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ORIGINAL PAPER

The Müller-Lyer illusion in the teleost fish *Xenotoca eiseni*

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Abstract In the Müller-Lyer illusion, human subjects usually see a line with two inducers at its ends facing outwards as longer than an identical line with inducers at its ends facing inwards. We investigate the tendency for fish to perceive, in suitable conditions, line length according to the Müller-Lyer illusion. Redtail splitfins (*Xenotoca eiseni*, family *Goodeidae*) were trained to discriminate between two lines of different length. After reaching the learning criterion, the fish performed test trials, in which they faced two lines (black or red) of identical length, differing only in the context in terms of arrangement of the inducers, which were positioned at the ends of the line, either inward, outward, or perpendicular. Fish chose the stimulus that appear to humans as either longer or shorter, in accordance with the prediction of the Müller-Lyer illusion, consistently with the condition of the training. These results show that redtail splitfins tend to be subject to this particular illusion. The results of the study are discussed with reference to similar studies concerning the same illusion as recently observed in fish. Contrasting results are presented. The significance of the results in light of their possible evolutionary implications is also discussed.

Keywords Visual perception · Illusions · Global versus local factors · Fish

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Introduction

So-called visual illusions are often considered instances of a systematic discrepancy between the physical properties of the external world and how they are perceived by the human visual system (Coren and Gyrus 1978; Gregory 1966; Oyama 1960; Wade 2005, 2010). However, owing to the pervasiveness of the tendency for humans to perceive illusions, they may be interpreted not as errors in signal processing but as efficacious tactical behavioral responses by living organisms to the environment that surrounds them and as furnishing advantages for survival (Guilford and Dawkins 1993). There is neither agreement about nor conclusive explanation for the nature, incidence, and role of the various perceptual illusions. Some studies (e.g., Henrich 2008; Henrich et al. 2010; Segall et al. 1963), relying on contrasting results found in subjects of different cultures (industrialized vs. small-scale societies) that show substantial variation across populations, explain some perceptual illusions (e.g., the Müller-Lyer) as culturally evolved by-products of some kind. Other studies highlight the variation in the strength of some illusions (e.g., the Ebbinghaus illusion) across different age groups, with children being less sensitive to them (Weintraub 1979;

Zanutti 1996; Kovacs 2000), supporting the hypothesis that contextual integrations (on which some illusions are held to depend) may be underdeveloped in young children.

The tendency to perceive visual illusions has been shown also in animal perception (see Kelley and Kelley 2014; Wyzisk and Neumeyer 2007) where some illusions are clearly related to advantage in male competition, courtship, and mate choice (Reaney 2009; Callander et al. 2011). Visual illusions in animals also afford insights into the brain mechanisms that integrate the visual stimulation into a coherent percept, making it possible to process objects as a whole by integrating sensory stimulation into a unified representation (Mascalzoni and Regolin 2011; Nieder 2002; Vallortigara 2004, 2006, 2009, 2012; Vallortigara et al. 2010). In particular, size geometrical illusions highlight how the appreciation of the properties of a target stimulus (e.g., length, width, or diameter) may be distorted by the surrounding context, so that contextual elements surrounding the target object distort perception of it.

Geometrical illusions thus provide an important tool for the study of the perceptual integration of local elements (e.g., smaller figures) into a global context (e.g., a global configuration consisting of smaller figures, as in the Ebbinghaus or the Müller-Lyer illusion) (Cavoto and Cook 2001; Deruelle and Fagot 1998; Fagot and Deruelle 1997; Kimchi 1992; Kinchla and Wolf 1979; Kinchla et al. 1983; Regolin et al. 2004).

