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ORIGINAL PAPER

Perception of the Ebbinghaus illusion in four-day-old domestic chicks (*Gallus gallus*)

O. Rosa Salva · R. Rugani · A. Cavazzana ·
L. Regolin · G. Vallortigara

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Abstract In the Ebbinghaus size illusion, a central circle surrounded by small circles (inducers) appears bigger than an identical one surrounded by large inducers. Previous studies have failed to demonstrate sensitivity to this illusion in pigeons and baboons, leading to the conclusion that avian species (possibly also nonhuman primates) might lack the neural substrate necessary to perceive the Ebbinghaus illusion in a human-like fashion. Such a substrate may have been only recently evolved in the primate lineage. Here, we show that this illusion is perceived by 4-day-old domestic chicks. During rearing, chicks learnt, according to an observational-learning paradigm, to find food in proximity either of a big or of a small circle. Subjects were then tested with Ebbinghaus stimuli: two identical circles, one surrounded by larger and the other by smaller inducers. The percentage of approaches to the perceptually bigger target in animals reinforced on the bigger circle (and vice versa for the other group) was computed. Over four experiments, we demonstrated that chicks are reliably affected by the illusory display. Subjects reinforced on the small target choose the configuration with big inducers, in which the central target appears perceptually smaller; the opposite is true for subjects reinforced on the big target. This result has important implications for the evolutionary history of the neural substrate involved in the perception of the Ebbinghaus illusion.

O. Rosa Salva (✉) · G. Vallortigara
Center for Mind/Brain Sciences, University of Trento,
Corso Bettini 31, 38068 Rovereto (TN), Italy
e-mail: orsola.rosasalva@unitn.it

R. Rugani · A. Cavazzana · L. Regolin
Department of General Psychology, University of Padova,
via Venezia 8, 35131 Padua, Italy

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Introduction

Accurate representations of the external world are necessary for adaptation to the environment, enabling an organism to identify food, to flee from predators and to avoid environmental dangers. Nevertheless, under some circumstances, a discrepancy can occur between reality and perception. In vision science, visual illusions have been used to gather an insight into the functioning of the visual systems and how it integrates the low-level aspects of the stimulation into a unified representation (Mascalzoni and Regolin 2011; Vallortigara et al. 2010; Wade 2005, 2010). By comparing the susceptibility to visual illusions in different animal species, we can gain information on the evolution of visual systems and the principles of perceptual organization. In recent years, geometric illusions (in which properties of a target stimulus, such as length, width, or diameter, are distorted by the surrounding context) have been increasingly used as a tool to compare the perceptual processes of human and nonhuman animals. Results suggested that a variety of nonhuman species experience size illusions much as humans do. Just to mention some examples, among mammals, the susceptibility to the Müller-Lyer illusion has been shown in capuchins and in rhesus monkeys (Suganuma et al. 2007; Tudusciuc and Nieder 2010), while the Ponzo illusion or the corridor illusion is perceived by horses (Timney and Keil 1996), monkeys (Barbet and Fagot 2002; Bayne and Davis 1983; see also Fujita 1996), and chimpanzees (Fujita 1997). In avian species, domestic chickens (Winslow 1933), ring doves (Warden and Baar 1929), pigeons (Fujita 2006; Fujita et al.

1991, 1993; Nakamura et al. 2006, 2009), and gray parrots (Pepperberg et al. 2008) are sensitive to various geometrical illusions (such as the Ponzo, the Müller-Lyer, and the horizontal–vertical illusion).

One of the strongest and most robust geometric size illusions is created by the Titchener circles. In this display, known also as the Ebbinghaus illusion, 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). Evidence available in the human literature indicates that this illusion reflects the action of grouping mechanisms (e.g., the entity of the illusion is modulated by the target-inducers distance, Roberts et al. 2005). Such grouping mechanisms seem to be spontaneously recruited by human subjects, as implied by the fact that the illusion is present in 5-month-old babies (Yamazaki et al. 2010) and emerges without adult participants being explicitly instructed to process the inducers (e.g., de Fockert et al. 2007). The Ebbinghaus illusion has been studied in adult baboons (Parron and Fagot 2007) and pigeons (Nakamura et al. 2008); neither species showed any evidence of perceiving this kind of illusion in the same way as humans. Baboons accurately judged the size of the central target, without being influenced by the surrounding inducers. Pigeons' size estimations were influenced by the inducers, but 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 (Nakamura et al. 2008). This has been interpreted as evidence of an assimilation effect: the size of the central circle is perceived as similar to that of the inducers. Based on these results, it has been theorized that the visual processes supporting the Ebbinghaus illusion were recently evolved within the primate lineage (Parron and Fagot 2007). The opposite effect of the Ebbinghaus illusion in pigeons and in humans seemed to imply a remarkable discrepancy in the perceptual mechanisms of the two species, which has been ascribed (e.g., by Nakamura et al. 2008) to anatomical differences between the visual pathways of birds and mammals (Shimizu 2004; Shimizu and Bowers 1999). In humans, the Ebbinghaus illusion is less pronounced in motor tasks than in purely perceptual tasks (Aglioti et al. 1995), suggesting that its neural substrate is localized in the neocortex, in which two independent pathways (the ventral and the dorsal streams, going from the primary visual cortex to the inferotemporal and the posterior parietal region, respectively) are dedicated to visual awareness and to subconscious control of actions (Goodale and Milner 1992). However, in contrast to the interpretation proposed by Nakamura et al. (2008), homologies between the avian *pallium* and the mammalian neocortex have been increasingly recognized in recent years (Jarvis et al. 2005; Reiner 2005; Reiner et al. 2005). Moreover, an argumentation based on a single avian species should be treated with caution, as revealed also by the results of the present study.

