurants or in marketing ploys (Van Ittersum and Wansink 2012; Wansink and Van Ittersum 2013; Erle and Zürn 2020). More recently, these phenomena have gained recognition as inexpensive, non-invasive tools to study the neurobiology of visual perception in several fields of basic and medical research (e.g. King et al. 2017; Makris et al. 2021). Despite an extensive body of literature covering visual illusions dating back to the 5th century B.C. (Wade 2017), the mechanisms underlying the perception of different visual illusions are still unknown, and therefore continue as the focus of many ongoing studies. Here, we attempt to gain insights into visual illusions by comparing commonalties and discrepancies in how different taxa respond to visual illusions under distinct methodological conditions, using information amassed by studies of perceptual illusions produced in the last decades.

Observational studies suggest that susceptibility to visual illusions is present in several species in various taxa (review in Kelley and Kelley 2014), while empirical studies in laboratory contexts have proven that many species are susceptible to a number of visual illusions, with some species perceiving them in the same way and others in the opposite way as humans do (Kelley and Kelley 2014; Feng et al. 2017; Parrish 2021; Watanabe 2021). The within and between species variability in the way animals perceive visual illusions is surprising but remains unexplained. How sensory information is captured and processed by the visual system can vary notably across species; such disparities can emerge from anatomical differences in the structure or position of the eyes, neural circuits underlying perception and the ecological requirements that have moulded the organism throughout its evolutionary history. Additionally, even the different methodological approaches of how we test the susceptibility to visual illusions in the same species can lead to contrasting results (Byosiere et al. 2020; Santacà et al. 2021).

In recent years, some effort was made to summarize the literature on visual illusion perception in animals in order to draw attention to possible flaws and shortcomings and highlight future research opportunities and promising areas. However, these reviews mostly focused only on a single species or animal group (Agrillo et al. 2013; Agrillo et al. 2020; Byosiere et al. 2020), a single methodological (Santacà et al. 2021) or biological aspect (Pecunioso et al. 2020) and none of them provided a quantitative analysis. Thus, the main goal of the present study is to identify the main factors behind the variance found in the susceptibility to geometrical illusions in a relatively wide range of taxa using a meta-analytic approach. Since a wide range of biological and methodological factors have been hypothesized to influence the direction or strength of the perception of visual illusions, in the present meta-analysis, we limit our examination to the list of moderators detailed below.

As biological moderators, we first examined their (a) *taxonomic class*. We decided to only include studies on different classes of the Vertebrata subphylum. Although there have been several studies on illusory perception in invertebrates, their eye structure and the underlying neural processes differ considerably from those of vertebrates, which makes any potential similarity or difference almost inexplicable. Next, we grouped the species into three broad categories according to their (b) *habitat* as a proxy for the environment they mostly live in and which may affect their visual perception: terrestrial (spend their life on the ground), aquatic (spend their life under water), or arboreal (spend all or partial time of their life above ground surface). We also grouped them according to the (c) *position of the eyes* and the resulting overlapping visual field, which in turn may reflect the connectivity of their neural circuits. The ecological niche requirements or even human selection may have shaped the morphological appearance of even closely related species in various directions.

As methodological moderators, we first examined the (d) *type of illusion*. We decided to include only those in the geometrical visual illusion category (Corridor, Delboeuf, Ebbinghaus, Horizontal‒vertical, Jastrow, Müller‒Lyer, Ponzo, Sander and Zöllner, see Supplementary Material for examples of each), which are among the most popular choices for animal testing. Ehm and Wackermann (2016) define geometric illusions as those in which the geometrical properties of an object (length, angle, size, etc.) are affected and systematically altered by the presence of other elements in the visual field. Comparing different illusions could reveal interesting information, as we know that humans are more susceptible to some types of illusion than others; susceptibility changes with age and even seemingly similar illusions may be processed by the nervous system differently (Billino et al. 2009; Schwarzkopf et al. 2011; Axelrod et al. 2017; Grzeczkowski et al. 2017; Grzeczkowski et al. 2018). We also further grouped these illusions according to the (e) *geometrical property* affected, namely the target object's area (Delboeuf, Ebbinghaus, Corridor, Jastrow), length (Horizontal−vertical, Müller−Lyer, Ponzo, Sander) or angle (Zöllner) (Supplementary material 1). Next, we classified the studies according to their (f) *testing method*, which could involve spontaneous choice or training. Testing spontaneous choice is basically an observation about the animals' natural behaviour repertoire by presenting to the subjects two or more groups of biologically relevant stimuli (e.g., food) in an illusory context or without it. In the training approach, subjects undergo extensive training in which some neutral stimuli are associated with a reward and their choice according to the training is taken as evidence of the susceptibility of the illusion. While both methods can be used to find the answer to the same question, a recent review by Santacà et al. (2021) contrasts the relevance and the potential weaknesses of these methodological approaches while also drawing attention on how they may lead to different results, even in the same species. Since not all the studies involved both (*g*) *sex*es, we decided to make an overall analysis on sex effect too.

We also examined the effect of the (h) *number of trials during training.* It has been criticized that usually mammals and birds are subjected to extensive training, which sometimes involves thousands of trials, and which results in a much better performance than lower order vertebrates, such as fishes, which usually are trained with only a few dozen trials (Agrillo and Bisazza 2014; Bisazza et al. 2014) Thus, any difference might be associated with the difference in the number of training trials. The studies by Bisazza and colleagues (2014) using a numerical discrimination task in guppies also support the notion that increasing the number of training trials could result in better performance (Bisazza et al. 2014). Training can also introduce a survival bias, as those who successfully complete the training may be those who are most sensitive to the illusions; Miletto (2018) showed that guppies that were faster in learning the numerical rule in the training phase were more sensitive to a certain visual illusion (Miletto Petrazzini et al. 2018). Similarly, we examined the (i) *number of trials during testing.* In illusion perception studies the desired result is that individual performance should match group performance. However, meeting the significance threshold for the binomial test at the individual level requires the repetition of a larger number of test trials for each subject. On one hand, increasing the number of trials per individual can result in more individuals reaching the significance threshold for the binomial test, thus increasing the strength of susceptibility. On the other hand, it can lead to two problems: animals might habituate to the behavioural assay, get satiated and become less responsive or they can associate additional rules and show a learning effect. (j) *Sample size* was also included as the studies varied considerably in the number of individuals they based their results on.

5.4 Methods

5.4.1 Search protocol and selection criteria

Where possible, we used the PRISMA Statement and checklist guidelines during the preparation of our report (Liberati et al. 2009; Moher et al. 2009). We used keyword searches in two online databases (Web of Science and Scopus) on November 7, 2022. We searched for studies containing the following search terms: “visual illusion*” and animal*. We searched across all years in both databases. We used the “Topic” search field in Web of Science in “All Databases” and the “Article title, Abstract, Keywords” search field in Scopus. This resulted in 946 articles in Web of Science and 320 articles in Scopus. We also collected all papers citing the two influential reviews (Kelley and Kelley 2014; Feng et al.

2017) in Web of Science, Scopus and Google Scholar. This resulted in 239 citing articles. Additionally, we extracted the empirical examples cited in these two reviews, resulting in 44 additional articles.

Four additional papers that were not located by the initial search were accessed because they were cited in the papers that were deemed relevant. Altogether, the search procedure yielded a total of 1553 papers reduced to 1218 after the removal of duplicates. Titles and abstracts of the remaining articles were screened with the strict inclusion criteria described below.

5.4.2 Inclusion criteria

A study had to meet several criteria for it to be included in our analysis. First, subjects should be non-human vertebrates. We decided not to include studies on invertebrates, since their visual system is highly different from that of vertebrates. We included only studies which tested geometrical visual illusions (see explanation in the Introduction). Also, we focused on studies that tested adult animals since studies on humans suggest that the emergence of susceptibility to some illusions change across the life span (Hanisch et al. 2001; Káldy and Kovács 2003; Duemmler et al. 2008; Doherty et al. 2010). In addition, only a few studies have been done on young animals (Dominguez 1954; Fuss et al. 2014; Nakamura et al. 2014; Fuss and Schluessel 2017; Bánszegi et al. 2021; Watanabe 2022). We also limited the analysis to experimental studies which were published in journal articles or theses in English.

The selection and exclusion process of all articles yielded in the search was done by two authors (O.B. and U.J.O.). Six hundred of all 1218 titles and, if necessary, abstracts were judged independently by two authors (O.B. and P.S.). Agreement on inclusion or exclusion of articles between these two researchers was evaluated for consistency, resulting in a Fleiss' Kappa of 0.901.

The full text of 63 articles was accessed and screened and a further 31 were excluded from the analysis yielding a total of 32 papers included in the final analysis (Table 1). The reasons for exclusion were that (a) the sample size was one (n = 4), (b) researchers tested only juvenile animals (n = 6), (c) the same individuals were tested with the same method as in another article (n = 1), (d) data and/or figures were not presented in a way which allowed us to extract the necessary information (n = 6), (e) the animals were not tested in a two-way choice method or there was not at least one test condition where the compared target objects were the same, one having a surrounding environment which could be responsible for the illusory effect (n=14).