However, while global perception seems to characterize the human species (Navon 1977), there is evidence in the literature that some nonhuman species, including pigeons and baboons, could have a more locally oriented perception than humans (Cavoto and Cook 2001; Cerella 1980; Chiandetti et al. 2014; Cook 1992; Deruelle and Fagot 1998; Fagot and Deruelle 1997; Wasserman et al. 1993; Kelley and Kelley 2014; Ushitani et al. 2001). But it would be an extreme oversimplification to draw a clear dichotomy between globally oriented humans and other locally oriented species. For example, the view that human and nonhuman animals may or may not show globally oriented perception depending on contextual variables (e.g., Fremouw et al. 2002; Kinchla et al. 1983; Navon 1977; Pomerantz 1983) is strongly supported by two recent studies on domestic chickens that used two very different procedures, obtaining opposite results within the same species (Rosa Salva et al. 2013; Nakamura et al. 2014). Recently, redtail splitfin fish (*Xenotoca eiseni*) have also been shown to preferentially process hierarchical stimuli at the global rather than local level (Truppa et al. 2010), confirming that remarkable similarities exist between the visual system of fish and other vertebrates. The experiments conducted on redtail splitfin fish are of particular relevance, because it is difficult to conceive the visual system of such fish as being closer to that of humans than that of any other species tested.

A well-known example of size geometric illusions is the Müller-Lyer illusion (Müller-Lyer 1889, 1894). It occurs when a line segment with two arrows facing outwards at the end appears to be longer than one with arrows facing inwards. In human perception, the illusion is well represented in the scientific literature; however, in this case too, no unitary or definitive explanation as to what perceptual principles account for the Müller-Lyer illusion has yet been provided (Chiang 1968; Dewar 1967; Gregory 1970, 1997; Erlebacher and Sekuler 1969; Pressey and Martin 1990; Predebon 1994, 2000; Purghé et al. 1999; Restle and Decker 1977; Roberts et al. 2005). The neural mechanism underlying the illusion was studied by Weidner and Fink (2007) and by Weidner et al. (2010) [for a review, see Bertulis and Butalov (2001)]. According to a well-known hypothesis (Gregory 1966**),** the Müller-Lyer illusion occurs because the line terminating with the arrows may be perceived as the outer edge of a box and thus in a location closer than the other line, which is perceived as the inner edge of a solid positioned farther away. However, it has also been shown that if the arrows are substituted with small circles or clusters, or on deletion of the inner lines, the illusion persists (Brentano 1892; Porac 1994; Watson et al. 1991; De Lucia et al. 1994).

In animal perception, the Müller-Lyer illusion (1889, 1894) has been tested in flies (Geiger and Poggio 1975), pigeons (Nakamura et al. 2006, 2008; Warden and Baar 1929), gray parrots (Pepperberg et al. 2008), capuchin monkeys (Suganuma et al. 2007), rhesus macaques (Tudusciuc and Nieder 2010), ring doves (Warden and Baar 1929), ants (Sakiyama and Gunji 2013), bamboo sharks (Fuss et al. 2014), and goldfish. In particular, the studies conducted with fish showed that neither bamboo sharks nor goldfish are particularly sensitive to differences in line length. There are task context differences, however, between the two studies. In Fuss et al. (2014), sharks could inspect the stimuli from very close-up (they were food-rewarded for pressing the snout against the wall just below/on the positive stimulus), while in the study with goldfish, they could go no closer than 5.5 cm to the stimuli. Also noteworthy is that bamboo sharks and goldfish, although not deceived by the Müller-Lyer illusion, have proved to be sensitive to Kanizsa's figures and subjective contours (Wyzisk and Neumeyer 2007). For a recent review on illusory contours in fish, see Agrillo et al. (2013) and Rosa Salva et al. (2014).

In our study, we investigated the perception of the Müller-Lyer illusion in redtail splitfin fish (*Xenotoca eiseni*), using a procedure analogous to that used by Sovrano and Bisazza (2008, 2009), Truppa et al. (2010), and

Sovrano et al. (2014) in other studies of vision in these fish. Because fish are sensitive to variations in contrast, it was decided to conduct the test both with all-black stimuli and also with the internal Müller-Lyer lines colored red (as in Pepperberg et al. 2008). The purpose was to verify whether color differences had any effect on perception of the entire configuration or on the strength of the illusion. However, because this manipulation of the stimuli did not produce any difference, we mention it in the description of the experimental design but will not discuss this aspect further.

