Animal Cognition (2025) 28:39
https://doi.org/10.1007/s10071-025-01957-y

ORIGINAL PAPER

Visual numerical cognition in pigeons: conformity to the Weber–Fechner law

Peng Wu[1,3] · Juncai Zhu[1,3] · Qingzhi He[1,3] · Zhizhong Wang[1,3] · Li Shi[2,3]

Received: 6 December 2024 / Revised: 21 April 2025 / Accepted: 24 April 2025

Abstract
As representatives of a basal bird lineage, pigeons have exhibited remarkable visual numerical cognition, comparable even to that of monkeys. Nevertheless, whether visual numerical cognition in pigeons conforms to the Weber–Fechner law remains unknown. To address this, we designed a fully automated apparatus tailored for pigeons and used it to train them to perform a delayed match-to-numerosity task. The results showed that on a linear scale, pigeons represented smaller numerosities with higher precision and larger numerosities with lower precision, exhibiting a numerical magnitude effect. When the linear scale was compressed into a logarithmic scale, this magnitude effect was offset, resulting in similar representational characteristics across different numerosities. This finding suggests that the mental number line of pigeons is logarithmic rather than linear, consistent with the Weber–Fechner law. While biological brains seek precision in representing numerical information, they must also take computational load into account. This representational strategy may be the optimal outcome of the trade-off between computational precision and computational load that biological brains have achieved through long-term evolution.

Keywords Pigeons · Birds · Numerosity · Mental number line · Logarithm

Introduction

Numerosity, that is, the number of elements in a set, is an important aspect of animals' perception of the external environment (Balestrieri et al. 2019; Bengochea et al. 2023; Benson-Amram et al. 2017; Gómez-Laplaza and Gerlai 2011; Lyon 2003; Wang et al. 2020). Behavioral studies have shown that numerosity representations in monkeys and corvids both conform to the Weber–Fechner law (Ditz and Nieder 2016; Kirschhock and Nieder 2023; Nieder and Merten 2007), i.e., their behavioral performance functions are best described by a logarithmically compressed number scale (Nieder 2016, 2017, 2020). Compared to pigeons, monkeys and corvids represent some of the most evolutionarily advanced species within their respective phylogenetic groups, both possessing an enlarged pallial telencephalon and sophisticated intellectual capacities (Emery and Clayton 2004; Güntürkün et al. 2021; von Eugen et al. 2020). Among them, corvids, due to their higher brain neuron density and a greater proportion of neurons located in the pallial telencephalon, even have a comparable number of pallial neurons to that of monkeys (Olkowicz et al. 2016), which is thought to support their advanced behavioral and cognitive complexity (Dicke and Roth 2016; Herculano-Houzel 2017). Although pigeons and corvids both belong to the avian class, pigeons represent a more basal avian lineage, possessing significantly fewer pallial neurons and total brain neurons (Olkowicz et al. 2016; Ströckens et al. 2022), their cognitive abilities are generally considered less advanced than those of corvids (Balakhonov and Rose 2017; Clayton and Emery 2015; Emery 2006; Güntürkün et al. 2017). For certain complex tasks, pigeons exhibit significantly poorer behavioral performance, or even fail to complete them, such as concept learning (Wright et al. 2017),

✉ Zhizhong Wang
wzz1982@zzu.edu.cn

✉ Li Shi
li_shi_edu@163.com

1 School of Electrical and Information Engineering, Zhengzhou University, Zhengzhou 450001, China

2 Department of Automation, Tsinghua University, Beijing 100084, China

3 Henan Key Laboratory of Brain Science and Brain-Computer Interface Technology, Zhengzhou 450001, China

Published online: 19 May 2025

rule transfer (Wilson et al. 1985), and tool use (Call 2010). Interestingly, in the field of numerical cognition, pigeons exhibit remarkable numerical discrimination abilities, comparable even to those of monkeys (Scarf et al. 2011). However, whether numerical cognition in pigeons conforms to the Weber–Fechner law, as observed in monkeys and corvids, requires confirmation through a more targeted experimental paradigm.