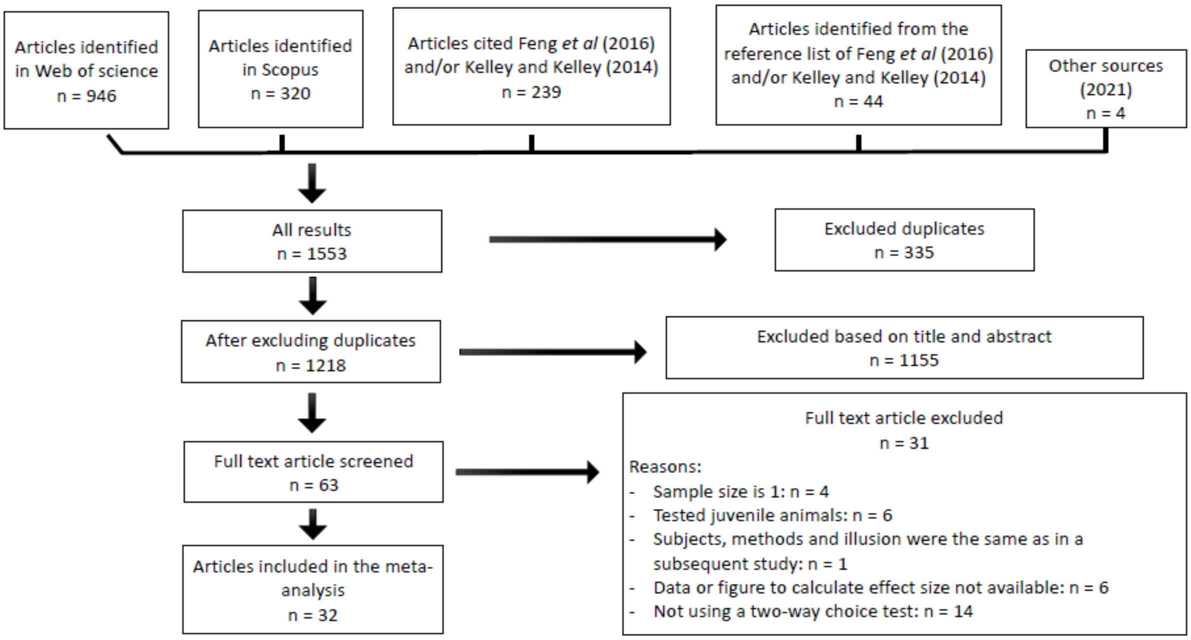


Figure 1. PRISMA figure. Flowchart showing systematic search process and study selection.

5.4.3 Calculating effect sizes

To quantify the susceptibility of different illusions in each paper for each of the included species, we needed to extract a standardized effect size from the reported results. First, we extracted the mean proportions of illusory choice either from the data reported or from the plots (Table 1) using WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/). llusory choice is the percentage of choices were an animal selects the stimulus that presents itself as illusion in the same way as humans would perceive it; in this sense, 0.8 would mean 80% of the choices are illusory choices made in the same way as humans, while 20% would mean 80% of illusory choices in the opposite way as humans. Thus, we also calculated the effect size for every study as the Cohen's h statistic, which is appropriate for proportion values (Cohen 1988). Since our main interest was in the strength and not in the direction of the illusion perception, we further transformed the magnitude of the illusory choice by subtracting 1 from the mean proportions that fell below 0.5. While the mean proportion is already scaled and can be used to compare studies, we also wanted a statistic that included the dispersion of each study. Using the sample size, mean and standard deviation, we also calculated standard errors. Confidence interval for the effect sizes were calculated as 95%CI = ES – (1.96*SE) to ES + (1.96*SE) where ES stands for effect size and SE is the asymptotic standard error for the effect size, as suggested by Nakagawa and Cuthill (2007).

In 8 out of the 32 studies we obtained more than one effect size since they tested multiple species with the same illusion (n = 4) or tested the same species or individuals with different illusions (n = 4). In 2 cases papers tested the same individuals with a slightly modified version of the same illusion, there we used only the largest value so as to avoid pseudo-replication by taking into account each individual only once.

5.4.4 Publication bias

We also examined the final dataset for evidence of bias against publishing studies with small effect sizes or those with small sample sizes; we tested whether there is a relationship between effect sizes or sample sizes and the year the study was published. We also tested whether there is a trend in the use of the two main types of testing methodology: training or spontaneous by means of a Pearson correlation.

Table 1. Studies included in the meta-analysis.

Authors	Species	Class	Habitat	Eyes position	Illusion	N males	N females	Stimuli	Training or Spontaeous	Compared to humans	Note
Agrillo et al. (2014)	Rhesus Monkey, *Macaca mulatta*	Mammal	Semi-arboreal	Frontal	Zöllner	3	0	Artificial	Training	Same direction	Mean was extracted for each individuals from Figure 3
Becker (2019)	Domestic dog, *Canis lupus familiaris*	Mammal	Terrestrial	Frontal	Ebbinghaus	10	12	Food	Spontaneous	No perception	Mean and SD was calculated from the reported raw data[1]
Benhar and Samuel (1982)	Baboon, *Papio anubis*	Mammal	Semi-arboreal	Frontal	Zöllner	2	0	Artificial	Training	Same direction	Mean and SD was calculated from the reported raw data
Byosiere et al. (2017b)	Domestic dog, *Canis lupus familiaris*	Mammal	Terrestrial	Frontal	Delboeuf	2	6	Artificial	Training	No perception	Mean and SD was reported [2]
					Ebbinghaus	2	5			Opposite direction	
Byosiere et al. (2018)	Domestic dog, *Canis lupus familiaris*	Mammal	Terrestrial	Frontal	Ponzo	2	6	Artificial	Training	No perception	Mean and SD was reported[3]
Cappellato et al. (2020)	Domestic horse, *Equus caballus*	Mammal	Terrestrial	Lateral	Müller-Lyer	5	5	Food	Spontaneous	Same direction	Mean and SE were extracted from Figure 3
Hanus et al. (2022)	Bonobo, *Pan paniscus*	Mammal	Terrestrial	Frontal	Ebbinghaus	2	3	Food	Spontaneous	Same direction	Mean and SD was calculated from the reported raw data[4]
					Horizontal-vertical	2	3			Same direction	
					Müller-Lyer	2	3			No perception	

					Sander	2	3			No perception	
	Capuchin, (species not specified)				Ebbinghaus	4	4			No perception	
					Horizontal-vertical	4	4			No perception	
					Müller-Lyer	4	4			Same direction	
					Sander	4	4			No perception	
	Chimpanzee, *Pan troglodytes*				Ebbinghaus	5	9			No perception	
					Horizontal-vertical	5	8			No perception	
					Müller-Lyer	5	8			No perception	
					Sander	5	8			No perception	
	Gorilla (species not specified)				Ebbinghaus	4	1			Same direction	
					Horizontal-vertical	3	1			No perception	
					Müller-Lyer	3	1			No perception	
					Sander	3	1			No perception	
	Orangutan (species not specified)				Ebbinghaus	1	3			No perception	
					Horizontal-vertical	1	3			No perception	
					Müller-Lyer	1	3			No perception	
					Sander	1	3			No perception	
Imura et al. (2008)	Chimpanzee, *Pan troglodytes*	Mammal	Semi-arboreal	Frontal	Corridor	1	2	Artificial	Training	Same direction	Mean and SE were extracted from Figure 3[5]
Keep et al. (2018)	Domestic dog, *Canis lupus familiaris*	Mammal	Terrestrial	Frontal	Müller-Lyer	0	6	Artificial	Training	Same direction	Mean and SE was reported[6]

Lucon-Xiccato et al. (2019)	Guppy, *Poecilia reticulata*	Fish	Aquatic	Lateral	Delboeuf	0	12	Food	Spontaneous	Opposite direction	Mean and SD was calculated from the reported raw data
						12	12	Artificial	Training	No perception	Mean and SD was calculated from the reported raw data
Miletto Petrazzini et al. (2017)	Domestic dog, *Canis lupus familiaris*	Mammal	Terrestrial	Frontal	Delboeuf	10	3	food	spontaneous	No perception	Mean and SD was reported
Mitchell (1971)	Domestic cat, *Felis silvestris catus*	Mammal	Semi-arboreal	Frontal	Zöllner	2	0	Artificial	Training	Opposite direcion	Mean and SD was reported[7]
					Müller-Lyer	3	2			Same direction	
Parrish and Beran (2014)	Chimpanzee, *Pan troglodytes*	Mammal	Semi-arboreal	Frontal	Delboeuf	2	1	Food	Spontaneous	Same direction	Mean and SD was calculated from the binominal test[8]
Parrish et al. (2015)	Capuchin monkey, *Cebus apella* (before *Sapajus apella*)	Mammal	Semi-arboreal	Frontal	Delboeuf	6	7	Artificial	Training	No perception	Mean and SD was calculated from the provided raw data from the authors
	Rhesus Monkey, *Macaca mulatta*					7	0			No perception	
Parron and Fagot (2007)	Baboon, *Papio anubis*	Mammal	Semi-arboreal	Frontal	Ebbinghaus	5	3	Artificial	Training	No perception	Mean and SD was extracted from Figure 3[9]
Santacà et al. (2017)	Ring-tailed lemur, *Lemur catta*	Mammal	Semi-arboreal	Frontal	Delboeuf	4	5	Food	Spontaneous	No perception	Mean and SD was calculated from the reported raw data
Santacà et al. (2019)	Bearded dragon, *Pogona vitticeps*	Reptilia	Terrestrial	Lateral	Delboeuf	4	8	Food	Spontaneous	Same direction	Mean and SD was calculated from the reported raw data[10]

Santacà and Agrillo (2020a)	Guppy, *Poecilia reticulata*	Fish	Aquatic	Lateral	Müller-Lyer	0	12	Artificial	Training	Same direction	Mean and SD was calculated from the reported raw data
Santacà and Agrillo (2020b)	Guppy, *Poecilia reticulata*	Fish	Aquatic	Lateral	Horizontal-vertical	0	12	Artificial	Training	Same direction	Mean and SD was calculated from the reported raw data [11]
Santacà et al. (2020a)	Redtail splitfin, *Xenotoca eiseni*	Fish	Aquatic	Lateral	Delboeuf	0	12	Food	Spontaneous	Opposite direction	Mean was reported and SD was calculated from the reported CI[12]
	Siamese fighting fish, *Betta splendens*					0	12			Opposite direction	
	Three-spot gourami, *Trichopodus trichopterus* (before *Trichogaster trichopterus*)					0	12			No perception	
	Zebrafish, *Danio rerio*					0	12			No perception	
Santacà et al. (2020b)	Bearded dragon, *Pogona vitticeps*	Reptilia	Terrestrial	Lateral	Müller-Lyer	4	8	Food	Spontaneous	Same direction	Mean and SD was calculated from the reported raw data
Santacà et al. (2020c)	Bearded dragon, *Pogona vitticeps*	Reptilia	Terrestrial	Lateral	Horizontal-vertical	4	5	Food	Spontaneous	Same direction	Mean and SD was calculated from the reported raw data