Methods

Subjects

The subjects were six male mature redtail splitfin fish, *Xenotoca eiseni* (ranging 2.5–4 cm in length), coming from a stock kept in our laboratory. Fish were reared in large tanks (100 cm long, 40 cm wide and 40 cm high; 150 l capacity), with rich vegetation (*Ceratophilllum* sp.) and polychromatic small gravel, provided with artificial illumination, 14:10 LD cycle. Water temperature was maintained at 25 ± 2° C. Fish were fed daily with dry fish food (Sera GVG-Mix®).

Apparatus

The apparatus was set up in a darkened room, and it replicated that used by Sovrano and Bisazza (2008, 2009), Truppa et al. (2010), and Sovrano et al. (2014) (see Fig. 1). Consisting of a square tank (15 cm long, 15 cm wide, and 15 cm high), it had uniform white walls and was centrally lit with a 75-W incandescent light bulb. The tank containing the test fish was within a larger one (60 cm × 36 cm × 25 cm) in order to create an external region with vegetation and food in which two other conspecifics (nontested females) were placed. This induced motivation for social reinstatement. Small tunnels (2.5 cm in length, 2 cm in size, 3 cm in height, and located 4.5 cm from the floor of the tank) were created in two diagonally opposite corners. These tunnels were made of white plastic material (Poliplack®), and the test fish could pass through them to rejoin the conspecifics in the external region in the outer tank (see Fig. 1). Each tunnel ended with a door (2.5 × 3.5 cm), of which the upper part consisted of a sheet of opaque plastic material and the lower part of a very flexible transparent plastic material. Although the two doors were visually identical, only one of them could be opened, because the other was blocked by an external plastic transparent panel. The test fish could thus open the correct door to rejoin its conspecifics by pressing on it with its snout. The choices of each door made by the test fish were clearly visible from video-recordings owing to characteristic movements of the fish's tail and the most caudal part of its body, which was visible outside the tunnel.

Fig. 1 The apparatus used in the experiment: the experimental square inner tank, placed in a larger one (*top*), with details of open and closed doors (respectively, in correspondence with the reinforced stimulus and of the not reinforced stimulus) (*down*)

The stimuli used for the visual discrimination learning and to test the illusions were located beneath each door (see Figs. 2, 3). Made of a special type of plastified cardboard,

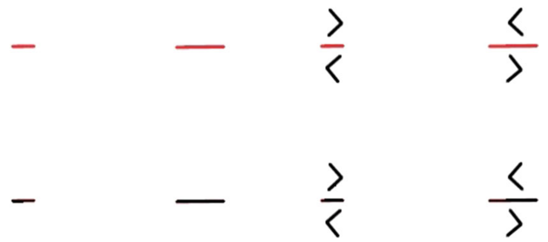


Fig. 2 The stimuli, located below the two doors, used during the training task: Two different lines, *black* and *red*, were presented in two different versions: *isolated lines* of different lengths and *lines* of *different lengths* with the presence of black inducers, positioned above and below the *target line*

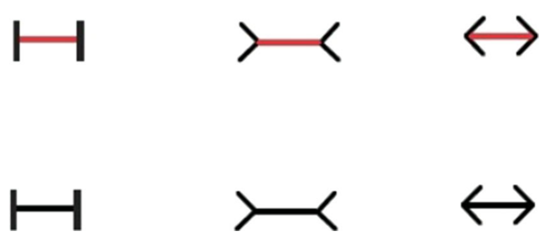


Fig. 3 The stimuli used during the test: The target lines were identical, in both the *black* and *red* versions, and inducing *brackets* were positioned at the ends of the *line*, either inward or outward, in order to create a Müller-Lyer illusion. In the control condition, the target lines (*black* or *red*) were flanked contiguously by two short perpendicular *black lines*

the stimuli were designed to resist the aquatic environment. Completely transparent screens (9 × 4 cm) were located 2.3 cm in front of the stimuli, in order to prevent visual exploration of stimuli in close proximity and, in this way, to allow a Gestalt-like perception of the overall pattern. During training, the stimuli to be discriminated consisted of two horizontal lines of different lengths: 0.5 and 1 cm. One group of fish was trained with the shorter line and the other with the longer line as positive. During training, the two different lines presented were either black or red and were presented in two different versions: isolated lines of different lengths and lines of different lengths with black inducers (two oblique lines—0.4 cm long—forming a right angle) positioned above and below the target line. The second version of the training stimulus (lines with inducers above and below) was inserted to accustom the fish to the subsequent presence of inducers in the test stimuli (see Fig. 2). This particular stimuli disposition has also been used by Nakamura et al. (2006). Both versions of the lines in two different colors (black and red) were presented to fish during training (Fig. 2).

