Animal Behavior and Cognition

ABC 2025, 12(3):461-472
DOI: https://doi.org/10.26451/abc.12.03.07.2025

Perception of Ebbinghaus and Delboeuf Illusions in Bottlenose Dolphins (*Tursiops truncatus*)

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Citation – Hamano, T., Nakamura, J., Watanuki, N., Azuma, R., Okuma, Y., Yamamoto C., & Kashiwagi, N. (2025). Perception of Ebbinghaus and Delboeuf illusions in bottlenose dolphins (*Tursiops truncatus*). *Animal Behavior and Cognition, 12*(3), 461-472. https://doi.org/10.26451/abc.12.03.07.2025

Abstract – This study investigated the perceptions of Ebbinghaus and Delboeuf illusions in captive bottlenose dolphins (*Tursiops truncatus*), aimed at understanding their visual information processing. Four female bottlenose dolphins were used for the Ebbinghaus illusion, and three for the Delboeuf illusion tests. The dolphins varied in age and were housed in the Kagoshima City Aquarium, Japan. A series of trials were performed for two types of Ebbinghaus and Delboeuf illusion experiments. The results showed that a few dolphins perceived the Ebbinghaus and Delboeuf illusions in a manner similar to humans. In addition, essential optical cognitive histological mechanisms and evolutionary background were discussed by comparing this study's results with previous studies' results. One or more evolutionary ecological factors might affect optical information processing.

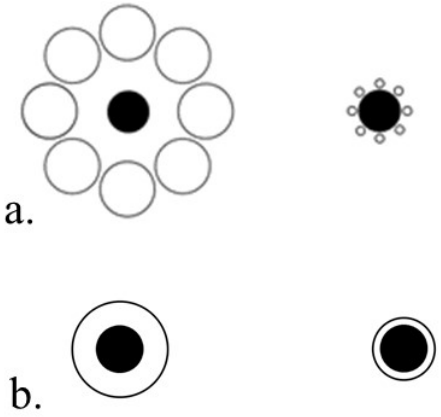
Keywords – Bottlenose dolphin, Delboeuf illusion, Ebbinghaus illusion, Neuroethology

The visual perception mechanism does not always perceive external optical information accurately and can interpret things differently from reality. For instance, we might perceive depth in a flat painting, fail to see something present, or misjudge an object's size because of interference, organization, fragmentation, or partial loss of visual information during processing. Visual masking and optical illusions are examples of how visual perception can misinterpret reality. The Ebbinghaus and Delboeuf illusions involve misjudging the size of two circles based on their surroundings (Figure 1). Humans (*Homo sapiens*) perceive a circle surrounded by smaller inducers as larger and one surrounded by larger inducers as smaller. Studies on such illusions in humans and non-human animals have led to scientific insights into brain functioning (Parron & Fagot, 2007; Schwarzkopf & Rees, 2013; Schwarzkopf et al., 2011). Studying the effects of illusions is crucial for understanding brain functions, especially in the visual cortex.

Specifically, the "global" process, which is the information processing of each element in aggregate as a whole set, and the "local" process, which is the information processing of each element in aggregate as an individual factor, are conceptual cores for understanding these illusionary phenomena (Han et al., 2002). In humans, the Ebbinghaus and Delboeuf illusions likely result from a global process, where both the inducer and central target are viewed together, creating a size contrast effect (Goto et al., 2007; Kelley & Kelley, 2014). The difference between global and local processing is influenced by brain structure (Han et al., 2002), which may result from natural selection. In other words, this difference may arise from whether

Figure 1

Example of (a) Ebbinghaus and (b) Delboeuf Illusions



the brain prioritizes local or global analysis of external information (Nayar et al., 2015). Naturally, animals do not rely solely on one process; instead, both are used separately or simultaneously, depending on the situation. The interspecies differences described below have been reported in several studies. These interspecies differences in illusion cognition are often explained by variations in visual processing, influenced by habitat adaptation, anatomy, and physiology (Bánszegi et al., 2021; Parron & Fagot, 2007). At least two hypotheses have been suggested: A single factor, i.e., the ecological strategy of searching for food, forms this difference. The other is that various factors, such as the ecological strategy of searching for food or searching for predators, convergent-evolutionary form global or local processing, respectively. It should not be forgotten that the possibility that different research methodological techniques lead to different research results is also pointed out (Kelley & Kelley, 2014). Accumulating information on interspecies differences and methodologically difference research is crucial for non-invasively studying visual processing and uncovering universal evolutionary mechanisms.

Research on perception of illusions in non-humans is gradually progressing. Studies have found that, unlike humans, the Ebbinghaus illusion produces the opposite effect (i.e., local precedence processing) in gray bamboo sharks (*Chiloscyllium griseum*) (Fuss & Schluessel, 2017), dogs (*Canis lupus familiaris*) (Byosiere et al., 2017), pigeons (*Columba livia*) (Nakamura et al., 2008), and bantams (*Gallus domesticus*) (Nakamura et al., 2014). For baboons (*Papio papio*) (Parron & Fagot, 2007) and starlings (*Sturnus vulgaris*) (Qadri & Cook, 2019), either no illusionary effect was identified, or the studies were inconclusive. Damselfish (*Chromis chromis*) (Fuss & Schluessel, 2017), chickens (*Gallus gallus*) (Rosa Salva et al., 2013), bottlenose dolphins (*Tursiops truncatus*) (Murayama et al., 2012), and redtail splitfins (*Xenotoca eiseni*) (Sovrano et al., 2015) have been reported to experience the same illusionary effect as humans (i.e., global precedence processing).