An intriguing possibility is that the opposite results obtained in humans and nonhuman animals would reflect a difference in the perceptual style prevalently adopted by each species under the testing circumstances employed by previous studies, in line with what is observed for different human populations (e.g., de Fockert et al. 2007; see also Happé 1996 for similar evidence in autistic individuals and Vallortigara et al. 2008). In comparison with humans (Navon 1977; but see Kimchi 1992), baboons and pigeons could have a more locally oriented perceptual style (Cavoto and Cook 2001; Cerella 1980; Deruelle and Fagot 1998; Fagot and Deruelle 1997; Ushitani et al. 2001; Vallortigara 2004, 2006; see also Watanabe 2001; Watanabe et al. 2011; but see Cook 1992; Cook et al. 1996; Wasserman et al. 1993; Fremouw et al. 1998). This could have favored attentional focus on the target circles, reducing or reversing the influence of the inducers. In order to perceive the Ebbinghaus illusion as a contrast illusion, subjects must simultaneously process several non-adjacent elements. The contrast effect determined by the Ebbinghaus illusion is related to the global aspect of the configuration. Erasing the most distant portions of the large inducing circles reverses the direction of the illusion, producing, in humans, an effect similar to that reported for pigeons (Oyama 1960; Weintraub 1979) (assimilation illusions are more likely to be originated by perceptual processing in the vicinity of the target and, remarkably, are more pronounced in pigeons than in humans, see Nakamura et al. 2008). Moreover, the learning paradigms, based on operant conditioning, employed with pigeons and baboons, could have enhanced any propensity to pay attention to local details of the configuration. In the study of Nakamura et al. (2008), pigeons were required to peck at the target circle before emitting the choice response, which could have favored focused attention on the target. Also, the final response that pigeons emitted consisted in pecking either of two response keys. Pecking is the main manipulative behavior of birds. Interestingly, in humans, studies employing manipulative responses (grasping) revealed reduction/absence of the illusion (Aglioti et al. 1995; Danckert et al. 2002).

The present study adopts a different approach from previous research and tests the sensitivity of few-day-old domestic chicks to the Ebbinghaus illusion. This animal model is considered an ideal choice for investigating the structuring of the visual space and its ontogenetic development in nonhuman animals. Domestic chickens are strongly dependent on visual input for orienting their behavior, making vision their primary sensory modality (Schmid and Wildsoet 1998; Vallortigara 2004, 2006). Moreover, chicks can be tested at an early age, in conditions of controlled visual experience and according to ecologically valid paradigms based on learning by exposure (Vallortigara 2012). In previous studies, newborn chicks have been found to be sensitive to a wide range of visual illusions, providing an interesting case of similarity with the functioning of human visual system. Chicks experience phenomena such as subjective contours (Zanforlin 1981), amodal completion (Lea et al. 1996; Regolin and Vallortigara 1995; Rugani et al. 2008), stereokinetic illusions (Clara et al. 2006), and biological motion (Regolin et al. 2000; Vallortigara et al. 2005; Vallortigara and Regolin 2006), being also able to recognize the configuration of features characterizing appropriate social companions (Rosa Salva et al. 2010, 2011, 2012), to categorize objects on the basis of perceptual features (Fontanari et al. 2011), to identify the number of a collection of objects (Rugani et al. 2010a, b), and to recognize physically plausible 3D objects (Regolin et al. 2011), which indicates that this animal model could be more relatively prone to spontaneously process global configurations, with respect to other animal species (for example, amodal completion has been quite difficult to prove in pigeons, see Fujita 2001). Moreover, chicks can be taught simple discriminations by means of learning by exposure (Mascalzoni et al. 2012), without resorting to shaping procedures that could lead animals to modify their spontaneous perceptual style.

Experiment 1

To study the effect of the Ebbinghaus illusion, we established the behavioral response of selecting a target circle according to its size, using to an observational-learning paradigm. This procedure consists in creating a contingency between food reinforcement and one of two stimuli present in the subjects' rearing environment. Half of the chicks could find food only by the big circle and the other half by the small circle. Only subjects that in a pretest phase showed the expected tendency to preferentially approach the circle of the reinforced size were then tested with Ebbinghaus stimuli.