At test, the target line was 0.8 cm in length, in both the black and red versions, and the inducing brackets (0.4 cm long) were positioned at the ends of the line, either inward or outward, in order to create the conditions for a Müller-Lyer illusion. In addition to the two canonical lines with inducing brackets, a control condition was created in which the target lines (black or red) were flanked contiguously by two short perpendicular black lines (0.7 cm long) (see Fig. 3).

The fish were trained to discriminate between two lines of different size. After reaching the learning criterion, fish were presented with two stimuli in which the sizes of the two lines were identical, but the context in which they were inserted (inward, outward, and perpendicular inducers) was changed in such a way as to produce the impression to a human observer of two lines of different lengths.

Procedure

Before being tested, the fish underwent a shaping procedure in their home tank (30 × 40 × 20 cm) for at least a week. For this procedure, a partition divided the home tank into two halves, one of which was "enriched" with food and vegetation, while the other, "un-enriched," half had no food and vegetation. Two tunnels with moveable doors identical to those subsequently used at test were inserted in the partition, so that the fish could move between the two compartments. The fish thus learned how to use the moveable doors before testing began. The stimuli (lines of different dimensions, long for one group of fish, and short for the other) to be used during the subsequent training were positioned below the tunnels, to accustom the fish to the stimuli and to facilitate training, by presenting exactly the same stimuli as were used in the training phase. The stimuli were two lines of different lengths, black or red, and presented as isolated lines or lines in the presence of black inducers (two oblique lines forming a bracket > or <) positioned above and below the target line (see Fig. 2). Note that, during the stimulus presentation, both moveable doors (with stimuli later associated with reinforcement during training) allowed the fish to move from one compartment to the other. Selective reinforcement by blocking one door was performed only during the subsequent training phase, in which the two stimuli of different sizes were presented together. Fish previously exposed to the long line were then rewarded for approaching the long line, while fish exposed to the short line were rewarded for approaching the short one.

The experiment comprised of two parts: training and test (see Fig. 2). Three fish were trained with the long line as positive (reinforced), and the other three fish with the short line as positive. The fish were given daily sessions of 10 trials, in which the four types of stimuli (Fig. 2) were presented twice consecutively, coupling long and short lines (isolated version before and version with inducers after), until the fish reached the learning criterion (at least 70 % of correct choices in two consecutive daily sessions).

This procedure can be considered reliable in light of the results obtained by previous work on perceptual illusions (Sovrano and Bisazza 2008, 2009; Truppa et al. 2010; Sovrano et al. 2014). In each trial, a fish was gently inserted into a transparent plastic cylinder placed in the center of the inner tank. The cylinder was removed after 20 s. The number of choices between the two doors made by the fish until it successfully exited and rejoined its conspecifics (the maximum time was 15 min) was recorded on each trial. A correction method (Sutherland and Mackintosh 1971) was used: If the fish made a wrong choice, it was allowed to change it until it successfully exited the inner tank, or until the overall time allowed for the trial had elapsed. The intertrial interval was 7 min after a correct choice, and 3 min if the choices by the fish consisted of mixed responses (incorrect and correct). The fish was allowed to remain in the outer region (reinforcement time) during the intertrial interval. Some food (the same as that used in the home tank) was put in the outer tank after some correct choices, but no more than twice for each daily session. The tank was rotated 90° after every two trials in order to avoid the possible use of any extra-tank cue during the course of the experiment. After reaching the learning criterion in the training phase, the fish performed the test trials in which they faced two stimuli: two lines (black or red) of identical length (1 cm), differing only in the context, in terms of arrangement of the inducers; as indicated above, inducing brackets were positioned at the ends of the line, either inward or outward. In addition, a control condition was created in which the target lines (black or red) were flanked contiguously by two short perpendicular black lines (0.7 cm long). The test involved four experimental conditions: comparisons between “inward brackets and outward brackets” and “inward brackets and perpendicular short lines” for both line colors (black and red) (see Fig. 3).