Compared with humans, the opposite illusionary effect in other species is thought to result from the size assimilation effect between the inducer and target, owing to local, rather than global, processing of both elements (Nakamura et al., 2008, 2014). Considering these differences in the view of evolutionary backgrounds, the effects vary even within animal groups such as primates or birds. Therefore, evolutionary ecological factors might contribute to these differences rather than mere genetic factors. For instance, when their ancestors searched for or hunted their foods, one requires attention to scattered objects or concentration focused on a single point in a group. In contrast, others require comprehensive insights into what exists in a group. Alternatively, one requires attention to a specific predator's shadow from broad habitat information. Moreover, the magnitude of illusions differs based on the society in which subjects are raised, indicating that acquired factors also influence the illusionary effect (Imada et al., 2013).

The Delboeuf illusion has the opposite effect on guppies (*Poecilia reticulata*) (Lucon-Xiccato et al., 2019) compared with humans. In the case of budgerigars (*Melopsittacus undulatus*) (Watanabe et al.,

2016), dogs (Byosiere et al., 2017), ring-tailed lemurs (*Lemur catta*) (Santacà et al., 2017), and red-footed tortoises (*Chelonoidis carbonaria*) (Santacà et al., 2019), the illusionary effect was either absent or inconclusive. In chimpanzees (*Pan troglodytes*) (Parrish & Beran, 2014), rhesus macaques (*Macaca mulatta*) (Parrish et al., 2015), capuchin monkeys (*Cebus apella*) (Parrish et al., 2015), cats (*Felis silvestris catus*) (Bánszegi et al., 2021), and bearded dragons (*Pogona vitticeps*) (Santacà et al., 2019), the effect was similar to that in humans. In humans, while the Delboeuf illusion operates through mechanisms similar to the Ebbinghaus illusion, one study found that it results from a combination of the contrast effect—from globally processing the inducer and target—and the assimilation effect (Agrillo et al., 2020). Several studies have explored the relationship between the Ebbinghaus and Delboeuf illusions (Byosiere et al., 2017; Fuss & Schluessel, 2017; Girgus et al., 1972). Regarding the Delboeuf illusion in non-human experiments, a method was sometimes used that could observe subjects' spontaneous food choices placed on a dish (Santacà et al., 2021). In experiments based on spontaneous food choices, there may be implicit assumptions, such as subjects always choosing the dish with more food or having conscious or unconscious motivations for their choices. While these assumptions can be correct, there are instances where non-optical factors influence subjects' choices or lack any specific reason, as observed in one experiment session; this suggests that food selectivity is not necessarily synonymous with visual cognition.

Cetaceans are an example of mammals that have adapted to a fully aquatic environment. Some experimental results have shown that cetaceans can clear their vision, to some extent, both underwater and above water (Rivamonte, 2009). Thus, cetacean vision has evolved for effective information gathering, especially in water. Behavioral and physiological studies show that cetaceans predominantly process visual information in their right visual field, suggesting that the brain's left hemisphere is more dominant in information processing (Delfour & Marten, 2006; Kilian et al., 2005). Despite cetaceans' unique visual processing abilities, challenges such as the limited number of housed cetaceans, emotional arguments about them, and technical problems such as staying dolphins out of water for extended hours hinder their use as experimental subjects, even for non-invasive studies. As a result, integrated *in vivo* experiments examining their central nervous system information processing are rare. Notably, there is only one case report on the Ebbinghaus illusion in a bottlenose dolphin (Murayama et al., 2012). However, data from a single case report is insufficient to draw complete conclusions (Feng et al., 2017). As noted, humans experience different illusions depending on their age and social backgrounds (Imada et al., 2013), and various methods can yield different results (Becker et al., 2021; Feng et al., 2017). While extensive data have been collected and analyzed in humans, only one case exists for dolphins (Murayama et al. 2012), which reported a similar illusionary tendency compared to humans when tested with the Ebbinghaus illusion. Further data accumulation and verification are required, as stated by the authors of that report. This study aimed to examine the Ebbinghaus and Delboeuf illusions in bottlenose dolphins by noninvasively examining their peculiar optic evolutionary neuroethology.

Methods

Ethics Statement

This research complied with Japanese law and was independently reviewed by the Kagoshima Aquarium Research Ethics Review Committee. We also complied with the World Zoo and Aquarium Animal Welfare Strategies, both in running this study and in daily practice.

Subjects and Housing

Four female bottlenose dolphins, primarily housed in a 750 m³ indoor pool at the Kagoshima City Aquarium, Japan, were selected for this study due to their training proficiency. The animals were fed a diet consisting of at least five different fish species, totaling approximately 10–15 kg per individual per day, administered in four to five feeding sessions. All four dolphins participated in the Ebbinghaus illusion test and three of the four were selected for the Delboeuf illusion test. Two of the four dolphins were estimated

to be 31 years old, one was 16 years old, and one was 2 years old; the 2-year-old, born to the 16-year-old, was the only captive-born dolphin.