Materials and methods

Subjects and rearing conditions

Subjects were 24 female "Hybro" (a local variety derived from the White Leghorn breed) domestic chicks (*Gallus gallus*), obtained from a local commercial hatchery (Agricola Berica, Montegalda, Vicenza, Italy) when they were only few hours old. On arrival at the laboratory, chicks were housed singly in standard metal home cages (28 cm wide × 32 cm long × 40 cm high) at controlled temperature (28–31 °C), with water available ad libitum in transparent glass jars (5 × 5 cm) placed in the middle of the home cage. The cages were constantly lit by fluorescent lamps (36 W), located 45 cm above the floor of each cage. According to an observational-learning paradigm, during the first four days of life, chicks were reared in the presence of four white plastic screens (10 × 14 cm), on the center of two of which there was a small orange target circle (0.5 cm of diameter), whereas on the other two, there was a larger orange target circle (0.9 cm) (the screens were placed one at each corner of the rectangular home cage). Based on this procedure, chicks could learn to recognize the reinforced screen either by memorizing the absolute size of the two target circles, or by learning to approach the bigger or the smaller circle (i.e., learning the discrimination in relative terms). The aim of the present study was not to determine the learning strategy adopted. However, it is likely that chicks learnt the discrimination in relative terms, since this might be the less demanding strategy in this context. All four screens presented, 2.5 cm above the orange target circle, an identical series of gray circles, in alternation, four big and six small (see Fig. 1a). This series of gray circles was irrelevant for discriminating between screens (being identical for all screens) and was used to accustom the animals to the presence of the gray circles that, in the following test phase, would constitute the inducers of the Ebbinghaus illusory configurations. Moreover, the series of gray circles also provided a visual reference point for judging the dimension of the orange target presented in each screen. For the Big-Target group ($N = 11$), food was available only behind the screens presenting the big orange circle, whereas for the Small-Target group ($N = 13$), food was available behind the screens presenting the small orange circle (an empty food dish was present behind the non-reinforced screens). Thus, for half of the chicks, the big circle was the positive target stimulus associated with food reinforcement (Big-Target group) and vice versa for the other half. The position of the screens in the rearing cage was constantly swapped during the day in order to avoid positional learning.

Apparatus

Testing took place in an experimental room whose temperature was 28 °C. The room was kept dark, except for the light coming from a 40-W lamp placed approximately 80 cm above the floor of the apparatus. This (Fig. 1b) consisted of a circular arena (95 cm diameter, 30 cm outer wall height) with the floor uniformly lined with white plastic sheets. At the beginning of each trial, a subject was

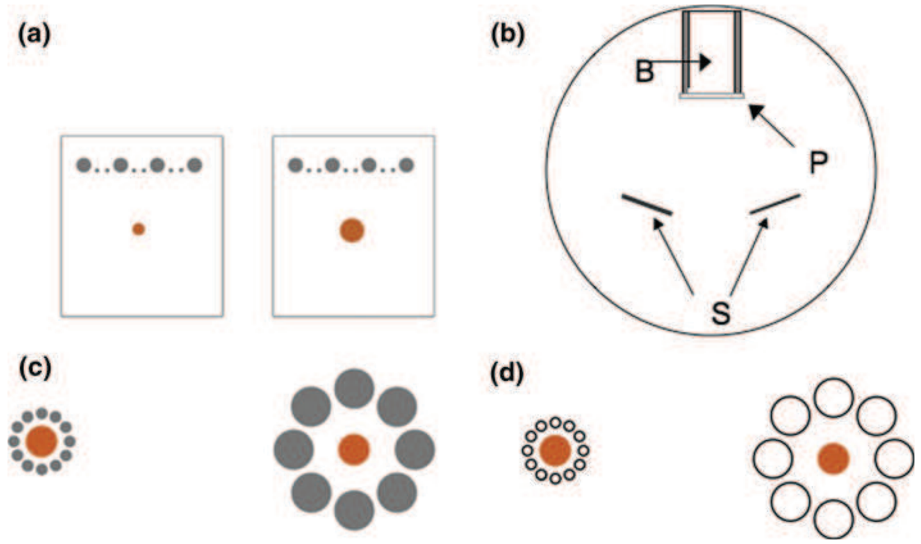

Fig. 1 **a** Reproduction of the stimuli used during the observational learning phase of Experiment 1; the *small* and the *big orange* target are represented on the *left* and on the *right* screen, respectively; the series or reinforcement-irrelevant gray inducers is depicted above the target. **b** View from above of the test apparatus employed in pretest and test phases, with the letter *B* indicating the starting box, *P* the translucent partition confining the chick inside the starting box, and *S* the position of the two screens. **c** Reproduction of the Ebbinghaus illusory configurations used as stimuli during the test phase of Experiment 1. *Left*: configuration with small inducers, which was expected to be chosen by the Big-Target group if the illusion was perceived; *right*: configuration with big inducers, which was expected to be chosen by group ST. **d** Reproduction of the Ebbinghaus illusory configurations employed during the test phase in Experiment 3, in which the inducers consist of empty circumferences

placed inside the apparatus, adjacent to the outer wall and facing two test screens, which were at a distance of 40 cm from the chick's position in the starting box (35 cm away from the closest side of the box, see Regolin et al. 2005a, b; Rugani et al. 2009, 2011) and at 20 cm from each other.