	Red-footed tortoise, *Chelonoidis carbonaria*	Reptilia	Terrestrial	Lateral		3	5			No perception	Mean and SD was calculated from the reported raw data
Santacà et al. (2020d)	Red-footed tortoise, *Chelonoidis carbonaria*	Reptilia	Terrestrial	Lateral	Delboeuf	3	5	Food	Spontaneous	No perception	Mean and SD was calculated from the reported raw data
Santacà et al. (2022)	Guppy, *Poecilia reticulata*	Fish	Aquatic	Lateral	Ebbinghaus	0	36	Crossing	Spontaneous	Same direction	Mean was reported and SD was calculated from the reported CI
					Delboeuf	0	36			Opposite direction	
Sovrano et al. (2015)	Redtail splitfin, *Xenotoca eiseni*	Fish	Aquatic	Lateral	Ebbinghaus	8	0	Artificial	Training	Same direction	Mean and SE was extracted from Figure 5b, percentage of first choice panel[13]
Sovrano et al. (2016)	Redtail splitfin, *Xenotoca eiseni*	Fish	Aquatic	Lateral	Müller-Lyer	6	0	Artificial	Training	Same direction	Mean and SE was extracted from Figure 4a[14]
Suganuma et al. (2007)	Capuchin monkey, *Cebus apella* (before S*apajus apella*)	Mammal	Semi-arboreal	Frontal	Müller-Lyer	5	5	Artificial	Training	Same direction	Mean and SD was calculated from the given values in the text[15]
Szenczi et al. (2018)	Domestic cat, *Felis silvestris catus*	Mammal	Semi-arboreal	Frontal	Delboeuf	10	8	Food	Spontaneous	Same direction	Mean and SD was calculated from the reported raw data
Timney and Keil (1996)	Domestic horses, *Equus caballus*	Mammal	Terrestrial	Lateral	Ponzo	0	2	Artificial	Training	Same direction	Mean was extracted for each individuals from Figure 4a
Warden and Baar (1929)	Dove, (species not specified)	Bird	Areal	Lateral	Müller-Lyer	No information provided about		Artificial	Training	Same direction	Mean and SD was calculated from the reported raw data

						the sex of the animals					
Watanabe et al. (2011)	Homing pigeon, *Columba livia domestica*	Bird	Areal	Lateral	Zöllner	6	0	Artificial	Training	Opposite direction	Mean and SE was extracted from Figure 4, left panel[16]
Watanabe et al. (2013)	Japanese bantam, *Gallus gallus domesticus*	Bird	Areal	Lateral	Zöllner	2	1	Artificial	Training	Opposite direction	Mean and SE was extracted from Figure 2 ’AVERAGE’ panel[16]

[1] Only data from adult dogs were included in the statistical analysis. Adult was defined as older than one year (Yu et al, 2020).

[2] Only the effect size from the Classical Ebbinghaus–Titchener illusion experiment was included. In both experiments the same individuals were tested on very similar illusions, but the sample size and the effect size were smaller in the latter.

[3] In Byosiere et al. (2017a) the same individuals were tested in a slightly modified version of the Ponzo illusion, thus we excluded the results of Byosiere et al. (2017a) in favor of the largest effect size of the present paper.

[4] In the statistical analysis we included only the data from adult individuals.

[5] For our calculation, we extracted the values where the illusion magnitude was the strongest for the animals from both, the floor and ceiling condition, different distance, 36-pixel size cylinder and calculated the mean value.

[6] In experiment 2 and 3 the same animals were tested in slightly modified version of the Müller-Lyer illusion, thus we decided to use only of the results of the Experiment 3 since it has a larger effect size.

[7] No clear description for the numbers of training and testing trials in Experiment thus we assumed the same l number of trials as in Experiment 2.

[8] *d* was calculated from the results of the binominal test of each individual, but since *p* is <0.001 which can mean 15 or 16 correct choices out of 16 trials, we chose the conservative option.

[9] Not specified, thus we assumed that the whiskers represent SD.

[10] We used only the data for the bearded dragon. The data from red-footed tortoise was included from the Santacà et al. (2020d) article.

[11] They tested the same individuals in two different illusion trials, thus we included the results from the classical T illusion only.

[12] Data from the Angelfish, *Pterophyllum scalare* was not included in the analysis, because they were immature animals.

[13] We included the data from the trials which used the visually most similar version of the Ebbinghaus illusion (see also Byosiere et al. 2017b; Becker 2019). The results of animals that were trained to select the smaller target stimulus have been reversed (and notated), then averaged by the results of the other animals trained to select the larger target stimulus (as in Watanabe et al. 2011; Watanabe et al. 2013; Byosiere et al. 2017b; Keep et al. 2018; Byosiere et al. 2019).

[14] We included the data from the two black target lines version of the Müller-Lyer illusion. The results of animals that were trained to select the short line have been reversed (and notated), then averaged by the results of the other animals trained to select the long line.

[15] Not specified, thus we assumed that the numbers after ± represent SD.

[16] We extracted the values for both, Boost-Upside-Wider and Boost-Downside-Wider condition, then calculated their mean.

5.4.5 Statistical analysis

We opted to use the proportion of illusory choice reported in each study and sample rather than significance values reported in the paper given that the latter is strongly tied to sample size and number of trials, which were inconsistently reported (e.g., in time, “we trained the animals for a month” rather than number of events) or applied (e.g., subjects were tested until a certain criterion was reached and number of trials varied between individuals). Additionally, we report the Cohen’s *h* values in the forest plot (made with the *escalc* and *forest* functions from the packages meta (Balduzzi et al. 2019) and metafor (Viechtbauer 2010), for R (R Core Team, 2021.) with Clopper-Pearson confidence intervals. We produced the funnel plots with the *funnel* function. We visualized the mean proportions of illusory choice per each of the grouping variables as a combination of violin plots and scatter plots, to illustrate the density estimates as well as the individual observations accompanied by their standard deviation. Plots were made using the package ggplot2 (Wickham 2016).

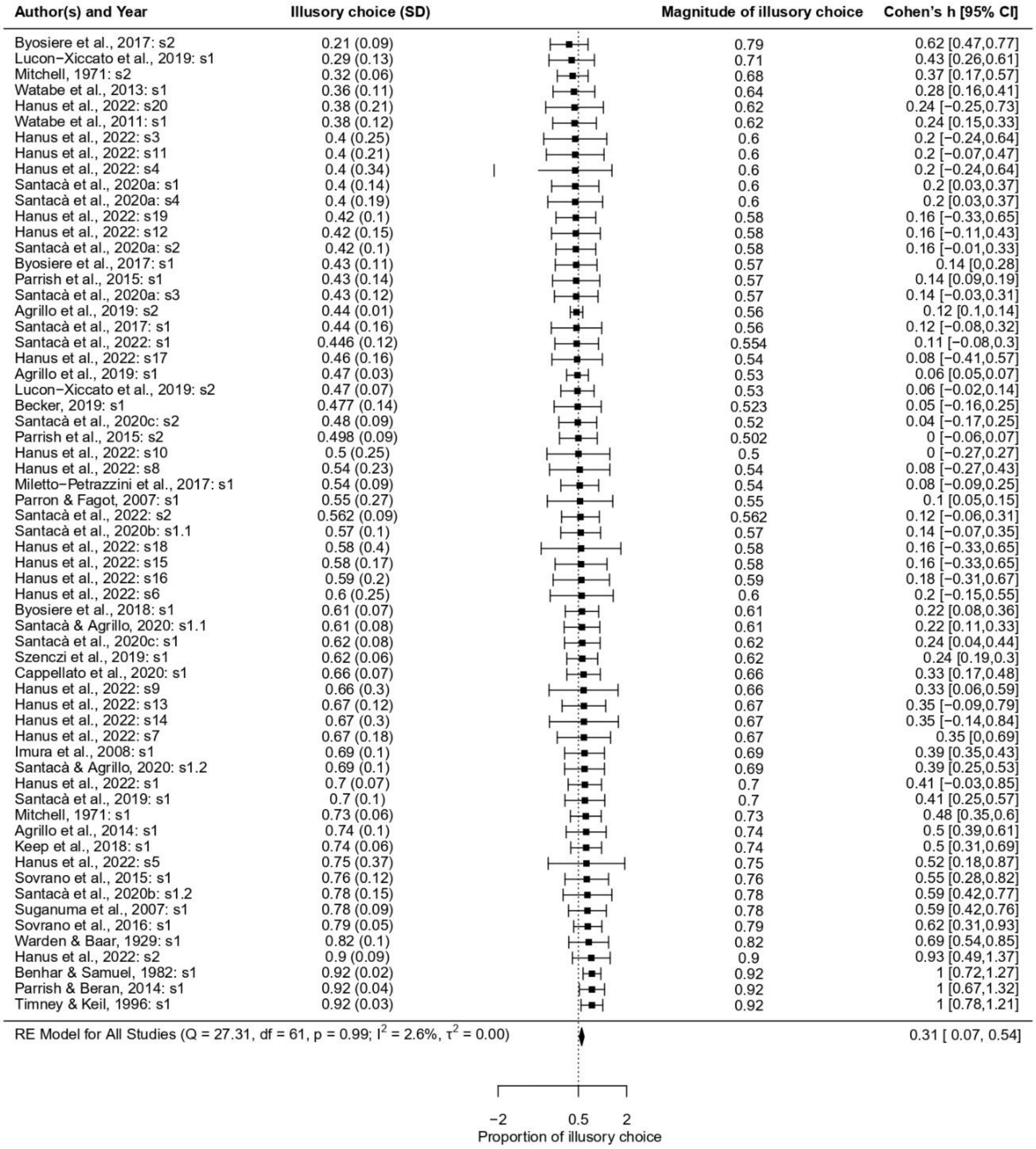
As proportions may not be normally distributed, the number of individual observations was small and the number of studies in each group was unbalanced, we opted for Kruskal-Wallis tests to evaluate differences between groups and Dunn tests with Bonferroni corrections for pairwise comparisons on those grouping variables with more than 2 categories.