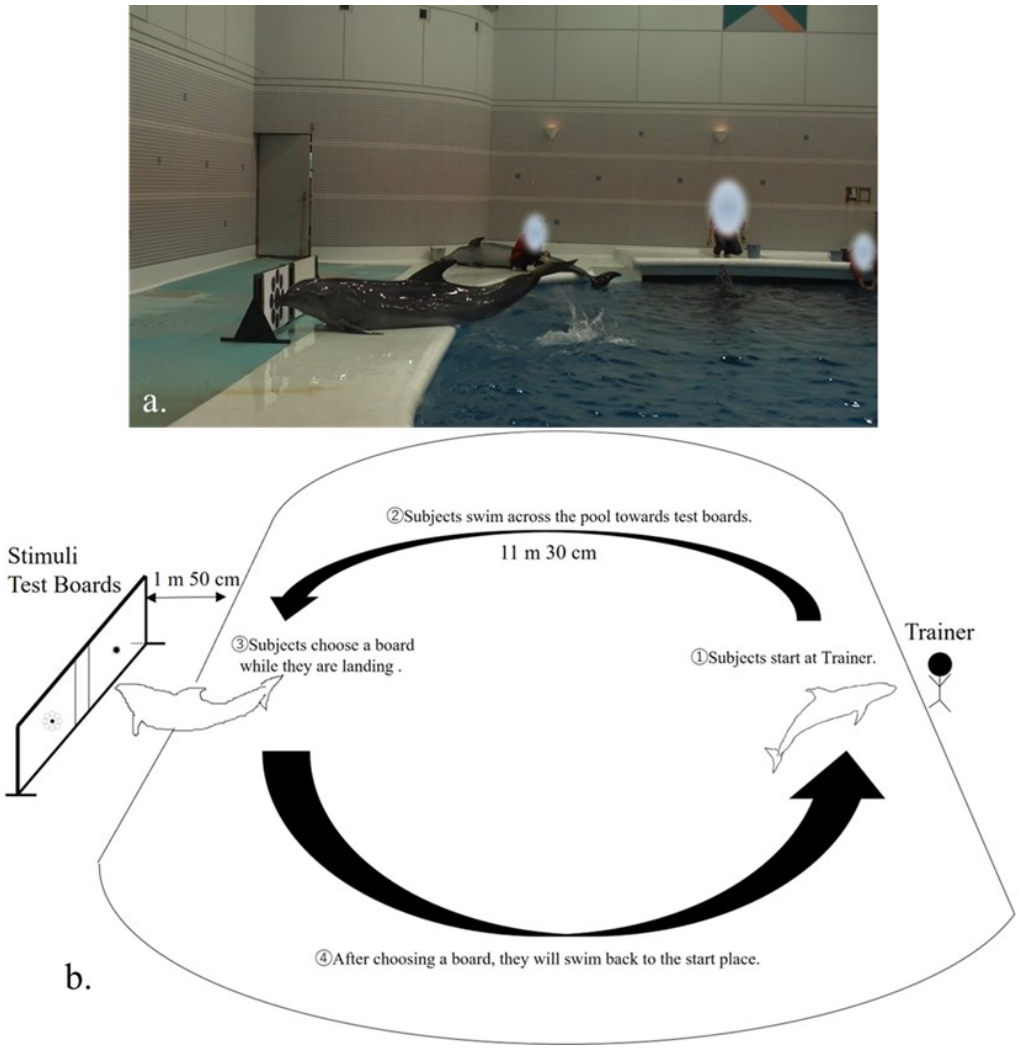
Protocol

Up to four dolphins shared the same pool, and during trials, other trainers kept non-participating dolphins at least 3 m away from test subjects to avoid influencing judgments. During the Ebbinghaus and Delboeuf illusion experiments, four types of boards and six combination patterns were used. Each board measured 55 cm × 91 cm with a centrally placed figure, and the two boards were set 20.5 cm apart. The dolphins started from the trainer's position, 11.3 m away from the boards, which were placed 1.5 m from the edge of the pool (Figure 2). The dolphins swam 11.3 m in response to the trainer's signal and selected a board once they reached the shore. The dolphins responded on land, using their snout-touch to indicate which board had the larger central circle. The subject's response was judged to finish with the subject touching one of the displayed boards. After choosing, the trainer sounded a whistle or a metallic noise to call them back. For control trials, the trainer whistled for correct answers and used a different sound for incorrect ones. In the test combinations, regardless of which option the dolphins chose, the trainer responded as if they had answered correctly in the control trials. After the trainer's reaction, the dolphins returned to the water and swam 11.3 m back to the trainer's position. Upon their return, the trainer rewarded them with two fish pieces for correct choices.

The experiments began once the dolphins were trained to select the larger central circle from the two presented. The trainer had at least three years of hands-on experience and understood key training techniques. During the experiments, the trainer was cautious not to react in any way other than what was previously agreed upon. The experiments comprised two main steps, with a maximum of two sessions conducted per day. Each session comprised 12 trials.