Procedure and test stimuli

On day 3 of life, chicks underwent the pretest. The test with illusory configurations took place on the following day. The same experimental procedure was employed for both phases. In their starting position within the arena, chicks faced two identical screens (both occluding a food dish) that could be distinguished only by the stimulus printed on them. When the chick looked behind a screen, a preference was scored and the trial ended. A test phase consisted of six trials. The left–right position of the two screens was swapped between the trials according to a semi-random sequence (the only constraint was that the same stimulus was never presented in the same position more than twice consecutively). In the pretest phase, chicks faced two screens depicting identical stimuli to those used at training. Only chicks that demonstrated a preference for the reinforced stimulus (i.e., that chose the correct screen on at least four out of six trials) during the pretest were then tested with the Ebbinghaus illusory stimuli (Fig. 1c). The stimuli used in the present paper resemble the configurations successfully employed with infants by Yamazaki et al. (2010) and comprise 12 small and 8 big inducers (3 and 10 mm). The two configurations had an overall diameter of about 16.5 and 39 mm, respectively (please note that the central target appears bigger in the configuration of smaller overall size). The orange target circle in the illusory configurations was 7 mm in diameter; the circle of small and big inducers was, respectively, 1.5 and 5.5 mm away from the central target.

Of the originally trained subjects, 27 did not met the learning criterion set in the pretest phase and did not accessed to the test phase (these are not included in the final sample of 24 chicks). The presence of a relatively high number of chicks that did not reach the learning criterion is likely to be due to the spontaneous nature of the incidental learning paradigm employed, which might have determined a reduced motivation to learn the discrimination proposed (due to the reduced cost of emitting a "wrong" choice during the incidental learning phase).

Our hypothesis for the test phase was that, if chicks perceive the illusion, those reinforced on the small target circle (Small-Target group) should preferentially approach the Ebbinghaus configuration with bigger inducers, in which the central circle is perceived as smaller by humans. Conversely, chicks reinforced on the bigger target circle (Big-Target group) should approach the screen representing the Ebbinghaus configuration with smaller inducers.

Results and discussion

During the test phase with illusory configurations, the behavior of Small-Target chicks appeared to be markedly different from that of Big-Target chicks. A Mann–Whitney U on the percentage of choices for the perceptually bigger stimulus revealed a marginally nonsignificant difference between the two groups ($U = 39.50$; $P = 0.063$). However, a Wilcoxon test revealed that the Small-Target group chose the perceptually bigger stimulus significantly below chance level (T^{+}=73.00; $P = 0.002$; mean = 26 %; s.e.m. = 6 %), that is, they preferentially approached the perceptually smaller target in line with our expectations. On the contrary, the Big-Target group was at chance level (T^{+}=18.00; $P > 0.05$; mean = 50 %; s.e.m. = 10 %) (Fig. 2). In order to exclude the possibility that only the Small-Target chicks expressed a significant preference at test, because of a different level of initial learning achieved by the two groups during the rearing phase, we compared the percentage of correct choices performed by the two groups in the pretest phase, without revealing any significant difference ($U = 68.00$; $P = 0.865$).

Thus, on the one hand, subjects belonging to the Small-Target group preferentially chose the configuration with bigger inducers, in which the central target appears perceptually smaller. In this group, the performance at test seems thus to reflect the illusion effect. On the other hand, the behavior of chicks belonging to Big-Target group did not conform to our predictions. We expected Big-Target chicks to preferentially choose the configuration with small inducers, whereas their performance was actually at chance level.

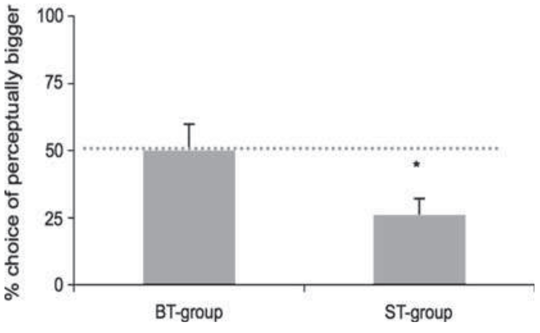

Fig. 2 Results of Experiment 1; the percentage of choice for the perceptually bigger stimulus (i.e., the configuration with smaller inducers) in the test phase with illusory configurations is reported on the *Y*-axis. The performance of the Big-Target group (reinforced on the big target) is represented on the *left column* and the performance of the Small-Target group (reinforced on the small target) is represented on the *right column* (means and standard errors are reported). The *dotted line* represents chance level and *asterisks* represent significant departures from chance level ($P < 0.05$). If the illusion is perceived, the Big-Target group is expected to choose the perceptually bigger stimulus above chance level and the Small-Target group is expected to chose the same configuration below chance level