We modified the delayed match-to-sample task, previously used to investigate numerical cognition in monkeys and corvids (Ditz and Nieder 2015, 2016; Nieder et al. 2002; Nieder and Miller 2003; Viswanathan and Nieder 2013), to better suit the behavioral characteristics of pigeons. Training pigeons to complete the behavioral task according to predefined rules poses significant challenges, and prolonged training also requires considerable effort from the experimenters. To address these challenges, we designed a fully automated training apparatus tailored for pigeons and used it to investigate their numerical cognitive abilities.

For larger numerosities, if biological brains are to maintain encoding precision similar to that of smaller numerosities, they must perform more neural computation, thereby consuming more energy (Jamadar et al. 2025; Lennie 2003). Therefore, biological brains must make a trade-off between encoding precision and energy consumption (Sengupta and Stemmler 2014). If pigeons, as representatives of a basal bird lineage, employ a similar strategy to monkeys and corvids in representing numerical information, it would suggest that this representation strategy offers advantages in biological computation. This may represent the optimal result of the trade-off between computational precision and energy consumption during the long-term evolution of biological brains, consistent with their real-time and efficient information processing characteristics. In-depth research into this encoding strategy will aid in the development of novel biologically inspired algorithms characterized by low power consumption. Additionally, it will provide biological insights into balancing computational precision and computational load in the field of artificial intelligence.

Through long-term evolution, biological brains of different species may select the optimal encoding strategy via convergent evolutionary mechanisms (Nieder 2016, 2017). Therefore, we hypothesized that, even though pigeons belong to the basal bird lineage, their numerical cognition also conforms to the Weber–Fechner law. To test this hypothesis, we trained pigeons to perform the designed delayed match-to-numerosity task. To control for the influence of low-level non-numerical visual features, both standard stimuli and control stimuli were used in each session, with the control group consisting of three sets of stimuli: "Density-fixed" stimuli, "Area-fixed" stimuli, and "Perimeter-fixed" stimuli. Subsequently, we used Gaussian fitting functions to assess the response characteristics of pigeons' behavioral performance functions across different numerical scales. If the hypothesis was supported, pigeons' behavioral performance functions would exhibit better symmetry and stability on the logarithmic scale.

Materials and methods

Animals

We trained two pigeons to perform the delayed match-to-sample task with the number of items in stimuli as the criterion for discrimination. During the training and testing phases, the pigeons were maintained on a controlled feeding protocol and received food as a reward only after completing the correct experimental trials. Following each session, the pigeons received a measured amount of specialized grit (1.2 g), automatically dispensed by the quantitative filling machine (see Table S1), to promote digestion and provide essential minerals, especially calcium, thereby helping them maintain health and nutritional balance. Pigeons lived in the experimental animal switching module of the fully automated apparatus. The main structure of the module is a customized, rotatable stainless steel cylinder (diameter: 120 cm, height: 55 cm), with each pigeon living independently in a sector-shaped area (central angle: 60°). The diameter, height, and sector angle of the cylinder were designed based on the pigeons' body size and behavioral characteristics, such as wing-spreading, ensuring that each pigeon is provided with suitable living space. Water was provided ad libitum. The experimental environment was maintained under a constant light-dark cycle, with 14 h of light and 10 h of darkness.

Delayed match-to-numerosity task and training

In the delayed match-to-numerosity task (Fig. 1a), a pigeon pecked at the small circle on the screen to start a trial. After an 800 ms presample period, a sample stimulus was displayed on the screen and remained for 800 ms (sample period). The pigeon had to extract the numerical feature from the sample stimulus and retain it for 600 ms (delay period) after the sample stimulus disappeared, for subsequent behavioral choice. During the choice period, a test stimulus containing a specific number of items and a purple triangle stimulus were simultaneously displayed on the screen. If the test stimulus contained the same number of items as the sample stimulus (match, 50% probability), the pigeon had to select the test stimulus to receive a food reward. Otherwise (non-match, 50% probability), the pigeon had to select the purple triangle stimulus to receive a food reward. The pigeon was