Correlations were performed with the *cor.test* function and we opted for the Spearman method, as not all values compared were continuous (e.g., sample size and year of publication). We report the correlation value and confidence intervals. All analysis and graphics were done using R v4.1.1 (R Core Team 2021). Significance was set at $p < 0.05$ and all tests were two-tailed.

5.5 Results

5.5.1 Final dataset and overall phenomena

The final dataset consisted of 32 studies and 62 effect sizes, testing 355 individuals in total. This included data for 22 species across a broad taxonomic range, tested on 9 different illusions. Figure 2 shows a summary of all studies included. A model for all studies suggests that less than three percent of the total variability can be attributed to between-studies variability, with a very small standard deviation of the distribution of true effect sizes ($Q = 27.31$, $df = 61$, $p = 0.99$, $H2 = 1.03$, $I^2 = 2.59\%$, $\tau^2 = 0.002 \pm 0.012$). Additionally, the mean proportions of choice are different from chance as seen in the summary mean proportion of illusory choice (0.57), marked by the grey diamond at the bottom of the figure. Studies that show a large effect (≥ 0.80) also have remarkably low sample sizes ($n = 2$ or $n = 3$).



Author(s) and Year	Illusory choice (SD)	Magnitude of illusory choice	Cohen's h [95% CI]
Byosiere et al., 2017: s2	0.21 (0.09)	0.79	0.62 [0.47,0.77]
Lucon−Xiccato et al., 2019: s1	0.29 (0.13)	0.71	0.43 [0.26,0.61]
Mitchell, 1971: s2	0.32 (0.06)	0.68	0.37 [0.17,0.57]
Watabe et al., 2013: s1	0.36 (0.11)	0.64	0.28 [0.16,0.41]
Hanus et al., 2022: s20	0.38 (0.21)	0.62	0.24 [−0.25,0.73]
Watabe et al., 2011: s1	0.38 (0.12)	0.62	0.24 [0.15,0.33]
Hanus et al., 2022: s3	0.4 (0.25)	0.6	0.2 [−0.24,0.64]
Hanus et al., 2022: s11	0.4 (0.21)	0.6	0.2 [−0.07,0.47]
Hanus et al., 2022: s4	0.4 (0.34)	0.6	0.2 [−0.24,0.64]
Santacà et al., 2020a: s1	0.4 (0.14)	0.6	0.2 [0.03,0.37]
Santacà et al., 2020a: s4	0.4 (0.19)	0.6	0.2 [0.03,0.37]
Hanus et al., 2022: s19	0.42 (0.1)	0.58	0.16 [−0.33,0.65]
Hanus et al., 2022: s12	0.42 (0.15)	0.58	0.16 [−0.11,0.43]
Santacà et al., 2020a: s2	0.42 (0.1)	0.58	0.16 [−0.01,0.33]
Byosiere et al., 2017: s1	0.43 (0.11)	0.57	0.14 [0,0.28]
Parrish et al., 2015: s1	0.43 (0.14)	0.57	0.14 [0.09,0.19]
Santacà et al., 2020a: s3	0.43 (0.12)	0.57	0.14 [−0.03,0.31]
Agrillo et al., 2019: s2	0.44 (0.01)	0.56	0.12 [0.1,0.14]
Santacà et al., 2017: s1	0.44 (0.16)	0.56	0.12 [−0.08,0.32]
Santacà et al., 2022: s1	0.446 (0.12)	0.554	0.11 [−0.08,0.3]
Hanus et al., 2022: s17	0.46 (0.16)	0.54	0.08 [−0.41,0.57]
Agrillo et al., 2019: s1	0.47 (0.03)	0.53	0.06 [0.05,0.07]
Lucon−Xiccato et al., 2019: s2	0.47 (0.07)	0.53	0.06 [−0.02,0.14]
Becker, 2019: s1	0.477 (0.14)	0.523	0.05 [−0.16,0.25]
Santacà et al., 2020c: s2	0.48 (0.09)	0.52	0.04 [−0.17,0.25]
Parrish et al., 2015: s2	0.498 (0.09)	0.502	0 [−0.06,0.07]
Hanus et al., 2022: s10	0.5 (0.25)	0.5	0 [−0.27,0.27]
Hanus et al., 2022: s8	0.54 (0.23)	0.54	0.08 [−0.27,0.43]
Miletto−Petrazzini et al., 2017: s1	0.54 (0.09)	0.54	0.08 [−0.09,0.25]
Parron & Fagot, 2007: s1	0.55 (0.27)	0.55	0.1 [0.05,0.15]
Santacà et al., 2022: s2	0.562 (0.09)	0.562	0.12 [−0.06,0.31]
Santacà et al., 2020b: s1.1	0.57 (0.1)	0.57	0.14 [−0.07,0.35]
Hanus et al., 2022: s18	0.58 (0.4)	0.58	0.16 [−0.33,0.65]
Hanus et al., 2022: s15	0.58 (0.17)	0.58	0.16 [−0.33,0.65]
Hanus et al., 2022: s16	0.59 (0.2)	0.59	0.18 [−0.31,0.67]
Hanus et al., 2022: s6	0.6 (0.25)	0.6	0.2 [−0.15,0.55]
Byosiere et al., 2018: s1	0.61 (0.07)	0.61	0.22 [0.08,0.36]
Santacà & Agrillo, 2020: s1.1	0.61 (0.08)	0.61	0.22 [0.11,0.33]
Santacà et al., 2020c: s1	0.62 (0.08)	0.62	0.24 [0.04,0.44]
Szenczi et al., 2019: s1	0.62 (0.06)	0.62	0.24 [0.19,0.3]
Cappellato et al., 2020: s1	0.66 (0.07)	0.66	0.33 [0.17,0.48]
Hanus et al., 2022: s9	0.66 (0.3)	0.66	0.33 [0.06,0.59]
Hanus et al., 2022: s13	0.67 (0.12)	0.67	0.35 [−0.09,0.79]
Hanus et al., 2022: s14	0.67 (0.3)	0.67	0.35 [−0.14,0.84]
Hanus et al., 2022: s7	0.67 (0.18)	0.67	0.35 [0,0.69]
Imura et al., 2008: s1	0.69 (0.1)	0.69	0.39 [0.35,0.43]
Santacà & Agrillo, 2020: s1.2	0.69 (0.1)	0.69	0.39 [0.25,0.53]
Hanus et al., 2022: s1	0.7 (0.07)	0.7	0.41 [−0.03,0.85]
Santacà et al., 2019: s1	0.7 (0.1)	0.7	0.41 [0.25,0.57]
Mitchell, 1971: s1	0.73 (0.06)	0.73	0.48 [0.35,0.6]
Agrillo et al., 2014: s1	0.74 (0.1)	0.74	0.5 [0.39,0.61]
Keep et al., 2018: s1	0.74 (0.06)	0.74	0.5 [0.31,0.69]
Hanus et al., 2022: s5	0.75 (0.37)	0.75	0.52 [0.18,0.87]
Sovrano et al., 2015: s1	0.76 (0.12)	0.76	0.55 [0.28,0.82]
Santacà et al., 2020b: s1.2	0.78 (0.15)	0.78	0.59 [0.42,0.77]
Suganuma et al., 2007: s1	0.78 (0.09)	0.78	0.59 [0.42,0.76]
Sovrano et al., 2016: s1	0.79 (0.05)	0.79	0.62 [0.31,0.93]
Warden & Baar, 1929: s1	0.82 (0.1)	0.82	0.69 [0.54,0.85]
Hanus et al., 2022: s2	0.9 (0.09)	0.9	0.93 [0.49,1.37]
Benhar & Samuel, 1982: s1	0.92 (0.02)	0.92	1 [0.72,1.27]
Parrish & Beran, 2014: s1	0.92 (0.04)	0.92	1 [0.67,1.32]
Timney & Keil, 1996: s1	0.92 (0.03)	0.92	1 [0.78,1.21]
RE Model for All Studies (Q = 27.31, df = 61, p = 0.99; I^2 = 2.6%, τ^2 = 0.00)			0.31 [0.07, 0.54]

Figure 2. Forest plot with all effect sizes. First column shows the studies included in the meta-analysis. They are arranged from lowest to highest according to the mean proportion of illusory choice. Each line includes first authors last name, year and, after colon, experiment number when a paper included more than one

species or illusory test (s1, s2, and so on). Other columns, from right to left, show the mean and between parenthesis, the standard deviation (SD) of the proportion of illusory choice, these same values expressed as a forest plot, then the magnitude of illusory choice and the and the effect size of the magnitude of illusory choice expressed as a Cohen’s h with the Clopper-Pearson 95% confidence interval (CI) between brackets. At the bottom of the plot are the statistical details for the random effect models as well as the summarized proportion of illusory choices for all studies, marked by a black diamond.

5.5.2 *Biological variables*

We found no statistical difference between the mean proportion of illusory choice according to the class of the animal tested, the habitat they live in or the position of their eyes. Despite this, the mean proportion of illusory choice observed in birds seems to be consistently above 0.69, however, there are only a few studies in this order. Table 2 shows the effect of biological variables and violin plots showing median and individual values can be found in Supplementary material.

5.5.3 *Methodological variables*

When comparing mean proportions of illusory choice between illusions, we found a significant effect, however, after performing post-hoc pairwise comparisons and then the corrections for multiple comparisons any significance was lost (Table 3). After grouping the illusions, we found an effect which was limited between the categories “area” versus “angle” (Table 3). We found no statistical difference between the mean proportions of illusory perception in studies that trained the individuals as compared with those that made spontaneous choice tests or between studies that used artificial or natural stimuli (food and holes). Table 2 shows the effect of categorical methodological variables and violin plots showing median and individual values, which can be found in Supplementary material.

Table 2. Results for the Kruskal-Wallis test corresponding to each moderator.

Type of moderator	Term	χ^2	Degrees of Freedom	*p*
Biological	Class	1.388	3	0.708
	Position of the eyes	0.489	1	0.484
	Habitat	3.532	3	0.317
Methodological	Illusion type	17.126	8	**0.029**
	Illusion grouping	6.343	2	**0.042**
	Training or spontaneous	3.511	1	0.061
	Artificial or natural stimuli	5.09	2	0.078

Table 3. Results for the Dunn post hoc test for those moderators with a significant contribution. Only raw significant comparisons are shown. Adjusted *p* values reflect Hochberg's correction.