Figure 2

Experimental Setup of the Ebbinghaus and Delboeuf Illusions in Bottlenose Dolphins



Note. a) Photograph of the experimental set up, and b) an illustration of a series of whole experiments.

First, the dolphins underwent pretest training to focus on the central circle on the boards and select the larger centered circles with no flankers. After a maximum of 2 weeks of pretest training, the dolphins proceeded to the first step of the experiment, which involved confirming their ability to compare the circles. Subsequently, Controls 1 and 2 (Figure 3) were presented to the dolphins, featuring centered targets of various sizes surrounded by large or small flankers of the same type. The first step was considered complete when the percentage of correct answers reached 100% in a single session. If a dolphin made a mistake, the session was suspended. We assumed that, if focused, the dolphins could choose correctly in Controls 1 and 2 without being confused by the surrounding flankers. The next step involved probe tests to assess illusion susceptibility in bottlenose dolphins. Controls 3 and 4 (Figure 3), featuring centered targets of various sizes surrounded by different types of large or small flankers, were alternated with Tests 1 or 2 (Figure 3), which used identical centered targets surrounded by various flankers. For example, the sequence would be in the following order: Control 3 →Test 1→ Control 4 →Test 1 → Control 3 → Test 1 → Control 4 → Test 1 → Control 3 → Test 1 → Control 4 → Test 1. Test 2 could replace Test 1, with control combinations constituting six trials in one session. Either Test 1 or 2 was used in a particular session.

In the second step, since the subjects achieved perfect accuracy with Control Combinations 1 and 2 in prior sessions, a session with a ratio of less than 100% correct responses from the control combinations (Controls 3 and 4) was deemed invalid, which was attributed to the subject being "unmotivated" or "distracted." Subsequently, such sessions were interrupted and excluded from analysis. We assumed that, if focused, the dolphins could choose correctly in Controls 3 and 4 without being confused by the surrounding flankers as First Step. The 16-year-old female could not concentrate on the Delboeuf illusion experiment, even when conducted over several days, leading to its abandonment. Consequently, four female bottlenose dolphins were selected for the Ebbinghaus illusion, and three were selected for the Delboeuf illusion.

All the figures were printed in 720 × 1,440 dpi on matt composite paper using an EPSON SC-P6000 printer. In each session, the appearance order pattern (left or right) in one session for the display was randomly decided to equal a 50–50 ratio by generating random numbers in a Visual Basic 6.0 program (Microsoft). Therefore, the correct board order in Control Combinations 1, 2, 3, and 4 appeared 50–50 left or right, as did in Test Combinations 1 and 2. After 48 valid trials (24 for each test combination), the response patterns in the valid test trial sessions were analyzed to assess the Ebbinghaus and Delboeuf illusions in bottlenose dolphins.

Analysis

A two-tailed Fisher's exact test was performed when the results of the test combinations were significantly different from the chance selectivity using GraphPad statistical software (GraphPad Software, Inc. La Jolla, CA, USA).

Results

After basic training, all dolphins passed the first step of the Ebbinghaus or Delboeuf illusion within a minimum of 12 trials in one session or a maximum of 20 trials in two sessions. For the second step, a minimum of 96 trials in eight sessions or a maximum of 140 trials in 14 sessions were individually required to collect the selectivity data of the 48 valid trials of the Ebbinghaus or Delboeuf test combinations. Invalid sessions were interrupted and discarded if the dolphins made a mistake in Controls 3 or 4. In this study, there were 18 trials in which the subjects made a mistake while selecting an answer in Controls 3 or 4 without apparent hesitation. In the Ebbinghaus illusion Test 1, the subjects' selectivity was not significantly different from random selectivity (50%) (Table 1). Furthermore, three of the four dolphins in Ebbinghaus illusion Test 2, one of the three dolphins in Delboeuf illusion Test 1, and one of the three dolphins in Delboeuf illusion Test 2 did not demonstrate statistically significant illusionary effects. However, some dolphins demonstrated illusionary effects.

Selectivity significantly differed from chance in the following cases: one approximately 31-year-old dolphin in Ebbinghaus illusion 2 ($p < .001$); one approximately 31-year-old ($p = .021$) and one 2-year-old dolphin ($p = .021$) in Delboeuf illusion 1; and one 31-year-old ($p < .001$) and one 2-year-old ($p < .001$) dolphin in Delboeuf illusion 2. Only one approximately 31-year-old dolphin was affected by both Ebbinghaus illusion 2 and Delboeuf illusions 1 and 2. Age-related selectivity was not observed in this study.