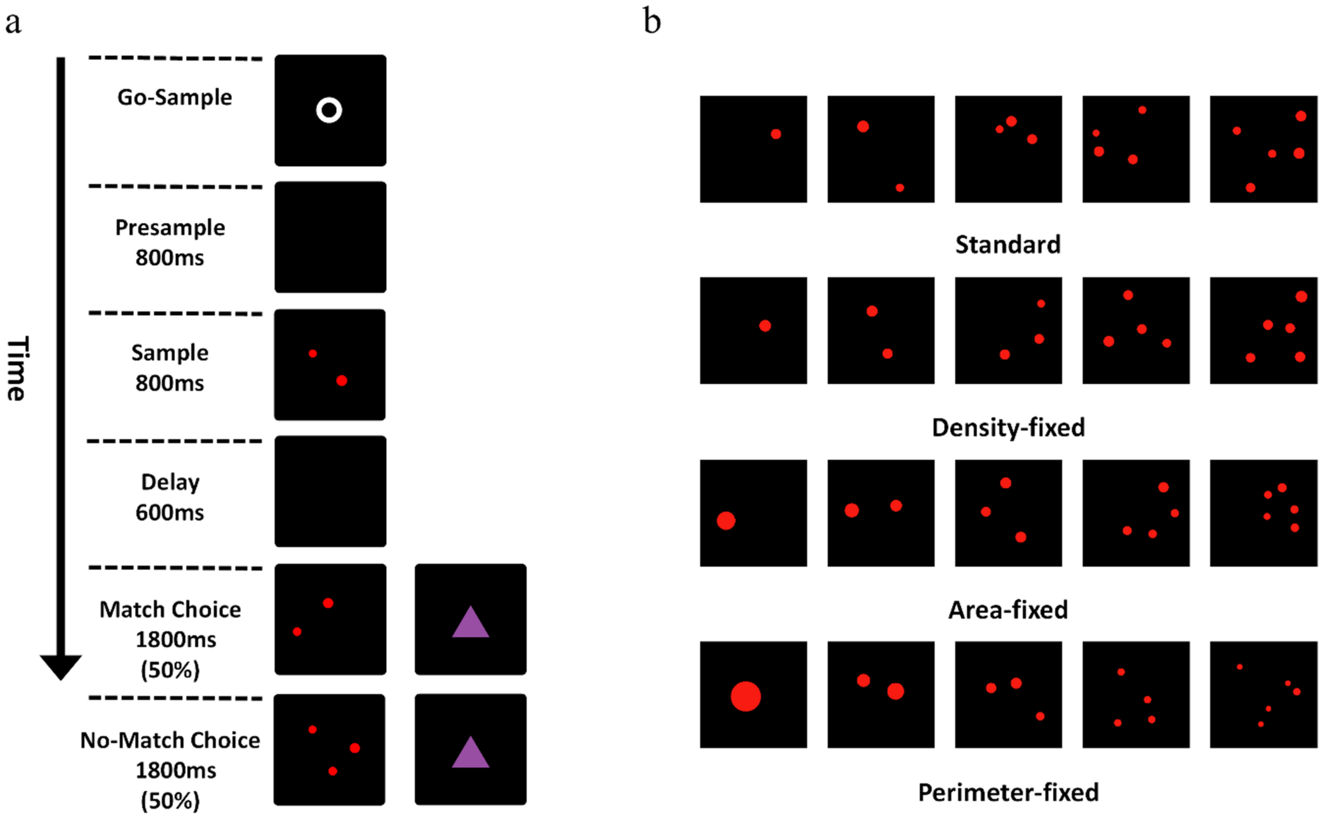

Fig. 1 Behavioral protocol and example stimuli. (**a**) Delayed match-to-numerosity task. In matching trials (probability = 50%), a test stimulus containing the same number of items as the sample stimulus and a purple triangle were simultaneously displayed during the choice period, and the pigeon had to select the test stimulus to obtain a food reward. In non-matching trials (probability = 50%), the test stimulus contained a different number of items from the sample stimulus, and the pigeon had to select the purple triangle stimulus to obtain a food reward. (**b**) Examples of standard stimuli and control stimuli, with the control group including three types of stimuli: "Density-fixed," "Area-fixed," and "Perimeter-fixed"

required to make a choice within 1800 ms; an incorrect choice or failure to choose led to a variable 10–15 s timeout.