The test consisted of four single sessions of 10 trials (each trial lasting 2 min), one session for each of the four test conditions, with both doors closed. If fish did not make a choice within 2 min, they were allowed to stay longer, until they produced at least one choice, up to a maximum of 15 min. This procedure was used to maintain motivation, reducing any tendency for the fish to stay in the central tank too long (Sovrano and Bisazza 2008, 2009; Truppa et al. 2010; Sovrano et al. 2014). Trials with the same stimuli as those used during training were intermixed every 2–3 test trials, in order to maintain the motivation of the fish. These trials were discarded in the test data analyses. Performance in these intermixed trials had to be perfectly correct in order for the fish to proceed to the next test trials. The presentation of the test stimuli followed a random order, different for different fish.

The first choice made in each trial, and the number of choices made for each of the two stimuli during the 2 min of the test were recorded for each fish. From these figures, the percentages of first choices and of overall choices for the configuration with lengthening inducers were computed. We expected that choice of the figure in which the line appeared shorter would be above chance level in the fish reinforced on the shorter line and below chance level in the fish reinforced on the longer line, and vice versa for choice of the figure in which the line appeared longer.

The data were subjected to an analysis of variance with the type of test (comparison between the long subjective condition with the short subjective condition in each of the four experimental conditions—black/red line and angular/perpendicular inducers) as a within-subject factor, and the stimulus (long line vs. short line) associated with reinforcement during training as a between-subjects factor. The significance of departures from random choice (50 %) was estimated by one-sample two-tailed t tests.

Results

There was no difference in the number of trials needed to reach the learning criterion between the two groups reinforced for approaching the long or the short line (short line: mean ± SEM: 20 ± 6.93; long line: mean ± SEM: 32 ± 24.98; $t(4) = -0.80$, $P = 0.47$).

The results of the tests are shown in Fig. 4a–h, separately for each reinforcement condition and for the four types of test stimuli. Data were analyzed as percentages of choices for the figure with the longer line (to a human observer). The graphs (Fig. 4a–h) show the percentages of the first choices and the total choices in 2 min of observation. The analysis of variance revealed a significant effect of the type of training, considering both only first choices ($F(1,4) = 188.46$, $P \leq 0.0001$) and total choices ($F(1,4) = 226.62$, $P \leq 0.0001$). There were no other statistically significant effects [first choices: type of test: $F(3,12) = 0.74$, $P = 0.55$; type of test × type of training: $F(3,12) = 0.37$, $P = 0.78$; total choices: type of test: $F(3,12) = 0.31$, $P = 0.82$; type of test × type of training: $F(3,12) = 0.54$, $P = 0.67$]. Thus, in further analyses, we collapsed the data of all the four types of test stimuli, running separate statistical tests for the two reinforcement conditions. One-sample t tests, comparing both the percentage of first choices and that of overall choices (two minutes of observation) to chance level, revealed that the fish significantly chose the line that appeared longer or smaller (to a human observer), consistent with the training phase. The results were as follows: Fish rewarded in the presence of the longer line chose to approach the perceptually longer stimulus significantly more often than would

Fig. 4 Percentages of choices for the subjectively long condition: above, first choices; below, total choices (group means with SEM are shown): **a**, **b** comparison between two black target lines with inward and outward inducers; **c**, **d** comparison between two *black target lines* with inward and perpendicular inducers; **e**, **f** comparison between two *red target lines* with inward and outward inducers; **g**, **h** comparison between two *red target lines* with inward and perpendicular inducers