Obviously, on the hypothesis that chicks' performance was determined only by the reinforcement contingencies and by the effect of the Ebbinghaus illusion, we expected both groups to show a preference for the configuration in which the perceived dimension of the target circle better corresponded to that of the previously reinforced stimulus. Thus, we must conclude that other unexpected factors are influencing subjects' behavior, one of which seems to be an idiosyncratic preference for the configuration with bigger inducers. However, based on our data, we cannot conclude that the only factor influencing chicks' behavior is such an idiosyncratic preference. If that was the case, chicks of both groups should show an identical preference in favor of the configuration with bigger inducers, and the Big-Target group's performance should be below chance level, rather than at chance level, because the hypothetical preference for the configuration with bigger inducers would drive them to choose the perceptually smaller stimulus. On the contrary, our results can be easily explained hypothesizing that the animals were simultaneously influenced by all the factors mentioned above: the reinforcement contingencies experienced at training, the illusory effect of the Ebbinghaus configurations, and an idiosyncratic preference for the stimulus with bigger inducers. According to this hypothesis, in the Big-Target group, the effect of the illusion would be masked by the spontaneous preference for the configuration with bigger inducers, resulting in the absence of preference actually observed. In the Big-Target group, in fact, a hypothetical preference for the configuration with bigger inducers would counterbalance the tendency to choose the target circle appearing perceptually bigger. Three further experiments were aimed at testing this interpretation.

Experiment 2

Results obtained in Experiment 1 suggest that chicks might perceive the Ebbinghaus illusion, even though the effect of the illusion was probably masked, in the Big-Target group, by a spontaneous idiosyncratic preference for the configuration with bigger inducers. The purpose of Experiment 2 was to test for the presence of such a spontaneous preference for approaching the configuration containing bigger inducers.

Materials and methods

Subjects and rearing conditions

Subjects were a new group of 12 female chicks. Rearing conditions were identical to those described for the first experiment. The only difference was that reinforcement was available behind both types of screens (depicting the big and the small orange circle), since we wanted to investigate the presence of a spontaneous preference for the configuration with bigger inducers, independent of reinforcement.

Test stimuli, apparatus, and procedure

During the test phase (which employed the same procedure and apparatus described for the first experiment), chicks were tested directly with the stimuli representing the Ebbinghaus illusion (without undergoing any pretest phase), in order to verify whether they presented a preference to approach the configuration with bigger inducers, as suggested by the results of Experiment 1.

Results and discussion

Results showed that chicks presented a clear tendency to choose the Ebbinghaus configuration with the bigger inducers ($T^{+} = 78.00$; $P < 0.000$; mean = 85 %; s.e.m. = 4 %, Fig. 3 left). This confirms our interpretation of the results obtained in Experiment 1, in which we hypothesized that in Big-Target group, the effect of the illusion was being masked by a spontaneous preference for the stimulus with bigger inducers. Such an idiosyncratic preference could be caused by the fact that subjects are attracted by the big gray inducers, possibly because of their perceptual salience. The investigation of the precise factors underlying chicks' spontaneous preference for the configuration with bigger inducers is beyond the aim of the present study. The following experiment was thus devoted to the development of a pair of stimuli that allowed us to test the perception of the Ebbinghaus illusion without incurring in such an idiosyncratic preference.

Experiment 3

In Experiment 3, we tested a different pair of illusory configurations in which the perceptual salience of the inducers was reduced, in order to prevent the emergence of a bias to approach the configuration with bigger inducers (as seen in Experiment 2). For this purpose, we employed a variant of the Ebbinghaus stimuli that have been described in the literature, in which the inducers were made up by empty circumferences instead of full color circles (Fig. 1d). As in Experiment 2, during the rearing phase, food was always available both behind screens depicting the big orange target circle and behind screens depicting the small orange target circle, since we wanted to study the presence of spontaneous preferences regardless of reinforcement contingencies. The aim of the present experiment was thus to validate this pair of stimuli by investigating whether chicks have an idiosyncratic preference for either of the two illusory configurations. If no such a preference was observed, the same stimuli would be employed to directly test chicks' susceptibility to the Ebbinghaus illusion.