Figure 3

Schedule and Conditions of the Experiment

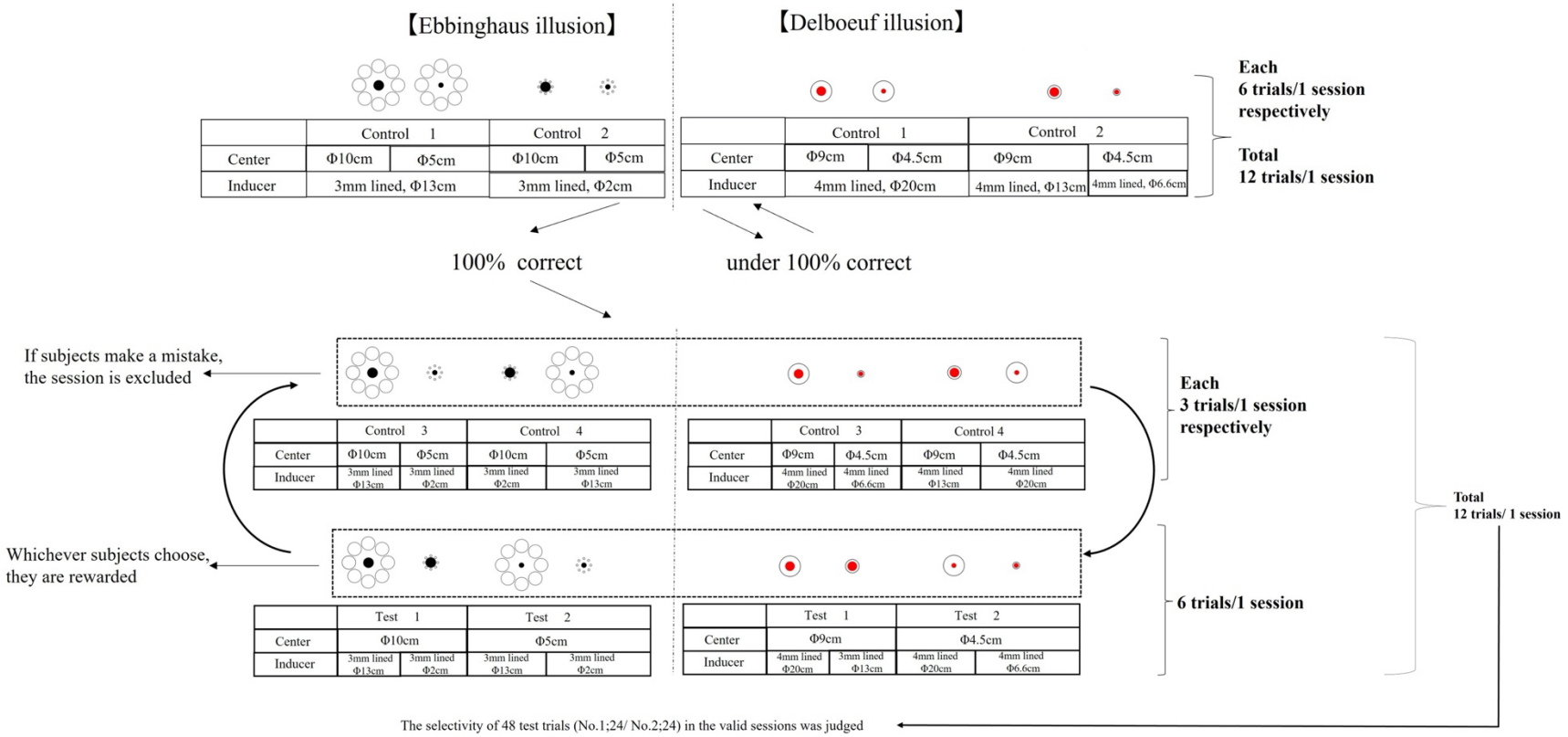
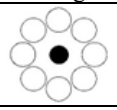
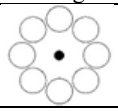


Table 1

Response Selections of Ebbinghaus and Delboeuf Illusions in Bottlenose Dolphins

Subject	Ebbinghaus Illusion Test 1			Ebbinghaus Illusion Test 2			Delboeuf Illusion Test 1			Delboeuf Illusion Test 2		
			*p*-value			*p*-value			*p*-value			*p*-value
Subject ① ♀estimated to be 31 years old	46%	54%	.671	4%	96%	< .001	33%	67%	.021	12%	88%	< .001
Subject ② ♀estimated to be 31 years old	50%	50%	1.0	46%	54%	.671	54%	46%	.671	46%	54%	.671
Subject ③ ♀estimated to be 16 years old	46%	54%	.671	50%	50%	1.0	N.D.	N.D.	-	N.D.	N.D.	-
Subject ④ ♀2years old	50%	50%	1.0	50%	50%	1.0	33%	67%	.021	8%	92%	< .001

Note. N.D. means no data. Subject ③ could not participate in the Delbouef illusion experiment because she showed disinterest in the examination procedure. *p*-values were calculated in two-tailed Fisher's exact test, which was conducted on each selectivity and chance selectivity (50%).

Discussion

The results showed that a few dolphins perceived the Ebbinghaus and Delboeuf illusion. Although the present study's methodological procedure differs from the previous study run with a dolphin (Murayama et al., 2012), this study also obtained similar results. Previous studies have described the various effects of methodological procedures (Rosa Salva et al., 2013). Specifically, individual comprehension of tasks could affect the results of illusion-related experiments in non-humans (Rosa Salva et al., 2013) because experimenters cannot communicate verbally with them. This study did not verbally confirm whether the dolphins could distinguish between the surrounding flankers and the centered target. However, alternating between different-sized (Controls 3 or 4) and same-sized (Tests 1 or 2) centered circles decreased the likelihood of the dolphins confusing surrounding flankers with centered targets. A strict 100% correct selectivity of the control combinations during the valid test sessions implied that each dolphin understood the task for that session.