Before the formal training on the delayed match-to-numerosity task, the two pigeons underwent only pre-training and did not participate in any other tasks. Pre-training followed the same protocol as shown in Fig. 1a, except that the stimulus set consisted of four images, each representing a different object with large appearance differences (dog, chair, banana, and cup). After 47 days of pre-training, with one session per day, each session lasting 3.5 h, their behavioral accuracy stabilized at over 90%, indicating that they had become highly familiar with the task protocol. In the initial sessions of the pre-training, in order to encourage the pigeons to actively complete the task, a reward of three food pellets was given each time, which was gradually reduced to a single food pellet in the later sessions. After the pre-training, we trained the pigeons to complete the delayed match-to-numerosity task (Fig. 1a) with one session per day. The session duration initially lasted 4.5 h but was gradually reduced to 3.5 h, depending on whether the pigeons stopped performing the task throughout the final part of the session. After 92 and 105 days of training, respectively, with an average of 526 and 591 trials per day, the behavioral accuracy of Pigeon B5 and Pigeon C3 reached a stable level (Fig. S2). Specifically, their accuracy no longer increased, and for each standard-control stimulus set combination, accuracy fluctuated within 5% across three consecutive sessions of the same combination. Subsequently, the testing phase began.

Numerical stimuli

The numerosity stimuli consisting of one to five red dots were generated using a custom-written Matlab script (Fig. 1b), with dot diameters on the stimulus screen ranging from 1 mm to 7 mm. To ensure that the pigeons made behavioral choices based on the number of items rather than low-level visual features that may covary with numerosity, we followed previous research by using both standard stimuli and control stimuli in each training and testing session (Ditz and Nieder 2015, 2016; Kobylkov et al. 2022). In the standard stimuli, dots with pseudo-random diameters were arranged pseudo-randomly but did not overlap on a black square background. The control group consisted of three sets of stimuli: “Density-fixed” stimuli, “Area-fixed” stimuli, and “Perimeter-fixed” stimuli. The average density was determined by calculating the mean distance between all dots in a numerosity stimulus. In the standard stimuli, the average density, total area, and total perimeter of the dots all increase with numerosity. In comparison, “Density-fixed” stimuli keep average density constant across all numerosities, while total area and total perimeter increase with numerosity. “Area-fixed” stimuli maintain a constant total area, while average density and total perimeter increase with numerosity. “Perimeter-fixed” stimuli maintain a constant total perimeter, while total area decreases with numerosity. Additionally, to prevent the pigeons from solving the task by memorizing visual patterns, each session used 60 newly generated numerosity stimuli, with 30 standard stimuli and 30 control stimuli. Each numerosity stimulus could serve as both the sample stimulus and the test stimulus, and the physical appearance of the sample and the test stimulus in each trial was never identical, including in the matching trials. Each session used a specific set of control stimuli, with the three control sets alternating across sessions. In each trial, numerosity, match vs. non-match, and standard vs. control were all randomized and unpredictable.

Fully automated training apparatus

We designed a fully automated apparatus based on the behavioral characteristics of pigeons and used it to train them to perform the delayed match-to-sample task (Fig. 2). The apparatus, controlled by a custom-written Python script, consisted primarily of four components: the main control module, the stimulus display and choice feedback module, the reward reinforcement module, and the experimental animal switching module.

Main control module was responsible for receiving data from various sensors, issuing corresponding control commands, managing the overall operation of the apparatus, and simultaneously recording the pigeons’ behavioral data.

Stimulus display and choice feedback module was responsible for displaying stimulus images and providing feedback on the pigeons’ behavioral choices via a customized infrared sensing frame.

Reward reinforcement module was responsible for precisely dispensing a single food pellet as a reward, with an average of 0.037 g per reward.