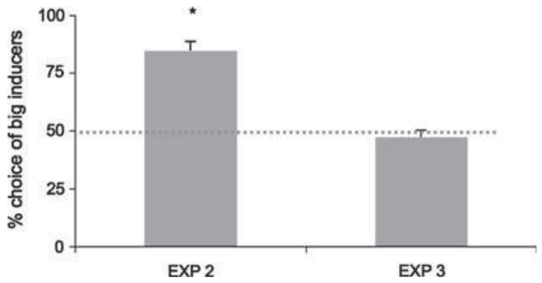

Fig. 3 Results of Experiments 2 (*left*) and 3 (*right*); the percentage of choice for the configuration with bigger inducers is reported on the *Y*-axis. The *dotted line* represents chance level and *asterisks* represent significant departures from chance level ($P < 0.05$)

Materials and methods

Subjects and rearing conditions

A new group of 12 female domestic chicks was tested. Animals were reared in the same conditions as described in Experiment 2.

Test stimuli, apparatus, and procedure

The stimuli used in the present experiment were identical to Experiments 1 and 2, with the sole exception that the inducers consisted of empty circumferences marked by a gray outline (0.5 mm thick) (see Fig. 1d). The procedure was the same as in Experiment 2 (the experimental apparatus was identical in all experiments).

Results and discussion

The percentage of choices for the configuration with bigger inducers was not significantly different from chance level ($T^{+} = 1.00$; $P > 0.05$; mean = 47 %; s.e.m. = 3 %, Fig. 3 right). This result shows that subjects do not show any spontaneous preference for choosing one of the two configurations. Therefore, it seems that chicks' spontaneous preference in Experiment 2 was due to the appearance of the inducers, since after reducing their perceptual salience, the bias to approach the configuration with bigger inducers disappeared.

Experiment 4

Since the stimuli used in Experiment 3 did not elicit any idiosyncratic preference in chicks, in Experiment 4, we employed these two configurations to test chicks' susceptibility to the Ebbinghaus illusion, using the same procedure as Experiment 1 (i.e., creating a contingency between food reinforcement and either the small or the big orange target circle present in subjects' rearing environment, see below).

Materials and methods

Subjects and rearing conditions

A new group of 16 female domestic chicks was used: 8 were randomly assigned to the Big-Target group and 8 to the Small-Target group (22 further subjects did not reach the learning criterion in phase 1 and were discarded from the experiment).

Stimuli, apparatus and procedure

In the present experiment, we used the same stimuli and procedures as Experiment 1, with the exception that we employed the test configurations validated in Experiment 3. During the incidental learning and pretest phase, chicks were exposed to the same configurations as in Experiment 1, with the series of aligned full gray inducers, since a pilot experiment revealed that this may enhance discrimination performance during this preliminary phase.

Results and discussion

The percentage of choices for the perceptually bigger stimulus was significantly different between the two groups ($U = 0.00$; $P < 0.001$). As predicted, the Big-Target chicks choose the perceptually bigger stimulus significantly above chance ($T^+ = 36.00$; $P = 0.003$; mean = 71 %; s.e.m. = 3 %) and the Small-Target chicks choose the same stimulus significantly below chance ($T^+ = 21.00$; $P = 0.015$; mean = 35 %; s.e.m. = 4 %) (Fig. 4).

That is to say that chicks reinforced on a bigger target preferentially approached the configuration with small inducers, in which the central target appears perceptually bigger, whereas chicks reinforced on a smaller target approached the configuration in which the central target appears perceptually smaller. Both experimental groups (Big-Target and Small-Target) were thus shown to be sensitive to the Ebbinghaus illusion when they were tested with the stimuli validated in Experiment 3. In this condition, in fact, both groups behaved on the basis of the reinforcement contingencies experienced at training and of the illusory effect induced by the Ebbinghaus configurations. To the best of our knowledge, the present experiment provides the first demonstration of susceptibility to the Ebbinghaus illusion in young animals reared under controlled visual experience.

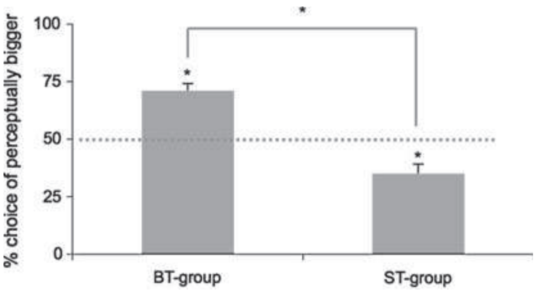

Fig. 4 Results of Experiment 4; the percentage of choice for the perceptually bigger stimulus in the test phase with illusory configurations is reported on the *Y*-axis. The performance of the Big- and Small-Target group is represented on the *left* and *right* column, respectively (means and standard errors are reported). The *dotted line* represents chance level and *asterisks* represent significant departures from chance level ($P < 0.05$)