This study used the sessions with 100% correct response rates for Controls 3 and 4 (which featured different-sized centered circles) as the accurate response data for Tests 1 and 2. Even in this context, the spontaneous choice tendency of Tests 1 and 2, presented alternatively between Controls 3 and 4, significantly differed from the 50% chance selectivity for some dolphins. These results suggest susceptibility to the illusion. Despite using the same training paradigm, some subjects were susceptible to illusion, while others were not. This situation does not indicate that the training method uniformly influenced the choice preferences of all dolphins. It is possible that the accidental choice in the early stage of the experiment gradually reinforced preferences in Tests 1 or 2, consequently producing a false-illusory tendency. However, the likelihood of this phenomenon occurring in all subjects susceptible to illusion is low.

While simplistic comparisons between studies using different training paradigms carry risks, the illusionary tendencies of the subjects partly align with those of humans and the single case report on a bottlenose dolphin. Visual information processing consists of two main types: global and local precedence, with global precedence being crucial for recognizing patterns as visual illusions (Parron & Fagot, 2007). Despite applying the same training paradigm to all dolphins, the two 31-year-old females produced different results under the same conditions. One dolphin demonstrated a clear illusionary effect, while the other showed an unclear illusionary effect. This difference may stem from acquired factors, including training, given this study's variations in illusionary tendencies.

Innate species differences may influence global precedence processing, including histological differences or similarities. In humans, fMRI studies of visual illusions indicate that various brain regions are involved, particularly in the visual cortex, including BA17 (V1), 18 (V2), 19 (V3, 4, 5), 21, 37, and 38. Additionally, cortical magnification in V1 to V3 may be involved (Chen et al. 2024; Han et al. 2002; Yan et al. 2011). Furthermore, the parahippocampal cortex, BA36 and 37, may also be implicated (Axelrod et al., 2017). However, applying these methodological techniques to large animals is challenging. Conversely, numerous postmortem histological studies have been conducted in various species. For instance, histological differences or similarities in V1 across species have been reported, including a study highlighting a thinner V1 in cetaceans compared with primates (Graïc et al., 2022). Graïc et al. (2022) also noted histological differences between cetacean V1 and hominidae V1, including a thinner layer 4 and variations in the cellular compositions of layer 5. By comparing histological studies of optical tissues, we can better understand the regions involved in global precedence processing. In other words, differences in brain structures and neuronal connections between humans and dolphins could be ruled out as candidate tissues involved in the evolutionary mechanisms of the illusion, given the generally consistent illusionary results between the two species. Further studies on the cetacean visual cortex are required.

According to previous studies on humans (Goto et al., 2007; Knol et al., 2015), the magnitude of the Ebbinghaus and Delboeuf illusions differs depending on various factors, including the distance between the inducer and the target. In the case of the two dolphins that exhibited the Delboeuf illusion in this study, the selectivity of the two combinations was biased when the distance between the inducer and the target increased. Furthermore, the illusion did not occur in Test 1 for the subject displaying the Ebbinghaus

illusion. Still, it did appear in Test 2, which had a greater distance between the inducer and the target. This result is consistent with that of a study on damselfishes (Fuss & Schluessel, 2017), indicating that both dolphins and damselfish experienced sufficient stimuli to induce the illusion, even with an increased distance between the target and inducer. Moreover, a greater distance between the target and the inducer may enhance global precedence processing, leading to a size contrast effect. Despite the significant genetic differences between damselfish and bottlenose dolphins, this suggests that ecologically relevant evolutionary factors may affect cognitive function in underwater species. As described above, considering that results showed the Ebbinghaus and Delboeuf illusion have illusionary effect on a few subjects regardless of subjects age and experimental methodology, bottlenose dolphin may be affected by these illusionary phenomena as species. The small fish that dolphins feed on frequently school with false deployment as a feint, which might form this global precedence processing in this species. Otherwise, dolphins' habit of forming female pods in a three-dimensional oceanic environment might also form this global precedence processing in this species. Intriguingly, damselfish eat copepods that form schools, and damselfish themselves form schools. It is important to note that various factors cause convergent evolution. Further assimilation of research might resolve this hypothesis.

This study has some noteworthy limitations. This study is a brief report of neuroethology, however, no direct data of neural mechanism were recorded. Although there are technical problems for applying fMRI into bottlenose dolphin, future advanced compact fMRI might resolve this difficulty. Additionally, subjects in this study were housed under human care, and the possibility that daily contact with trainers may affect an individual's cognitive ability or behavioral responses should not be excluded. Fundamentally different methodology might be required for resolving this problem.

In summary, this is the first cross-sectional study investigating the Ebbinghaus and Delboeuf illusions in bottlenose dolphins of varying ages. Regardless of methodological differences, this study also builds on a previous case report (Murayama et al., 2012), and similar to this case report, this study suggests that some bottlenose dolphins may process visual information with global precedence, similar to humans. The comparison with illusionary experiments with other species might bring the histological slight insights and the evolutionary backgrounds including various convergent-evolutionary factors in the information processing.

Author Contributions: Hamano designed the research and wrote the manuscript. Nakamura and Watanuki conducted the research. Azuma and Okuma supported the research. Yamamoto and Kashiwagi supervised the research.