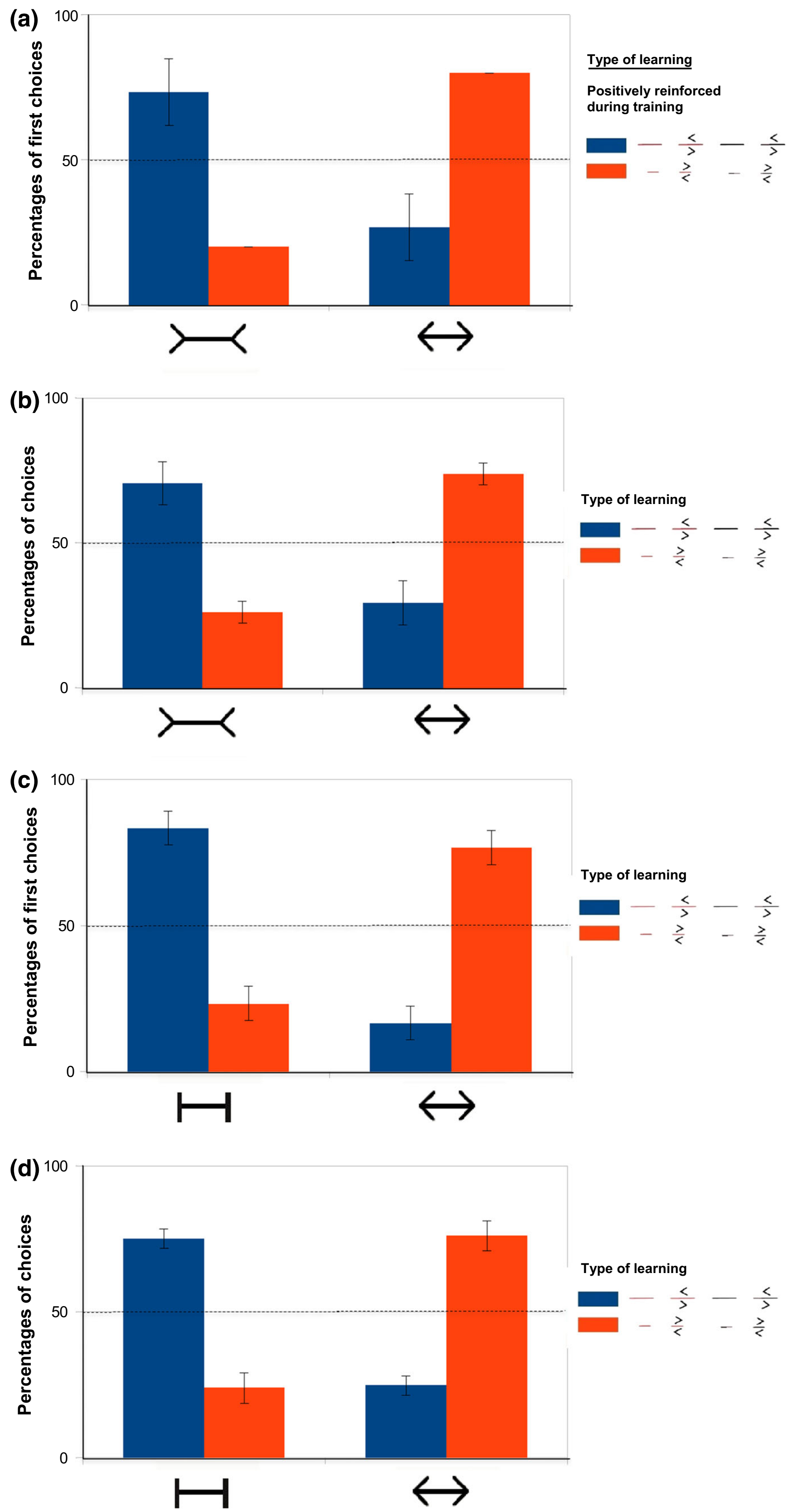