Experimental animal switching module was responsible for switching the experimental animals once the preset conditions were met.

The main contributions of this apparatus included: (1) fully automated training, with daily automatic activation and deactivation, automated training of experimental animals, automated recording of behavioral data, and automated switching of experimental animals, which did not require any involvement from the experimenters throughout the entire process; (2) precise dispensing of a single food pellet for each reward, which significantly increased the total number of behavioral trials completed in each session.

Data analysis

To investigate whether numerical cognition in pigeons conforms to the Weber–Fechner law, we first calculated the probability that pigeons judged the test stimulus as containing the same numerical feature as the sample stimulus. That is, the probability of making the correct choice in match trials and the incorrect choice in non-match trials. The resulting behavioral performance functions were then plotted on four different scales: linear, a power function with an exponent of 0.5, a power function with an exponent of 0.33, and a logarithmic (log2) scale. These scales were selected because Fechner suggested that the just noticeable difference is constant on a logarithmic scale of stimulus magnitude (Fechner 1860), i.e., the perceived magnitude is logarithmically related to the actual stimulus magnitude. In contrast, Stevens proposed that the just noticeable difference remains constant on a power scale (Stevens 1961), i.e., the perceived magnitude follows a power law in relation to the actual stimulus magnitude. Among these, power functions with exponents of 0.5 and 0.33 are the most representative scaling models of the mental number line, each reflecting a different degree of nonlinear compression (Ditz and Nieder 2016; Kobylkov et al. 2022; Nieder and Merten 2007). To further evaluate the symmetry and stability of the behavioral performance functions, we fitted Gaussian functions to the behavioral performance curves plotted on the aforementioned scales. The Gaussian function is defined as:

$$R_{fit}(n) = A \bullet exp(-\frac{(n-\mu)^2}{2\sigma^2}) \quad (1)$$

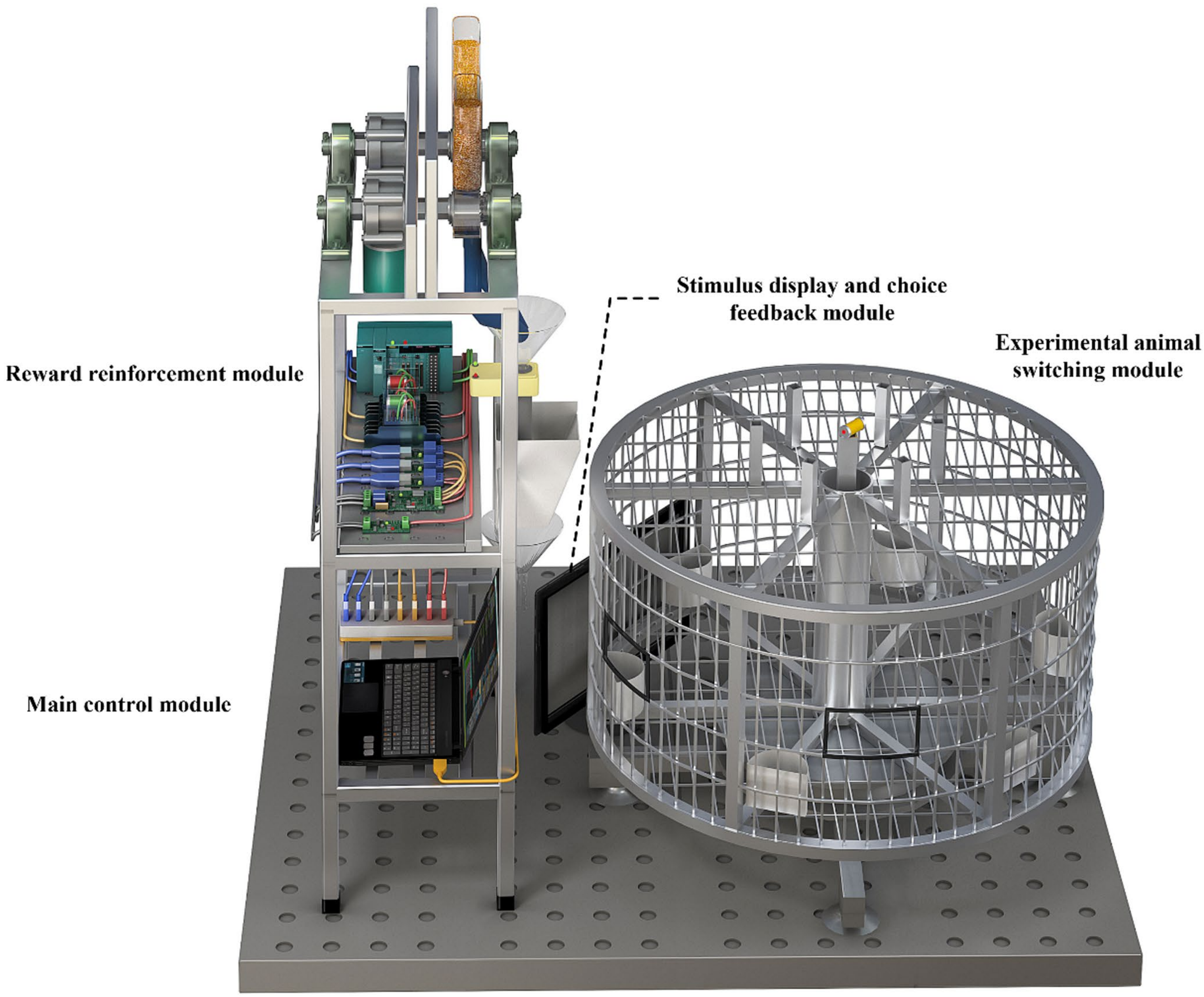

Fig. 2 Fully automated training apparatus. On the left side of the figure is a stainless steel frame (40 cm × 50 cm × 145 cm), which is divided into three layers. The bottom layer contains the apparatus' main control module, while the first and second layers house the reward reinforcement module. On the right side of the figure are the stimulus display and choice feedback module, as well as the experimental animal switching module. The apparatus automatically trained pigeons to complete the experimental task, and by accurately dispensing a single food pellet for each correct trial, it significantly increased the number of trials completed in each session

In this equation, A represents the peak height of the Gaussian fitted curve, μ represents the center position, and σ represents the width. The total sum of squares (SS_{tot}) of the observed values was calculated as follows:

$$SS_{tot} = \sum_{i=1}^{N} \left(R_{obs}(n_i) - \bar{R}_{obs}\right)^2 \quad (2)$$

Where $\bar{R}_{obs}$ was the mean of the target fitted data:

$$\bar{R}_{obs} = \frac{1}{N}\sum_{i=1}^{N} R_{obs}(n_i) \quad (3)$$

The sum of squared residuals (SS_{res}) was calculated as follows:

$$SS_{res} = \sum_{i=1}^{N} \left(R_{obs}(n_i) - R_{fit}(n_i)\right)^2 \quad (4)$$

Finally, the goodness-of-fit (R^2) value of the Gaussian function was calculated as:

$$R^2 = 1 - \frac{SS_{res}}{SS_{tot}} \quad (5)$$

R^2 values were used as a quantitative measure of the symmetry of the behavioral performance curves, while σ

values were used to assess the stability across the behavioral performance curves.

Results

Behavioral accuracy

During the testing phase, Pigeon B5 was recorded for 54 sessions, with an average of 543 trials per session and an average accuracy of 73.98% ± 0.23. Pigeon C3 was recorded for 60 sessions, with an average of 585 trials per session and an average accuracy of 72.79% ± 0.21 (Fig. S2). The behavioral accuracy of pigeon B5 for the standard stimuli and the three sets of control stimuli is shown in Fig. 3a, with no significant differences across the four stimulus sets ($p = 0.287$, Kruskal-Wallis test). The behavioral accuracy of pigeon C3, as shown in Fig. 3b, was consistent with that of pigeon B5 and also exhibited no significant differences across the four stimulus sets ($p = 0.523$, Kruskal-Wallis test). Pigeons exhibited similar behavioral performance for the standard stimuli and the three sets of control stimuli, indicating that they relied on numerosity rather than covarying low-level visual features such as average density, total area, and total perimeter to solve the delayed match-to-sample task.