Moderator	Term 1	Term 2	n_1	n_2	Statistic	*p*	Adjusted *p*
Illusion type	Delboeuf	Müller-Lyer	16	13	2.773	**0.006**	0.154
	Delboeuf	Zöllner	16	5	2.384	**0.017**	0.154
	Jastrow	Müller-Lyer	2	13	2.4	**0.016**	0.154
	Jastrow	Ponzo	2	2	2.067	**0.039**	0.264
	Jastrow	Zöllner	2	5	2.401	**0.016**	0.154
	Müller-Lyer	Sander	13	5	-1.987	**0.047**	0.264
Illusion grouping	Angle	Area	5	29	-2.189	**0.029**	0.086

We also evaluated the relationship between the effect size and methodological variables such as the number of trials during the training methods, number of trials during testing, sex ratio, and the sample size. Effect size and sample size was the only significant correlation (Table 4, Supplementary material).

Table 4. Correlation of methodological values with the absolute effect size.

Comparison	r	95% Conf. Int.	P
Number of trials during training	0.01	[-0.59; 0.58]	0.98
Number of trials during testing	0.17	[0.12; 0.43]	0.19
Sex ratio	0.14	[-0.12; 0.37]	0.29
Sample size	-0.47	[-0.64; -0.24]	< **0.001**

There was also a statistical difference in the strength of the perception of geometrical illusions depending on whether it reflected the same or opposite way how humans perceive the illusion. Out of the 62 experiments reported here, 31 found no significant effect, 23 found an effect in the same way humans do, and only 8 found an effect in the opposite way as humans. Additionally, the magnitude was larger in the same direction with a mean of 0.69, vs that in the opposite direction which had a mean of 0.59 ($W = 719.5$; $p < 0.001$).

5.5.4 Publication bias

A rank correlation test for funnel plot asymmetry (Kendall's = -0.08, $p = 0.39$), as well as a visual inspection of the funnel plots of the standard error and the inverse standard error did not suggest publication bias (Supplementary material). We found a negative correlation between the publication year and mean of proportion of illusory choice and absolute effect size ($r = -0.3$, $p = 0.017$, CI [-0.55, -0.04], $r = -0.3$, $p = 0.017$, CI [-0.51, -0.01], respectively; Supplementary material) and a positive correlation between the publication year and sample size ($r = 0.26$, $p = 0.042$, CI [-0.024, 0.53]; Supplementary material).

When comparing the publication year, we found that older studies tended to train the animals to respond, although the dates span for a large range (mean year 2005 ± 22.7), while more recent studies tend to implement spontaneous testing (mean year 2019 ± 2.07; Supplementary material).

5.6 Discussion

In general, we found that half (n = 31) of the mean proportions of illusory choice differ from chance, and the analysis on the effect sizes suggests that geometrical illusion perception is a phenomenon that is present in all the vertebrate groups reported in the studies we found. Our study also supports the hypothesis that some of the moderators can influence the strength of susceptibility of geometrical visual illusions. The analysis revealed that although none of the biological moderators (taxonomical class, habitat, or position of the eyes) seems to influence visual illusion perception, several of the methodological moderators did.

The type of illusions seems to significantly influence the magnitude of susceptibility, but after correcting for multiple comparisons, any significant values were lost. A better understanding of the perception of each type of illusion could be managed if studies incorporated the susceptibility scores for each individual tested. Recent studies in humans have focused on intra- and inter-subject variability of susceptibility on different visual illusions and show that the magnitude of perception by the same individual can be very different (Axelrod et al. 2017; Grzeczkowski et al. 2017). Only a weak connection, if any, has been found between the perception of different types of illusions even when they are considered to belong to the same category (Schwarzkopf et al. 2011; Grzeczkowski et al. 2018). This supports the notion that there is no unique common neural path that can account for the perception of all visual illusions. Studies testing the same subjects with different illusions and reporting the relationship between the strength of perception should be favoured and welcomed. Progress in this direction might also change our approach to illusion categorization – the classical method is to divide them according to their appearance – however, the new approach would be to group them in terms of the direction and magnitude in which they can be perceived in an effort to approximate a classification based on the underlying neural mechanisms (Oyama 1960; Coren et al. 1976; Gregory 1997; Ninio 2014; Hamburger 2016).

The sample size also significantly influences the strength of the response to an illusory effect at the group level. The negative correlation between the sample sizes and effect sizes suggests that the fewer individuals are tested, the greater the effect found. This happens most likely because individuals that are slower to train or show no interest in the test are often excluded from the studies. We would therefore like to emphasise the importance of proper sample size selection and clarity when reporting the individual data (as well as that of any excluded animals). Larger samples can also help to elucidate individual differences in visual perception, since, for example, the susceptibility to a certain type of visual illusion can vary markedly between individuals (see above).

Animals tested using spontaneous choice tasks showed a marginally weaker response to illusions than those which were under a training paradigm. This suggests that in planning a study, one should consider how the main question of the study influences the methodological choice: training animals might be the better choice if the aim of the study is to reveal the neurological substrate involved in the perception of an illusion as it may lead to a more consistent and stronger effect size with a lower sample size. It is important to note, however, that with training we cannot exclude the possibility that such processes may involve reinforcement learning towards other environmental cues and not only those responsible for illusory perception (e.g., for instance, when training an animal for the Delboeuf illusion, they may respond to the ratio between the plate and the food or the size of the plate on the training trials rather than on the actual illusory factor). If the question involves understanding on how the visual illusion is perceived as part of an animal’s natural behavioural repertoire, using spontaneous choice may be the better methodological approach, even if it involves testing a larger number of subjects and may yield lower effect sizes (for additional comparison of the two methods see Agrillo and Bisazza 2014; Santacà et al. 2021). Realistically, selecting a testing method may not possible, as spontaneous testing might not be suitable for all species (see example in Becker et al. 2021 were they suggest that sponaneus choice test may invoke an inhibitory control problem in dogs). Finally, another aspect which is often overlooked in these forms of testing is motivation, which plays a key role in spontaneous testing – and a reason not to interpret null results as a lack of susceptibility.

An ancillary methodological observation is that almost all spontaneous choice tests rely on food as a stimulus. Food is a universal motivator, but not the only thing an animal needs. A clever deviation from food-based paradigms is the study methods of Santacà et al. (2022), where guppies were tested using a paradigm involving different sizes of holes that the animals needed to cross, then modifying the environment around the holes in order to create the illusory effect. The development of new testing paradigms can also give the opportunity to spontaneously test animals in more naturalistic situations, or even in their natural environment. This could provide information about the acquisition and relevance of certain sensory information in an animal's everyday life. Finally, testing the susceptibility of the same illusion but in different contexts would also provide the opportunity to cross validate the phenomena within the same species or reveal that it is limited to a single scenario, providing clues as to which mechanisms may be behind it (i.e., relevant for food but not for mating or escaping).

Some species perceive geometrical visual illusions in the opposite way that humans do. Although, our analysis shows that the effect is stronger if the perception is the same as in humans. However, this result can be misleading. Since there is more interest in the visual perception of species that are more similar to humans, such as mammals, this result may be biased. As shown here, many more mammalian species are chosen as test subjects, while studies in other taxa (for example, fishes) where species are more likely to perceive illusions in the opposite way that humans do are less numerous.

Publication bias was present in the current data set and showed a trend with time; recent publications show smaller effect sizes, larger sample sizes and opt for spontaneous testing. As it is commonly observed in other fields, bias against publishing studies with small effect with non-significant results seems to be fading (Jennions and Møller 2002). Additionally, while training animals used to be the classical approach in illusory perception studies, spontaneous testing seems to be trending and continues to gain ground as the method of choice.

This meta-analysis highlights some of the gaps in the field. An area of opportunity is to evaluate underrepresented taxonomical groups; for example, we found no studies on amphibians and only a few on reptiles and birds and they all have small sample sizes (Supplementary material). Regarding the taxa and habitat, few or no studies have taken the opportunity to evaluate the effect of permutations by testing, for instance, water-bound mammals (e.g. dolphins, see Murayama et al. 2012, however only one animal was tested), flightless birds (e.g. ostriches or kiwis), or flying mammals (bats). A similar pattern can be observed for the illusion types; while some are used to test several species (e.g., Delboeuf) others have been barely studied (e.g., Ponzo or Jastrow). Additionally, we would invite research groups that have established model species to expand their tests to a wider range of illusions, allowing the field to have a better comparability of susceptibility (e.g. Hanus et al. 2022).

Finally, since most modern journals have the option to include supplementary material or have even made sharing raw data via online repositories compulsory, an effort should be made by authors and reviewers to ensure the availability of data at the individual level. In statistical terms, the bare minimum required should be to include the systematic report of the mean, standard deviation and effect sizes. Additional standardization of the number and type of trials during spontaneous food choice task should also be beneficial for researchers studying specific species to easily implement the methods and contribute to the pool of information.

Conflict of interest. The authors declare that they have no conflict of interest.

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Availability of data and materials.

Dataset can be accessed at: https://doi.org/10.6084/m9.figshare.22674559.v1

Appendix A. Supplementary material.

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6. Discusión

Nuestros resultados indican que los moderadores biológicos (clase taxonómica, posición de los ojos y hábitat) no parecen tener una influencia significativa en la susceptibilidad de los animales para percibir ilusiones visuales geométricas.

Revisiones como la de Kelley y Kelley., (2014) y Feng et al., (2017) atribuyen la percepción a ilusiones visuales a errores en la forma en que se procesan los estímulos visuales, no a los órganos sensoriales, probablemente esta es la razón por la cual la posición de los ojos y el hábitat de los vertebrados no influye en su percepción a las ilusiones visuales. Además, trabajos como el de Santacà y Agrillo (2021) sugieren que la percepción a ilusiones visuales podría atribuirse a los circuitos neuronales subyacentes a la percepción visual y la ontogenia de los sistemas visuales.