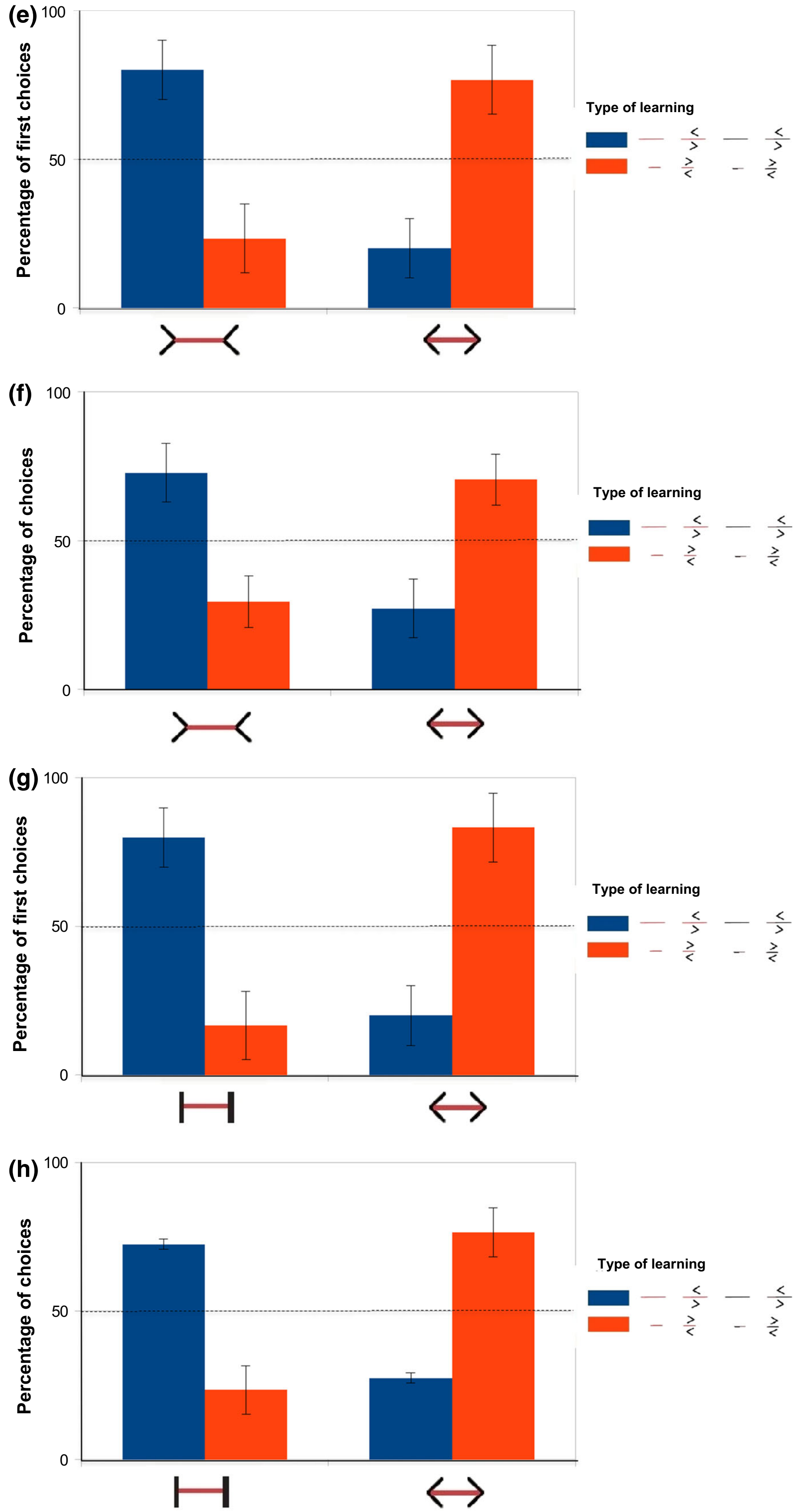