General discussion

Here, we demonstrated that few-day-old domestic chicks perceive the Ebbinghaus illusion as a contrast illusion: like human beings, chicks treated the central target circle surrounded by big inducers as smaller than an identical circle flankered by small inducers (Exp. 4). This conflicts with previous evidence reported in the literature for other animal species (baboons, Parron and Fagot 2007; and pigeons, Nakamura et al. 2008). The result sheds new light on the origin of the perceptual mechanisms underlying the susceptibility to the Ebbinghaus illusion. The difficulty that pigeons and baboons have in perceiving the Ebbinghaus illusion as a contrast illusion has been ascribed to the recent evolution in primates of the implicated perceptual and neural mechanisms (Parron and Fagot 2007; Nakamura et al. 2008). The results obtained here, however, are in contrast to this explanation, indicating that in principle, the avian visual system can produce the perception of this illusion. Why did previous studies fail to reveal sensitivity to the Ebbinghaus illusion in baboons and pigeons? Based on the present evidence, it is only possible to propose speculative hypotheses, since our study differs from those of Nakamura et al. (2008) and Parron and Fagot (2007) in many respects, such as the species tested, the age of the animals, the illusory configurations, and the procedures employed.

An important consideration, however, is that different species might be characterized by dissimilar perceptual styles. Of potential relevance for the perception of the Ebbinghaus illusion (Roberts et al. 2005), human adults are generally considered to have a globally oriented perceptual style (Navon 1977), even though a variety of factors can influence the actual type of processing adopted, including attentional factors and stimulus properties (see Kimchi 1992 for a review). In some animals, proximity grouping mechanisms might not be as efficient recruited as for humans (Deruelle and Fagot 1998; Fagot and Deruelle 1997; Spinozzi et al. 2003). It would be an oversimplification to present a clear dichotomy between humans as purely global processers and other species as merely local processers. For example, attentional requirements can modulate the perceptual style of both humans (Kimchi 1992) and pigeons, which can flexibly shift between prioritization of the global or of the local level (Fremouw et al. 1998). Moreover, similarities between the perceptual style of pigeons and humans have been observed with hierarchical texture stimuli (Cook 1992; Cook et al. 1996), showing that under some circumstances, both species integrate global information. Also, a recent study revealed that a species of fish (*Xenotoca eiseni*) may present a globally oriented perceptual style in the perception of hierarchical Navon stimuli (Truppa et al. 2010). Despite that, data on nonhuman species, including baboons and pigeons, have often failed to reveal a global precedence in the perception of hierarchical stimuli, or have even revealed a local precedence (Cavoto and Cook 2001; Deruelle and Fagot 1998; Fagot and Deruelle 1997; see also Cerella 1980; Ushitani et al. 2001; Watanabe 2001; Watanabe et al. 2011 and Vallortigara 2004 for a theoretical discussion). Nakamura et al. (2008) suggested that ecological factors might play a role in determining pigeons' altered perception of the Ebbinghaus illusion, hypothesizing that a somehow more locally oriented perceptual style might be easier to implement in the light brain required for flight (see Nakamura et al. 2008). Pigeons also feed on small grains, which could favor attention to local features and fine details of the substrate. However, it should be noted that the feeding habits of domestic chickens, which are a good candidate species for having a relatively globally oriented perceptual style (Lea et al. 1996; Regolin and Vallortigara 1995; Regolin et al. 2000, 2011; Rosa Salva et al. 2010, 2011; Vallortigara et al. 2005), are not so different from those of pigeons. Moreover, domestic chickens closely descend from the red junglefowl, a species capable of flying, at least over short distances. Another, related, explanation for the difficulty of demonstrating the perception of the Ebbinghaus illusion in animal species susceptible to other visual illusion (pigeons, Nakamura et al. 2008; baboons, Parron and Fagot 2007) has been proposed by Parron and Fagot (2007). These authors pointed out that several visual illusions demonstrated in nonhuman animals are based on figures made of spatially connected elements (e.g., the horizontal–vertical illusion, Dominguez 1954; Harris 1968; the corridor illusion, Barbet and Fagot 2002; stereokinetic illusions, Clara et al. 2006), a property that can favor attention to the illusory figures as wholes. Thus, according to Parron and Fagot (2007), the Ebbinghaus illusion would be particularly difficult to perceive for some animal species, since it is composed of disconnected elements. Future studies could further investigate this issue by investigating the perception of geometrical size illusions involving spatially disconnected elements (e.g., the Delboeuf illusion, Nicolas 1995) in different species, including also the splitfin fish *Xenotoca eiseni* (Truppa et al. 2010).

