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The Ebbinghaus illusion in a fish (*Xenotoca eiseni*)

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Abstract The tendency of fish to perceive the Ebbinghaus illusion was investigated. Redtail splitfins (*Xenotoca eiseni*, family Goodeidae) were trained to discriminate between two disks of different sizes. Then, fish were presented with two disks of the same size surrounded by disks of large or small size (inducers) arranged to produce the impression (to a human observer) of two disks of different sizes (in the Ebbinghaus illusion, a central disk surrounded by small inducers appears bigger than an identical one surrounded by large inducers). Fish chose the stimulus that, on the basis of a perception of the Ebbinghaus illusion, appeared deceptively larger or smaller, consistent with the condition of training. These results demonstrate that redtail splitfins tend to perceive this particular illusion. The results are discussed with reference to other related illusions that have been recently observed to be experienced by fish (such as the Navon effect), and with regard to their possible evolutionary implications.

Keywords Visual perception · Visual illusions · Ebbinghaus illusion · Titchener circles · Fish

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Introduction

Visual illusions are instances of systematic discrepancy between the physical properties of the external world and their representation in the visual system. Thus, visual illusions offer insight into the brain mechanisms that integrate the visual stimulation in a coherent percept, through its representation in the visual system (Mascalzoni and Regolin 2011; Vallortigara 2004, 2006, 2009, 2012; Vallortigara et al. 2010; Wade 2005, 2010). The comparative study of visual illusions provides us with information on the evolution of visual systems and the principles of perceptual organization. In geometric size illusions, the appearance of the properties of a target stimulus (e.g., length, width or diameter) is distorted by the surrounding context, providing an important tool for the study of perceptual integration of local elements into the global context created by the surrounding visual elements. Geometrical illusions such as the Ponzo, the Müller-Lyer and the horizontal–vertical illusion, seem to be perceived by species as distant as apes (chimpanzees, Fujita 1997), monkeys (e.g., Barbet and Fagot 2002; Bayne and Davis 1983; Suganuma et al. 2007; Tudusciuc and Nieder 2010; see also Fujita 1996), ungulates (e.g., horses, Timney and Keil 1996) and birds (domestic chickens, Winslow 1933; Rosa Salva et al. 2013; ring doves, Warden and Baar 1929; pigeons, Fujita et al. 1991, 1993; Nakamura et al. 2006, 2009; and gray parrots, Pepperberg et al. 2008).

Despite the paucity of research on geometric illusions in fish, they are a promising model for the comparative investigation of such phenomena (see Agrillo et al. 2014; Rosa Salva et al. 2014 for reviews). In fact, redtail splitfin, goldfish and two species of reef fish have been found to be susceptible to perceptual phenomena such as amodal completion and perception of illusory contours (Darmaillacq et al. 2011; Sovrano and Bisazza 2008, 2009; Wyzisk and Neumeyer 2007; see Fuss et al. 2014 for evidence in elasmobranchs; see Regolin and Vallortigara 1995; Regolin et al. 2004; Forkman and Vallortigara 1999 for similar evidence in other taxonomic groups). This is particularly remarkable in light of the phylogenetic distance between these three fish species (Steinke et al. 2006) and from other vertebrates (Kumar and Hedges 1998).

Studies on visual illusions in fish species are very informative about the phylogenesis of these traits. The susceptibility of this taxonomic group to amodal completion and illusory contours suggests a conserved trait rather than a case of convergent evolution in fish, birds and mammals. Within fish, illusory contours are perceived by teleosts as distant as Ostariophysi (redtail splitfin fish, *Xenotoca eiseni*) and Acanthopterygii (goldfish, *Carassius auratus*) (Sovrano and Bisazza 2009; Wyzisk and Neumeyer 2007). Similarly, amodal completion is observed in two species of Acanthopterygii (*Variola louti* and *Scarus niger*), in addition to the redtail splitfin fish (Darmaillacq et al. 2011; Sovrano and Bisazza 2008). Recently, it has been found that even cartilaginous fish (bamboo sharks, *Chiloscyllium griseum*) are susceptible to amodal completion and illusory contours (Fuss et al. 2014). Surprisingly, redtail splitfins also recognized illusory shapes created by phase shifts or by interruption of diagonal lines (Sovrano and Bisazza 2009), whereas in another study, goldfish did not recognize phase-shifted illusory shapes (Wyzisk and Neumeyer 2007). However, this may be due to a methodological problem in the stimuli of Wyzisk and Neumeyer (2007), which consisted of very thin lines, reducing the strength of the illusory perception.