Entonces, podemos inferir que la capacidad visual de diferentes especies de vertebrados o craneados no es el factor principal que determine si pueden percibir ilusiones visuales, por lo que la manera en la que cada especie procesa y comprende la información que recibe del ambiente a través de sus ojos debe ser el factor clave; de acuerdo con Ohzawa, (1999) “De ser así, entonces sus cerebros (de los animales) cometen los mismos errores que nosotros (humanos), lo que implica que las estrategias y suposiciones que utilizan los sistemas visuales son similares entre las especies”.

Sin embargo, es posible que los mecanismos visuales subyacentes a la percepción de ilusiones difieran entre las especies, provocando que solo algunas puedan experimentarlas (Byosiere et al., 2018), lo que podría explicar por qué algunas especies las perciben de forma opuesta a como lo hacen los seres humanos y porque otras no las perciben.

En el caso de la clasificación taxonómica, desde la clase hasta la especie se presenta una alta variabilidad de resultados que no permiten deducir si las relaciones filogenéticas entre los taxa tienen alguna influencia en la percepción a ilusiones visuales. Incluso, si la variabilidad intra e inter-sujeto en la susceptibilidad a diferentes ilusiones visuales nos muestra que la magnitud de la percepción puede ser muy diferente en la misma persona (Axelrod et al., 2017; Grzeczkowski et al., 2017). Aunque estudios recientes únicamente han encontrado una conexión débil, si es que la hay, entre la forma en que se perciben diferentes tipos de ilusiones (Grzeczkowski et al., 2018; Schwarzkopf et al., 2011)

Por otro lado, en el caso de varios moderadores metodológicos (Tipo de ilusión, propiedad geométrica, método de pruebas, sexo, número de repeticiones durante el entrenamiento, número de repeticiones durante las pruebas y tamaño de muestra), nuestros resultados parecían sugerir que tenían un efecto, como fue el caso del tipo de ilusión, sin embargo, al realizar las correcciones para comparaciones múltiples se perdió esta significancia, por lo que el tipo de ilusión no demuestra tener algún efecto. Nuestros resultados no hacen posible realizar un comparativo con la mayoría de las observaciones realizadas en otras revisiones.

Encontramos una correlación negativa entre el tamaño de muestra y el tamaño de efecto, lo cual nos indica que mientras menos individuos se pongan a prueba mayor es el tamaño efecto, lo cual afecta significativamente a la fuerza de respuesta a efectos ilusorios a nivel de grupo. Esto ocurre porque posiblemente se excluyeron de varios estudios a aquellos individuos que no mostraron interés en las pruebas o que fueron de entrenamiento lento, lo anterior implica una lección con relación a la importancia de seleccionar correctamente el tamaño de muestra y la claridad al reportar los datos de individuos incluso para animales excluidos de los análisis, debería ser una prioridad en futuros estudios.

El uso de tamaños de muestra mayores podría ayudar a eliminar las diferencias individuales y a su vez podría dar una idea sobre sus posibles mecanismos lo que podría ayudar a avanzar en el campo, tal como mencionan Santacà y Agrillo (2021): “En experimentos de selección espontanea normalmente se evalúa una muestra de mayor tamaño para evaluar el desempeño grupal y, por lo tanto, superar cualquier preferencia individual por el estímulo.”

Además, encontramos que los animales que fueron puestos a prueba usando pruebas de selección espontánea muestran una respuesta marginal débil a las ilusiones comparada a aquellos donde fueron entrenados previamente.

Por otro lado, también es posible que la exclusión de estudios que incluyeran individuos juveniles pudo ser un factor importante durante el análisis de nuestros datos, por ejemplo, en especies como el gato domestico *Felis silvestris catus*; estudios previos donde se utilizaron individuos juveniles se reporta que estos no son susceptibles de percibir las ilusiones visuales (Bánszegi et al., 2021a), caso contrario es el ejemplo del estudio de la especie *Gallus gallus* donde Salva et al (2013) reportan que juveniles con 4 días de edad fueron capaces de percibir la ilusión de Ebbinghaus. En muchos casos tampoco se ha estudiado la misma ilusión en diferentes especies, lo cual puede ser un factor que impida realizar una mejor comparación. En el futuro, nuevos estudios que llenen este hueco de información nos proveerían de un mejor panorama para analizar este fenómeno.

Una posible respuesta al porqué de la diferencia en la percepción entre individuos juveniles y adultos pueden ser las diferencias en el desarrollo entre las especies precociales como lo es *Gallus gallus* y especies altriciales el gato doméstico o los mismos humanos. Bánszegi et al., (2021) nos mencionan una variedad hipótesis para el caso del gato doméstico donde se comparan sus resultados y los reportados en humanos, puesto que en ambas especies se encontraron similitudes en como responden a la ilusión de Delboeuf en individuos adultos y como en ambas especies no perciben la ilusión visual cuando los organismos son demasiado jóvenes. Estas hipótesis en resumen nos dicen que muy probablemente estas especies requieran experiencia en estímulos visuales para poder ser capaces de percibir ilusiones, teniendo también como requerimiento la madurez de sus sistemas de procesamiento visual.

Santacà et al., (2021) nos mencionan dos ejemplos sobre como los animales podrían explotar las ilusiones visuales. Para las ilusiones de tamaño o brillo estas podrían estar presentes en el cuerpo de las especies y tener influencia en diferentes contextos sociales como la elección de pareja y los conflictos intersexuales […] las ilusiones de movimiento o las ilusiones que obscurecen la forma del cuerpo podrían jugar un papel importante en el camuflaje de los animales y con ello reducir el riesgo de ser depredados o para incrementar la probabilidad de depredar.

Es por estas razones que suponemos que se requiere de una madurez sensorial equivalente a la de un adulto para poder percibir ilusiones y, por lo tanto, cobra sentido el hecho de que individuos muy jóvenes o sin un desarrollo total de los sistemas visuales a temprana edad, no sean capaces de percibir ilusiones visuales. Aunque en el trabajo de Feng et al., (2017) nos mencionan que "hay evidencia reciente que sugiere que los mecanismos subyacentes a la percepción de ilusiones visuales podrían no depender enteramente en la experiencia personal".

Al analizar de nuevo datos de varias investigaciones publicadas se vuelve evidente que todas cuentan con resultados distintos y diferentes sesgos, ya que los criterios de cada estudio y sus objetivos eran diferentes. Con el objetivo de poder reducir este sesgo, sugerimos que en estudios posteriores se reporten los datos de todos los individuos analizados, ya que varios artículos reportan haber excluido individuos de los análisis estadísticos con base en sus propios criterios, esto dificulta el poder establecer criterios de inclusión y exclusión para seleccionar artículos, aunque ello no representa propiamente una limitante o desventaja del método del metaanálisis sino del campo de investigación.

En algunas investigaciones se trabajó con individuos de un solo sexo y pocos de los que trabajaron con machos y hembras reportaron la inexistencia de diferencias por el sexo. Estos datos, en combinación y bajo nuestros análisis tampoco indicaron que exista una diferencia entre los mecanismos de percepción visuales que sea dependiente del sexo.

Algunas investigaciones reportan a especies que usan ilusiones visuales en sus conductas de apareamiento, por ejemplo, en el trabajo de Kelley & Endler, 2012 reportan que en aves de la familia Ptilonorhynchidae los machos construyen nidos con decoraciones llamativas y realizan movimientos que crean una ilusión de perspectiva que aumenta sus probabilidades de ser seleccionados por la hembra. El ejemplo anterior sugiere que el uso de ilusiones visuales puede resultar benéfico para los animales con dimorfismo sexual.

Es posible que estos resultados se deban a que la mayoría de las especies con las que trabajaron no presentaban un dimorfismo sexual muy marcado, tanto física como conductualmente. Sugerimos que en el futuro se investigue en especies con las características antes mencionadas.

La cantidad de repeticiones que cada estudio realizó, tanto para entrenamiento como para pruebas con las ilusiones, es un factor determinante en la fiabilidad y veracidad de los resultados. Durante el entrenamiento, una basta cantidad de repeticiones puede conducir a que los sujetos lleven a cabo de forma correcta las pruebas con ilusiones, y a su vez, una cantidad alta de repeticiones en estas últimas pruebas permite obtener resultados significativos que nos indiquen con mayor certeza si los individuos pueden percibir ilusiones visuales geométricas. Detectamos que para una cantidad representativamente grande de los artículos analizados se trabajó con una cantidad baja de repeticiones (tanto para entrenamiento de ser el caso o en pruebas de ilusión) que aumenta la probabilidad de sesgo en sus resultados. En los estudios de Bánszegi et al., (2021) y Petrazzini et al., (2018) nos mencionan que mientras mayor sea el número de repeticiones de las pruebas de ilusión y de entrenamiento, se reducirá el sesgo en los resultados.

El desempeño de uno o varios individuos con datos extremos en pocas repeticiones puede llevar a que los resultados a nivel de grupo no sean representativos, por lo cual sugerimos que en futuros trabajos se utilicen cantidades adecuadas de repeticiones las cuales permitan minimizar el sesgo a nivel individual y grupal.

7. Conclusiones

Nuestros resultados no indican que los moderadores biológicos tengan alguna influencia significativa en la percepción a ilusiones visuales geométricas, caso contrario a los moderadores metodológicos donde varios de ellos mostraron tener influencia significativa, con excepción del tipo de ilusión cuya significancia desapareció con análisis posteriores. La variabilidad en los resultados parece estar más relacionada a variables como el tamaño de muestra, la cantidad de repeticiones realizadas durante el entrenamiento o las pruebas de ilusión y el haber trabajado con datos provenientes de investigaciones que trabajaron con objetivos y especies diversas donde en algunos de ellos fueron eliminados datos. Nuestro trabajo revela una serie de áreas de oportunidad, factores de sesgo y brechas metodológicas que sugerimos tomar en cuenta a la brevedad para poder obtener resultados con una mayor veracidad y que esto permita conocer mejor como los moderadores biológicos y metodológicos influencian la percepción de ilusiones visuales en vertebrados no humanos.