Behavioral performance functions

The behavioral performance functions of pigeon B5 and pigeon C3 are shown in Fig. 3c and d, respectively (see Fig. S3 for further details). The different colored lines represent different sample numerosities, and each point on the lines corresponds to the average probability that the pigeons judged the test stimulus as containing the same number of items as the sample stimulus. As shown in the figures, the greater the numerical difference between the test stimulus and the sample stimulus, the lower the probability that the pigeons chose the test stimulus, exhibiting the numerical distance effect. At the same numerical distance, the larger the number of items in the sample stimulus, the higher the probability that the pigeons chose the test stimulus. Accordingly, the behavioral performance curves became wider, indicating that the pigeons' numerical cognition also aligns with the numerical magnitude effect.

To further investigate pigeons' numerical cognition, we conducted a statistical analysis on the behavioral data collected from all 114 sessions during the testing phase (54 sessions from Pigeon B5 and 60 from Pigeon C3; see Fig. S2), with the results shown in Fig. 4b. The figure includes the pigeons' average behavioral performance across all combinations of sample and test numerosities, where darker colors indicate smaller numerical distances. Pigeons' behavioral performance was evaluated based on numerical distance, as shown in Fig. 4a. The results further reflect the numerical distance effect and suggest that pigeons encode numerical information in a manner similar to band-pass filtering. The behavioral performance curves obtained across all sessions were separately plotted on a linear scale (Fig. 4c) and a logarithmically compressed scale (Fig. 4d). The curves appeared noticeably steeper on the left side under the linear scale, whereas they exhibited better symmetry under the logarithmically compressed scale. Under the linear scale, the behavioral performance curves exhibited the numerical magnitude effect, the essence of which is higher representation precision for smaller numerosities and lower representation precision for larger numerosities. In contrast, under the logarithmic scale, the larger the numerosity, the greater the degree of compression on the number line, which resulted in behavioral performance curves for different sample numerosities exhibiting similar response widths (see also Fig. 5d), thereby offsetting the numerical magnitude effect.

Scale of the mental number line

Gaussian fitting was used to quantitatively describe the symmetry and stability of behavioral performance functions under different numerical scales. Examples of the fitting results for the linear scale and the logarithmically compressed scale are shown in Fig. 5a and b, respectively, where the different-colored lines represent the performance functions for different sample numerosities, and the red curves represent the Gaussian fitting results. Under a given numerical scale, the closer the performance function is to the fitted curve, the better its symmetry; that is, the response characteristics to numerosities at equal distances on both sides of the sample numerosity become more consistent. Additionally, the smaller the variation in the widths of the fitted curves, the higher the stability across the performance functions; that is, the performance functions for different sample numerosities become more similar.

The goodness-of-fit (R^2) values of the Gaussian functions were used to evaluate the symmetry of the behavioral performance functions under different numerical scales, as shown in Fig. 5c. The mean R^2 values for the linear scale, the power function with an exponent of 0.5, the power function with an exponent of 0.33, and the logarithmic scale were 0.70 ± 0.01, 0.80 ± 0.01, 0.83 ± 0.01, and 0.85 ± 0.01, respectively. The R^2 values on the four numerical scales were significantly different ($p < 0.001$, Friedman test, $n = 114$), with post-hoc pairwise comparisons using the Wilcoxon signed-rank test showing significant differences in all pairs (all $p < 0.001$, $n = 114$). Furthermore, the sigma values of the Gaussian functions were used to evaluate the stability across the performance functions, with the results shown in