Fig. 4 continued



be expected by chance (first choice, $t(2) = 13.23$, $P = 0.006$; overall choices, $t(2) = 14.78$, $P = 0.005$), whereas fish rewarded in the presence of the shorter line chose the perceptually longer stimulus significantly less often than would be expected by chance (first choice $t(2) = -8.03$, $P = 0.015$; overall choices $t(2) = -8.92$, $P = 0.012$).

Discussion

The aim of our research was to verify whether redtail splitfins (*Xenotoca eiseni)* have the tendency to be affected by the Müller-Lyer illusion, which to date has been demonstrated only for other species. The purpose of the experiment was therefore to test whether one segment was seen as longer and the other as shorter. Studies conducted by Fuss et al. (2014) with bamboo sharks and by Wyzisk and Neumeyer (2007) with goldfish have shown the tendency for fish to be sensitive to illusory contours but not to line length.

Our hypothesis was that the long and short appearances would be affected by the direction of the terminations, that is, by the illusion. We also checked the difference between conditions with vertical bars and inclined bars (|—| < —>), to see whether the illusory effect was due to the area occupied by the figure or merely to the perceived length (see Malott et al. 1967). The areas in our test were, respectively, 0.29, 0.56, and 0.80 cm^2: with equal lengths, the areas were different; the smaller one was almost half (0.52) of the control, and the largest one was almost one and a half (1.4) of the control. These data are in agreement with the explanation of the illusion given by Müller-Lyer himself, because the illusion of length entails (or even follows) a difference in area, according to the principle of assimilation (Da Pos and Zambianchi 1996, p. 156; Pressey 1971).

In our research, the fish performed test trials in which they faced two stimuli. The latter were two horizontal lines of identical length, with the context changing only in terms of arrangement of the inducers: two right angles facing inwards and outwards on the target lines, and the target line flanked contiguously by two short perpendicular black lines.

Two tests were conducted. In the first, stimuli of uniform black color were used, and in the second, stimuli of different colors (red for the internal lines). Unlike previous studies (Sovrano and Bisazza 2008, 2009; Truppa et al. 2010), we considered, as dependent variables, not only the total choices in the two minutes of the test, but also the first choices in each trial; the results for the two measures were consistent. This strengthens the evidence for the illusory effect in these fish.

In our research, redtail splitfins rewarded in the presence of the longer line chose to approach the longer stimulus significantly more often than would be expected by chance, whereas fish rewarded in the presence of the shorter line chose the longer stimulus significantly less often than would be expected by chance, irrespective of the color of the internal lines (black or red). Our results confirm those obtained with other species, i.e., flies (Geiger and Poggio 1975), pigeons (Nakamura et al. 2006, 2009; Warden and Baar 1929), gray parrots (Pepperberg et al. 2008), sharks (Fuss et al. 2014), capuchin monkeys (Suganuma et al. 2007), and ring doves (Warden and Baar 1929). However, our results differ from those obtained with bamboo sharks (Fuss et al. 2014) and goldfish (Wyzisk and Neumeyer 2007) in which the fish were not deceived by this illusion. However, the design and the procedure of the above experiments with fish were different from ours, so that a direct comparison among the results seems very difficult.

As regards the contrasting results between ours and those of Fuss et al. (2014), one could hypothesize that the difference is due to the different methodologies.

These comparative studies also shed light on the phenomena of vision with regard to their possible evolutionary implications. In fact, the overall evidence suggests that the perceptual processes leading to the perception of the Müller-Lyer illusion, allowing the appreciation of objects as global entities, may be present in mammals, birds, and fish. Fish are particularly interesting for the analysis of perceptual phenomena, both because they are amenable to traditional training procedures and because their abilities can be investigated through naturalistic incidental learning tasks as in our study, where fish were allowed to freely choose the viewing distance from the stimuli. As proposed by Rosa Salva, Sovrano, and Vallortigara (2014), however, caution is necessary when comparing results obtained for different species, in different settings, and with different task procedures. Further studies might, for example, adapt fish species to the touch screen/skinner box procedures usually used with pigeons and other birds, to verify whether the subjects show a more locally oriented behavior. In such a situation, the bamboo sharks tested in Fuss et al. (2014), for example, were trained to respond by pressing their snout on the stimuli. More generally, fish species, given their great taxonomic diversity and the phylogenetic distance from other vertebrates, if viewed as a model of object processing in the visual system, may offer important insights for understanding the evolution of the vertebrate visual system, providing information on the neural correlates of perceptual organization in species belonging to different taxa.

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Compliance with ethical standards

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

Ethical standard The experiments reported here comply with the current Italian and European Community laws for the ethical treatment of animals.

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