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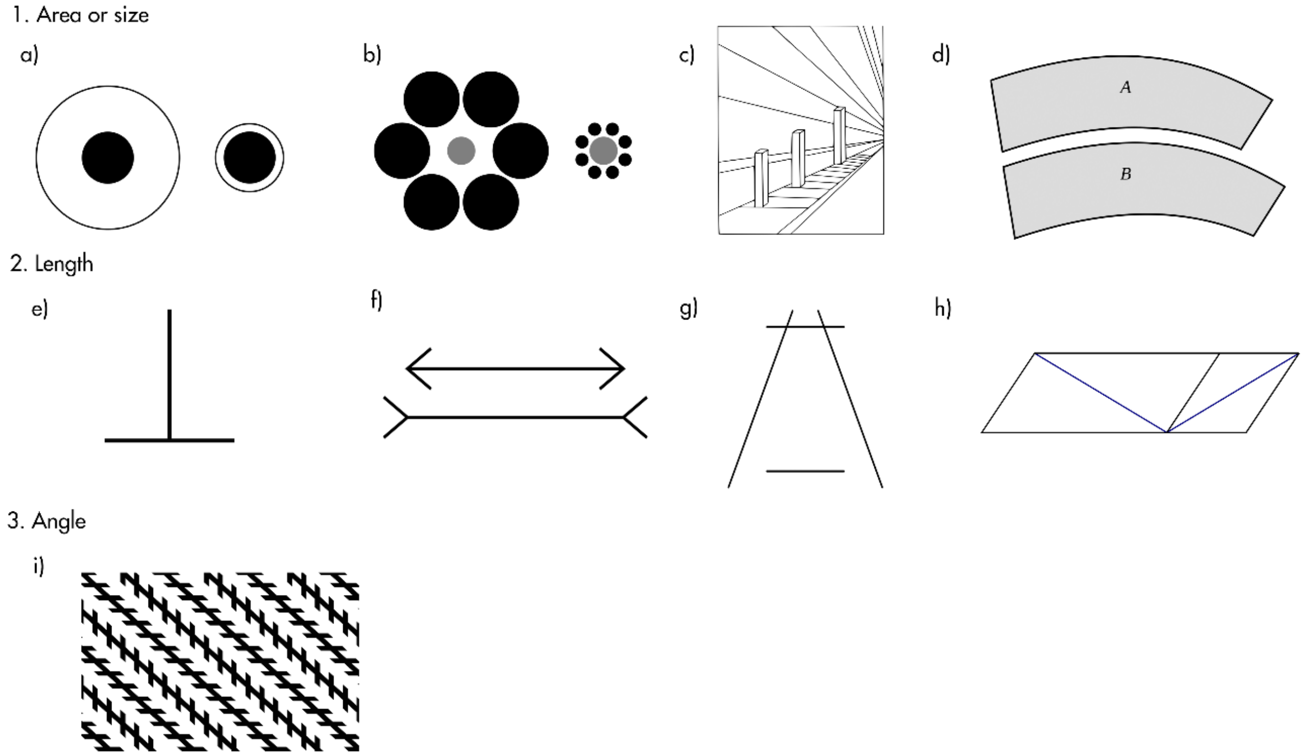
9. Material suplementario del articulo

Appendix A. Supplementary material.



a) Delboeuf illusion, the dot with the smaller surrounding ring appears larger. b) Ebbinghaus illusion, the central circle surrounded by large circles appears smaller. c) Corridor illusion, objects of equal size in a perspective picture appear larger the further away they seem to be. d) Jastrow illusion, one of the identical curved shapes looks larger. e) Vertical–horizontal illusion, observers to overestimate the length of a vertical line relative to a horizontal line of the same length. f) Müller - Lyer illusion, of two lines with equal length, the one with the open fins appears longer. g) Ponzo illusion, the upper of two parallel horizontal lines of equal length appears to be longer than the bottom when they are flanked by oblique lines that are closer together at the top than they are at the bottom. h) Sander illusion. the diagonal line bisecting the larger parallelogram appears to be longer than the diagonal line bisecting the smaller parallelogram. i) Zöllner illusion, alternating pattern of crossing line surrounding parallel lines creates the illusion that they are not parallel

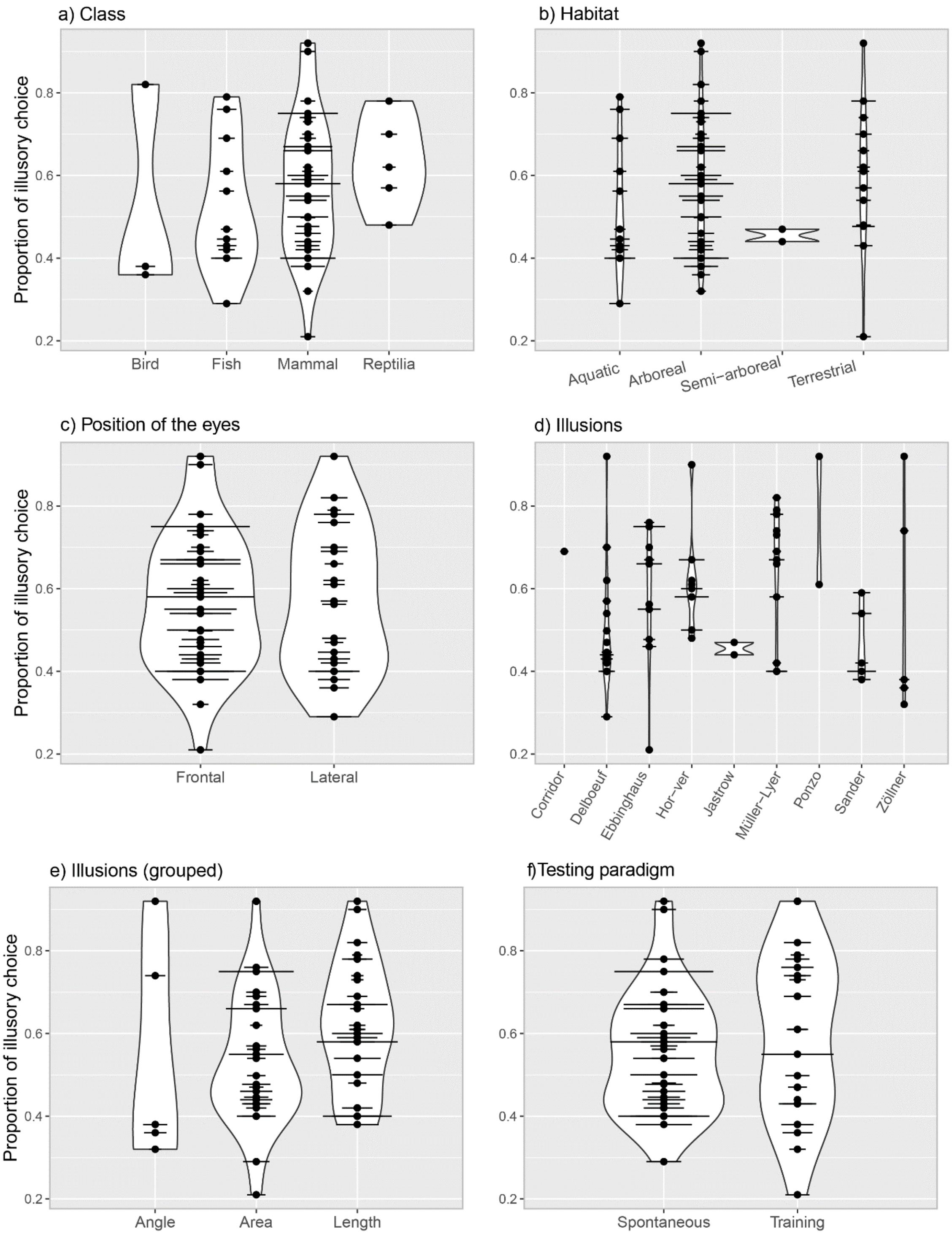


Figure 1. Violin plots for biological and methodological factors: a) class, b) habitat, c) position of the eyes, d) illusions, e) illusions, but grouped and f) training paradigm. For each of the samples included in the meta-analysis, a dot represents the mean proportion of illusory choice (in the same direction), while horizontal lines represent the standard deviation. Areas are the mirrored density plots.