The evidence discussed up to the present moment could suggest a scenario of evolutionary analogy, according to which some phylogenetically distant species (humans and domestic chicks) independently evolved the perceptual mechanisms subtending the susceptibility to the Ebbinghaus illusion, whereas other species (baboons and pigeons, phylogenetically related to the above mentioned ones) did not. This scenario is supported also by considerations about the neural substrate of the Ebbighaus illusion, which has been hypothesized to be influenced by contour interaction implemented by lateral inhibition at the neural level (e.g., Coren et al. 1988; Weintraub and Schneck 1986; Ganz 1966). Recent studies have provided evidence that, in humans, the perception of the Ebbinghaus illusion might be mediated by the primary visual cortex (Murray et al. 2006; Schwarzkopf et al. 2011; Song et al. 2011), which is retinotopically organized (Holmes 1918, 1944; Horton and Hoyt 1991). In birds, most visual discriminations (including size discriminations) are carried out by the collothalamic visual pathway (functionally analogous to the mammalian lemnothalamic pathway, Shimizu and Bowers 1999; Shimizu et al. 2010), projecting from the retina to the optic tectum, nucleus rotundus, and entopallium (Bessette and Hodos 1989; Cohen 1967; Hodos and Bonbright 1974; Hodos and Karten 1966, 1970, 1974; Hodos et al. 1984, 1986, 1988; Kertzman and Hodos 1988; Macko and Hodos 1984). In this pathway, retinotopic organization is absent from the nucleus rotundus onward (Fredes et al. 2010; Benowitz and Karten 1976; Hellmann and Güntürkün 1999; Wang et al. 1993), raising the intriguing possibility that in birds, the neural processing that causes the illusion may be completed in the midbrain.

We would like, however, to add a note of caution, since the training paradigms employed for pigeons (Nakamura et al. 2008) and baboons (Parron and Fagot 2007) were based on operant conditioning procedures and involved pecking responses for pigeons, whereas the chicks in the present experiment spontaneously learnt the association between food and their target stimulus in an observational-learning paradigm (Mascalzoni et al. 2012), making it difficult to directly compare the behavior of different species. Notably, the study of Truppa and collaborators (2010) in fish employed a paradigm based on learning associations between stimuli and fitness relevant items (escape routes) during free explorations of the environment. This evidence converges to suggest that procedures allowing the animal to spontaneously learn relevant environmental contingencies might be particularly appropriate to investigate phenomena associated with a high degree of perceptual grouping. This is also consistent with evidence that the perceptual style adopted can be influenced by attentional factors, as well as by stimulus size and eccentricity (e.g., in pigeons Fremouw et al. 1998; see Kimchi 1992 for a review on human data). Thus, different procedures may influence the viewing strategy adopted. In the present study, chicks were unconstrained in their behavior prior to the emission of the relevant response, being able to inspect the stimuli at various distances. In the study of Nakamura et al. (2008), the use of an operant chamber and the requirement of the emission of a pecking response on the stimuli might have promoted a frequent use of the frontal visual field (Goodale 1983). Notably, the use of the central versus lateral visual field has been associated with focalized versus integrated processing (e.g., Lamb and Robertson 1988; pigeons' central and lateral visual field could be, respectively, specialized for foraging on the ground and for predator detection/flight control, Goodale 1983; Martinoya et al. 1984). Also, slightly different stimuli might have contributed to the differences observed. The use, in the present study, of a variant of the illusion in which the small inducers are closer to the central target (similar to that used by Yamazaki et al. 2010) might have enhanced the illusory percept (Girgus et al. 1972; Duemmler et al. 2008), possibly also by promoting global processing of the configuration. In order to clarify the evolutionary origins of the mechanisms subtending to the susceptibility to the Ebbinghaus illusion, future studies should devise comparable procedures to be employed with different species and identical stimuli, allowing to discern the presence of homologies versus analogies in their perceptual adaptations. For instance, it would be interesting to compare the perception of the Ebbinghaus illusion in chickens and pigeons using tasks based either on pecking or on approach behavior; similarly, it would be informative to compare the two species when both are trained according to operant conditioning versus observational-learning paradigms and in conditions in which the viewing strategy adopted by the animals is similarly constrained/unconstrained.

Another intriguing aspect of this illusion, revealed by cross-cultural studies, is that in humans, it seems to be influenced by cultural factors (de Fockert et al. 2007; Doherty et al. 2008). This would suggest that the mechanisms determining the susceptibility to the Ebbinghaus illusion are not innately specified, being influenced by previous experience. Research on the ontogenetic development of the perception of this illusion has revealed partially contradictory results about whether the Ebbinghaus illusion is perceived similarly by adults and children (see Bondarko and Semenov 2004; Doherty et al. 2010; Duemmler et al. 2008; Hanisch et al. 2001; Kaldy and Kovacs 2003; Weintraub 1979; Zanuttini 1996). In contrast to the idea of a major role of enculturation in the development of this phenomenon, the illusion may already be perceived at 5–6 months of age (Yamazaki et al. 2010). Our results seem to support this view, since we demonstrated susceptibility to the Ebbinghaus illusion in few-day-old animals, whose visual experience had been strictly controlled. It would be interesting to verify whether the susceptibility to the Ebbinghaus illusion can be found in human newborns (known to have a global bias in the perception of hierarchical stimuli, Macchi Cassia et al. 2002).

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

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