Funding: This research received no specific grant from any funding agency.

Conflict of Interest: The authors declare no conflicts of interest.

Availability of Data and Materials: The data and materials are available from the corresponding author upon reasonable request.

References

Agrillo, C., Santacà, M., Pecunioso, A., & Miletto Petrazzini, M. E. (2020). Everything is subjective under water surface, too: visual illusions in fish. *Animal Cognition, 23*(2), 251–264. https://doi.org/10.1007/s10071-019-01341-7

Bánszegi, O., Szenczi, P., Urrutia, A., Martínez-Byer, S., & Hudson, R. (2021). Visual discrimination of size and perception of the Delboeuf illusion in the domestic cat (*Felis silvestris catus*): a developmental disjunction? *Journal of Comparative Psychology, 135*(4), 505–515. https://doi.org/10.1037/com0000288

Becker, N., Prasad-Shreckengast, S., & Byosiere, S. -E. (2021). Methodological challenges in the assessment of dogs' (*Canis lupus familiaris*) susceptibility of the Ebbinghaus-Titchener illusion using the spontaneous choice task. *Animal Behavior and Cognition, 8*(2), 138–151. https://doi.org/10.26451/abc.08.02.04.2021

Byosiere, S.-E., Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). Visual perception in domestic dogs: susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Animal Cognition, 20*(3), 435–448. https://doi.org/10.1007/s10071-016-1067-1

Chen, L., Wu, B., Yu, H., & Sperandio, I. (2024). Network dynamics underlying alterations in apparent object size. *Brain Communications, 6*(1), fcae006. https://doi.org/10.1093/braincomms/fcae006

Delfour, F., & Marten, K. (2006). Lateralized visual behavior in bottlenose dolphins (*Tursiops truncatus*) performing audio-visual tasks: The right visual field advantage. *Behavioural Processes, 71*(1), 41–50. https://doi.org/10.1016/j.beproc.2005.09.005

Feng, L. C., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). Why do animals differ in their susceptibility to geometrical illusions? *Psychonomic Bulletin & Review, 24*(2) 262–276. https://doi.org/10.3758/s13423-016-1133-3

Fuss, T., & Schluessel, V. (2017). The Ebbinghaus illusion in the gray bamboo shark (*Chiloscyllium griseum*) in comparison to the teleost damselfish (*Chromis chromis*). *Zoology, 123*, 16–29. https://doi.org/10.1016/j.zool.2017.05.006

Girgus, J. S., Coren, S., & Agdern, M. (1972). The interrelationship between the Ebbinghaus and Delboeuf illusions. *Journal of Experimental Psychology, 95*(2) 453–455. https://doi.org/10.1037/h0033606

Goto, T., Uchiyama, I., Imai, A., Takahashi, S., Hanari, T., Nakamura, S., & Kobari, H. (2007). Assimilation and contrast in optical illusions. *Japanese Psychological Research, 49*(1), 33–44. https://doi.org/10.1111/j.1468-5884.2007.00330.x

Graïc, J.-M., Peruffo, A., Corain, L., Finos, L., Grisan, E., & Cozzi, B. (2022). The primary visual cortex of Cetartiodactyls: organization, cytoarchitectonics and comparison with perissodactyls and primates. *Brain Structure and Function, 227*(4), 1195–1225. https://doi.org/10.1007/s00429-021-02392-8

Han, S., Weaver, J.A., Murray, S.O., Kang, X., Yund, E.W. & Woods, D.L. (2002). Hemispheric asymmetry in global/local processing: effects of stimulus position and spatial frequency. *NeuroImage*, *17*(3), 1290–1299. http://doi.org/10.1006/nimg.2002.1255

Imada, T., Carlson, S. M., & Itakura, S. (2012). East-West cultural differences in context-sensitivity are evident in early childhood. *Developmental Science, 16*(2), 198–208. https://doi.org/10.1111/desc.12016

Kelley, L. A., & Kelley, J. L. (2014). Animal visual illusion and confusion: The importance of a perceptual perspective. *Behavioral Ecology, 25*(3), 450–463. https://doi.org/10.1093/beheco/art118

Kilian, A., von Fersen, L., & Güntürkün, O. (2005). Left hemispheric advantage for numerical abilities in the bottlenose dolphin. *Behavioural Processes, 68*, 179–184. https://doi.org/10.1016/j.beproc.2004.11.003

Knol, H., Huys, R., Sarrazin, J.-C., & Jirsa, V. K. (2015). Quantifying the Ebbinghaus figure effect: Target size, context size, and target-context distance determine the presence and direction of the illusion. *Frontiers in Psychology, 6*, 1679. https://doi.org/10.3389/fpsyg.2015.01679

Lucon-Xiccato, T., Santacà, M., Miletto Petrazzini, M. E. M., Agrillo, C., & Dadda, M. (2019). Guppies, *Poecilia reticulata*, perceive a reversed Delboeuf illusion. *Animal Cognition, 22*(3), 291–303. https://doi.org/10.1007/s10071-019-01237-6

Murayama, T., Usui, A., Takeda, E., Kato, K., & Maejima, K. (2012). Relative size discrimination and perception of the Ebbinghaus illusion in a bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals, 38*(4), 333–342. https://doi.org/10.1578/AM.38.4.2012.333