Fewer attempts have been made to test fishes' tendency to perceive geometrical optical illusion. Two existing studies have failed to demonstrate susceptibility to the Müller-Lyer illusion in either bamboo sharks (Fuss et al. 2014) or goldfish (Wyzisk 2005). Contradictory results have been obtained in animals with regard to the perception of the Ebbinghaus illusion (or Titchener circles): In this display, a central circle surrounded by large circular inducers is perceived as smaller than an identical circle surrounded by small inducers (Aglioti et al. 1995; Choplin and Medin 1999; Coren and Enns 1993; Ebbinghaus 1902; de Grave et al. 2005; Girgus et al. 1972; Massaro and Anderson 1971; Weintraub 1979). It is one of the strongest and most robust geometric size illusions spontaneously reported by human observers (de Fockert et al. 2007), apparent already in pre-verbal infants (Yamazaki et al. 2010; but see Happé 1996; Kaldy and Kovacs 2003; Phillips et al. 2004). The Ebbinghaus illusion has initially been studied in baboons (Parron and Fagot 2007) and pigeons (Nakamura et al. 2008), revealing a different perception of the Titchener circles than that in the human species (see also Murayama et al. 2012 for a preliminary study on a single bottlenose dolphin). While baboons were not affected by the illusory display, estimating the size of the central target accurately, pigeons responded to the Ebbinghaus illusion in an opposite way with respect to humans, overestimating the size of a target surrounded by large inducers and underestimating that of a target encircled by small inducers. This suggested an assimilation effect in the study of Nakamura and colleagues, with the size of the central circle assimilated to that of the inducers. These results led to theories that the perceptual mechanisms at the basis of our perception of the Ebbinghaus illusion were evolved in primates (Parron and Fagot 2007). In particular, the neural substrate determining the perception of the Ebbinghaus illusion is thought to be located in the human neocortex, where the two independent neural pathways, the dorsal and the ventral stream, are responsible for visual awareness and for action control (Goodale and Milner 1992). This could explain why the Ebbinghaus illusion is reduced when tested through motor tasks (Aglioti et al. 1995; Danckert et al. 2002). In non-mammalian species, the neural circuits composing the visual pathways are differently organized than that in mammals (e.g., birds, Shimizu 2004; Shimizu and Bowers 1999; but see Reiner et al. 2005). These differences have been claimed to be the cause of the different processing of the Ebbinghaus illusory configuration in mammalian and non-mammalian species (Nakamura et al. 2008; see Rosa Salva et al. 2013 for a discussion focused on avian species).

In humans, the Ebbinghaus illusion is believed to reflect the action of perceptual grouping mechanisms, i.e., the fact that human subjects perceive objects in relation to the surrounding context. This is supported by the negative correlation of the target-inducers' distance with the magnitude of the illusion (Roberts et al. 2005). Moreover, erasing the distant portions of larger inducers reverses the effect of the illusion (Oyama 1960; Weintraub 1979). This indicates that when humans perceive only the immediate surroundings of the target, they also perceive the Ebbinghaus illusion as an assimilation illusion. It has thus been proposed that human's globally oriented perceptual tendencies (Navon 1977) determine their perception of the Ebbinghaus illusion as a "contrast illusion," in which the size of the central target is contrasted with that of the inducers. Conversely, species characterized by a more locally oriented perceptual style would be immune to the illusion or perceive it in the opposite direction, assimilating the size of the central circle to that of the inducers, since they would focus only on the target and the parts of the inducers that are located in its close proximity (Nakamura et al. 2008, 2014). Previous studies indicate that some nonhuman species, including pigeons and baboons, could have a more locally oriented perception than humans (Cavoto

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