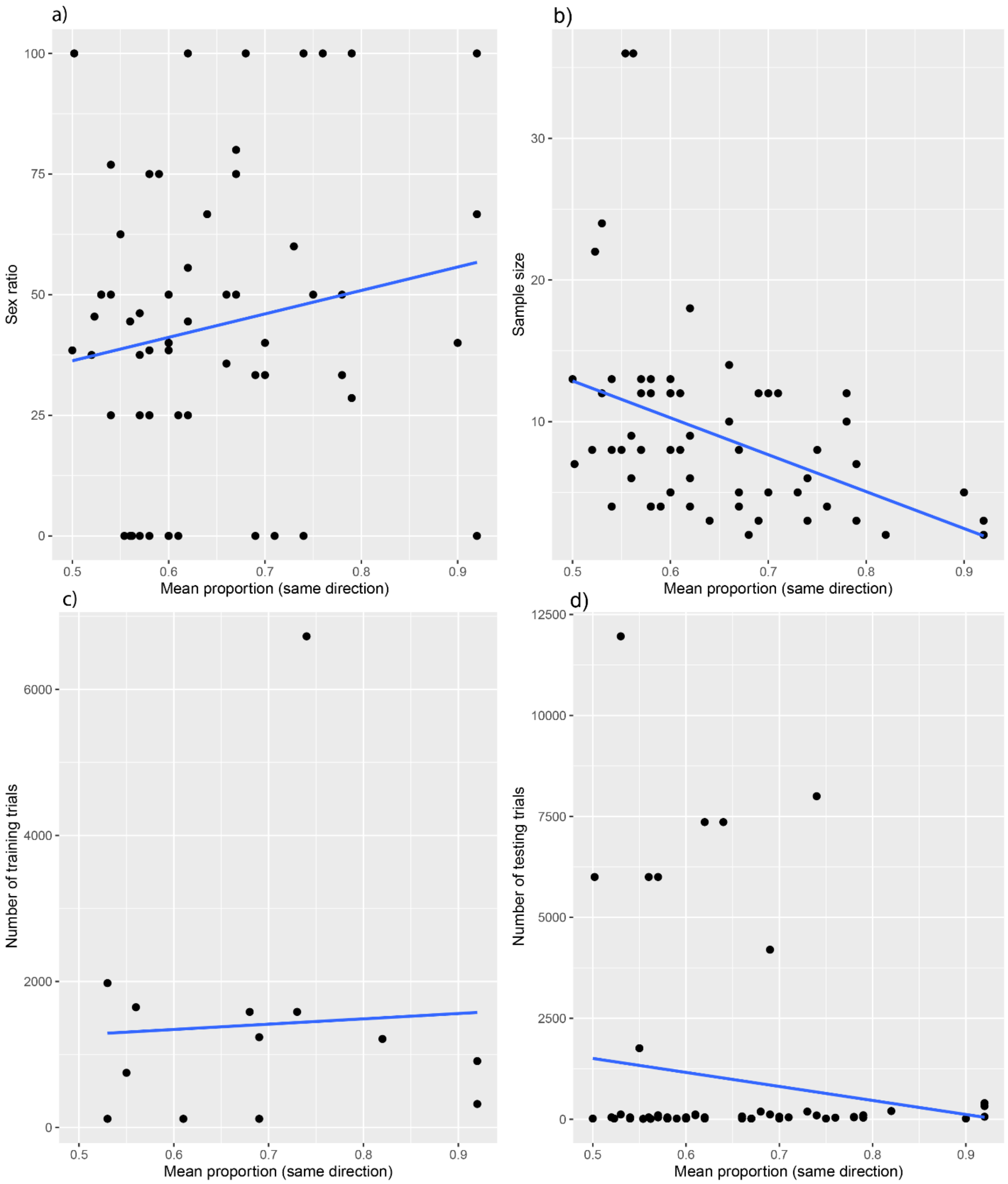


Figure 2. Scatterplots illustrating the correlation between the mean and a) the sex ratio, b) sample size, c) the number of training trials, d) the number of testing trials. Blue line marks the linear relationship between these variables.

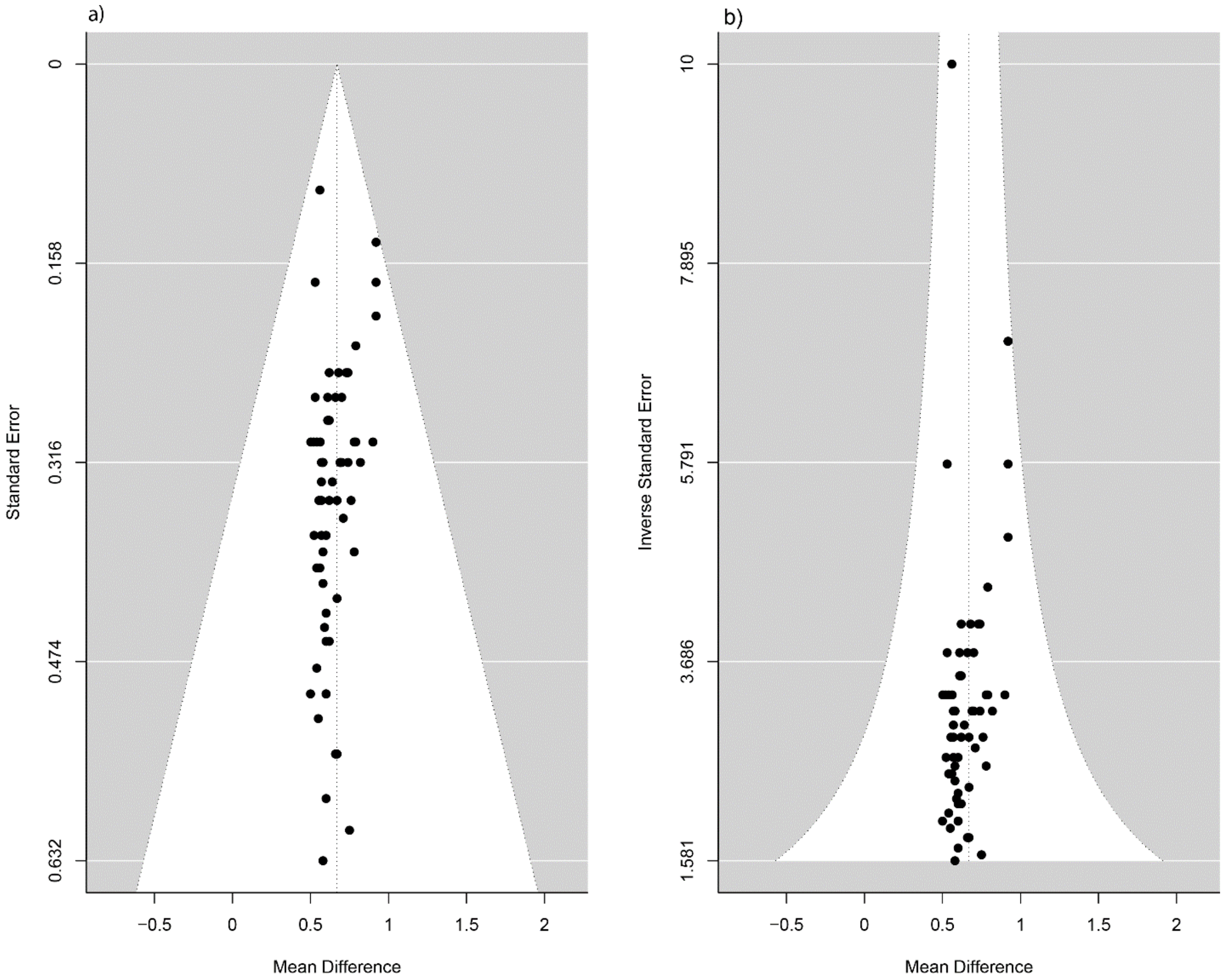


Figure 3. Funnel plots showing the relationship between the mean difference and the a) standard error and b) inverse standard error. White contour marks the pseudo 95% confidence intervals.

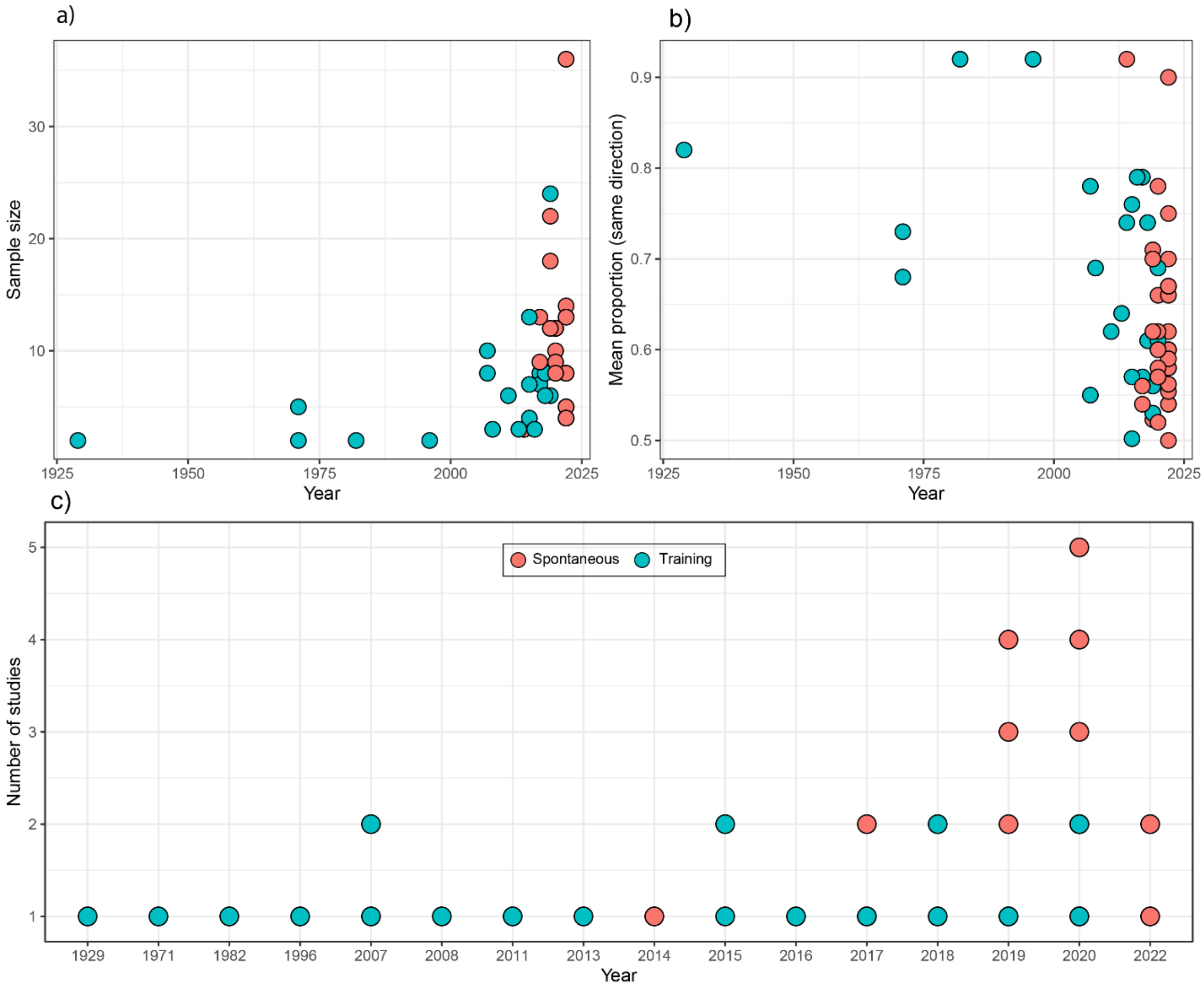


Figure 4. Scatter plots of a) sample size and year, b) mean proportion of illusory choice and year and c) number of studies published per year. Blue dots show studies using the training paradigms while pink dots mark those using spontaneous choice paradigms.