Nakamura, N., Watanabe, S., & Fujita, K. (2008). Pigeons perceive the Ebbinghaus-Titchener circles as an assimilation illusion. *Journal of Experimental Psychology: Animal Behavior Processes, 34*(3), 375–387. https://doi.org/10.1037/0097-7403.34.3.375

Nakamura, N., Watanabe, S., & Fujita, K. (201). A reversed Ebbinghaus–Titchener illusion in bantams (*Gallus gallus domesticus*). *Animal Cognition, 17*, 471–481. https://doi.org/10.1007/s10071-013-0679-y

Nayar, K., Franchak, J., Adolph, K. & Kiorpes, L. (2015). From local to global processing: the development of illusory contour perception. *Journal of Experimental Child Psychology*, *131*, 38–55. https://doi.org/10.1016/j.jecp.2014.11.001

Parrish, A. E., & Beran, M. J. (2014). When less is more: like humans, chimpanzees (*Pan troglodytes*) misperceive food amounts based on plate size. *Animal Cognition, 17*, 427–434. https://doi.org/10.1007/s10071-013-0674-3

Parrish, A. E., Brosnan, S. F., & Beran, M. J. (2015). Do you see what I see? A comparative investigation of the Delboeuf illusion in humans (*Homo sapiens*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Learning and Cognition, 41*(4), 395–405. https://doi.org/10.1037/xan0000078

Parron, C., & Fagot, J. (2007). Comparison of grouping abilities in humans (*Homo sapiens*) and baboons (*Papio papio*) with the Ebbinghaus illusion. *Journal of Comparative Psychology, 121*(4), 405–411. https://doi.org/10.1037/0735-7036.121.4.405

Potier, S., Mitkus, M., & Kelber, A. (2020). Visual adaptations of diurnal and nocturnal raptors. *Seminars in Cell & Developmental Biology, 106*, 116–126. https://doi.org/10.1016/j.semcdb.2020.05.004

Qadri, M. A. J., & Cook, R. G. (2019). Perception of Ebbinghaus–Titchener stimuli in starlings (*Sturnus vulgaris*). *Animal Cognition, 22*, 973–989. https://doi.org/10.1007/s10071-019-01289-8

Rivamonte, L. A. (2009). Bottlenose dolphin (*Tursiops truncatus*) double-slit pupil asymmetries enhance vision. *Aquatic Mammals, 35*(2), 269–280. https://doi.org/10.1578/AM.35.2.2009.269

Rosa Salva, O., Rugani, R., Cavazzana, A., Regolin, L., & Vallortigara, G. (2013). Perception of the Ebbinghaus illusion in four-day-old domestic chicks (*Gallus gallus*). *Animal Cognition, 16*, 895–906. https://doi.org/10.1007/s10071-013-0622-2.

Santacà, M., Agrillo, C., & Miletto Petrazzini, M. E. (2021). The challenge of illusory perception of animals: The impact of methodological variability in cross-species investigation. *Animals (Basel), 11*(6), 1618. https://doi.org/10.3390/ani11061618

Santacà, M., Miletto Petrazzini, M. E., Agrillo, C., & Wilkinson, A. (2019). Can reptiles perceive visual illusions? Delboeuf illusion in red-footed tortoise (*Chelonoidis carbonaria*) and bearded dragon (*Pogona vitticeps*). *Journal of Comparative Psychology, 133*(4), 419–427. https://doi.org/10.1037/com0000176

Santacà, M., Regaiolli, B., Miletto Petrazzini, M. E., Spiezio, C., & Agrillo, C. (2017). Preliminary study to investigate the Delboeuf illusion in ring-tailed lemurs (*Lemur catta*): Methodological challenges. *Animal Behavior and Cognition, 4*(3), 365–377. https://doi.org/10.26451/abc.04.03.13.2017

Schwarzkopf, D. S., & Rees, G. (2013). Subjective size perception depends on central visual cortical magnification in Human V1. *PLOS ONE, 8*(3), e60550. https://doi.org/10.1371/journal.pone.0060550

Schwarzkopf, D. S., Song, C., & Rees, G. (2011). The surface area of Human V1 predicts the subjective experience of object size. *Nature Neuroscience, 14*, 28–30. https://doi.org/10.1038/nn.2706

Sovrano, V.A., Albertazzi, L., & Rosa Salva, O. (2015). The Ebbinghaus illusion in a fish (*Xenotoca eiseni*). *Animal Cognition, 18*, 533–542. https://doi.org/10.1007/s10071-014-0821-5

Watanabe, S., Hase, Y., & Nakamura, N. (2016). Do budgerigars (*Melopsittacus undulatus*) perceive the Delboeuf illusion?: A preliminary study with a simultaneous discrimination task. *Psychologia, 59*(2-3), 121–135. https://doi.org/10.2117/psysoc.2016.121

Yan, T., Wang, B., Yamasita, Y., Yu, B., Guo, Q. & Wu, J. (2011). Attention influence response in the human visual area V1 for Ebbinghaus illusion. *The 2011 IEEE/ICME International Conference on Complex Medical Engineering*, 582–587. https://doi.org/10.1109/ICCME.2011.5876808