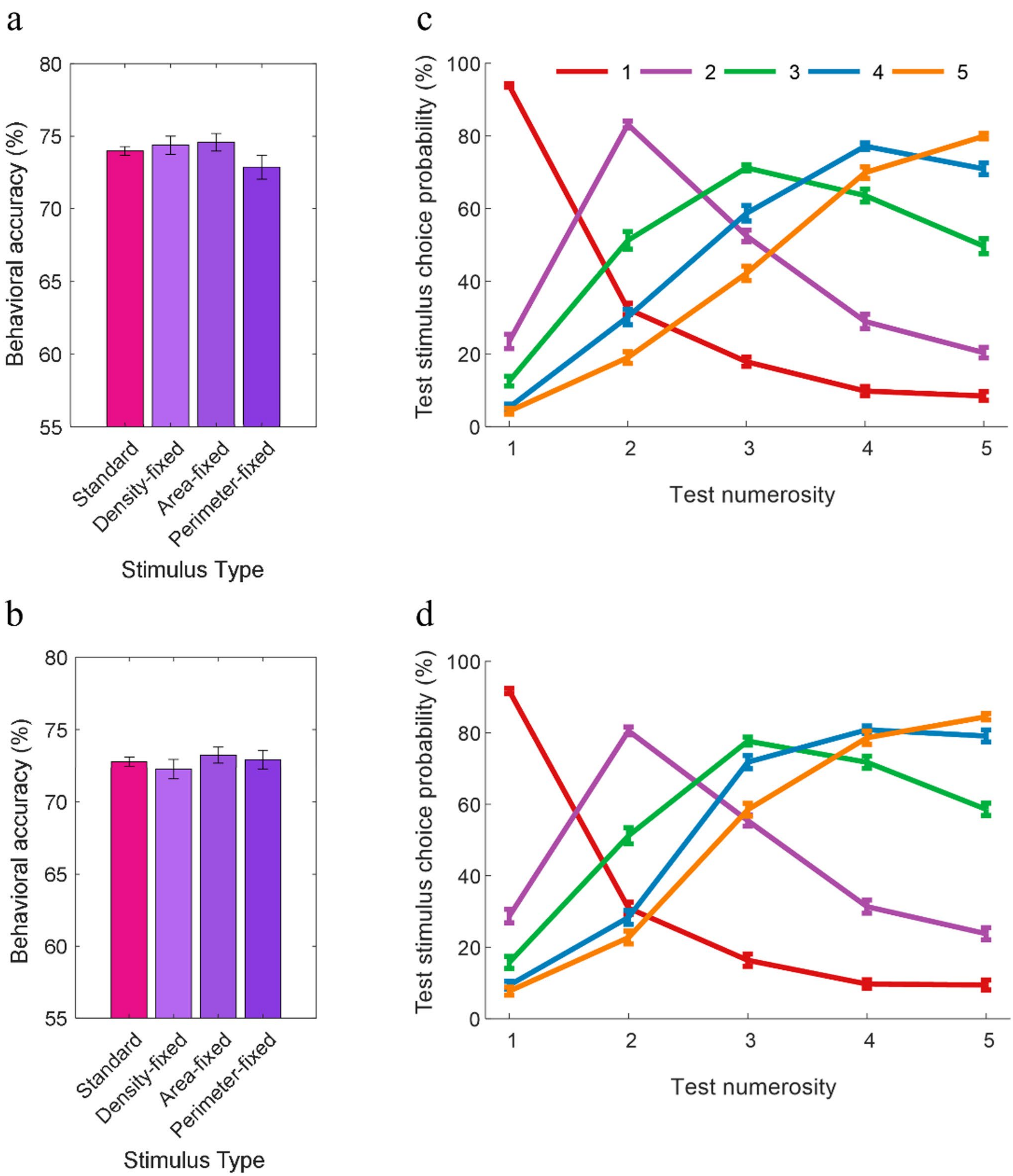

Fig. 3 Behavioral accuracy and performance functions. (**a**) Behavioral accuracy of pigeon B5 (standard stimulus set: 54 sessions; three control stimulus sets: 18 sessions each). (**b**) Behavioral accuracy of pigeon C3 (standard stimulus set: 60 sessions; three control stimulus sets: 20 sessions each). (**c**) Behavioral performance functions of pigeon B5. (**d**) Behavioral performance functions of pigeon C3. Each color represents one sample numerosity. Error bars correspond to SEM

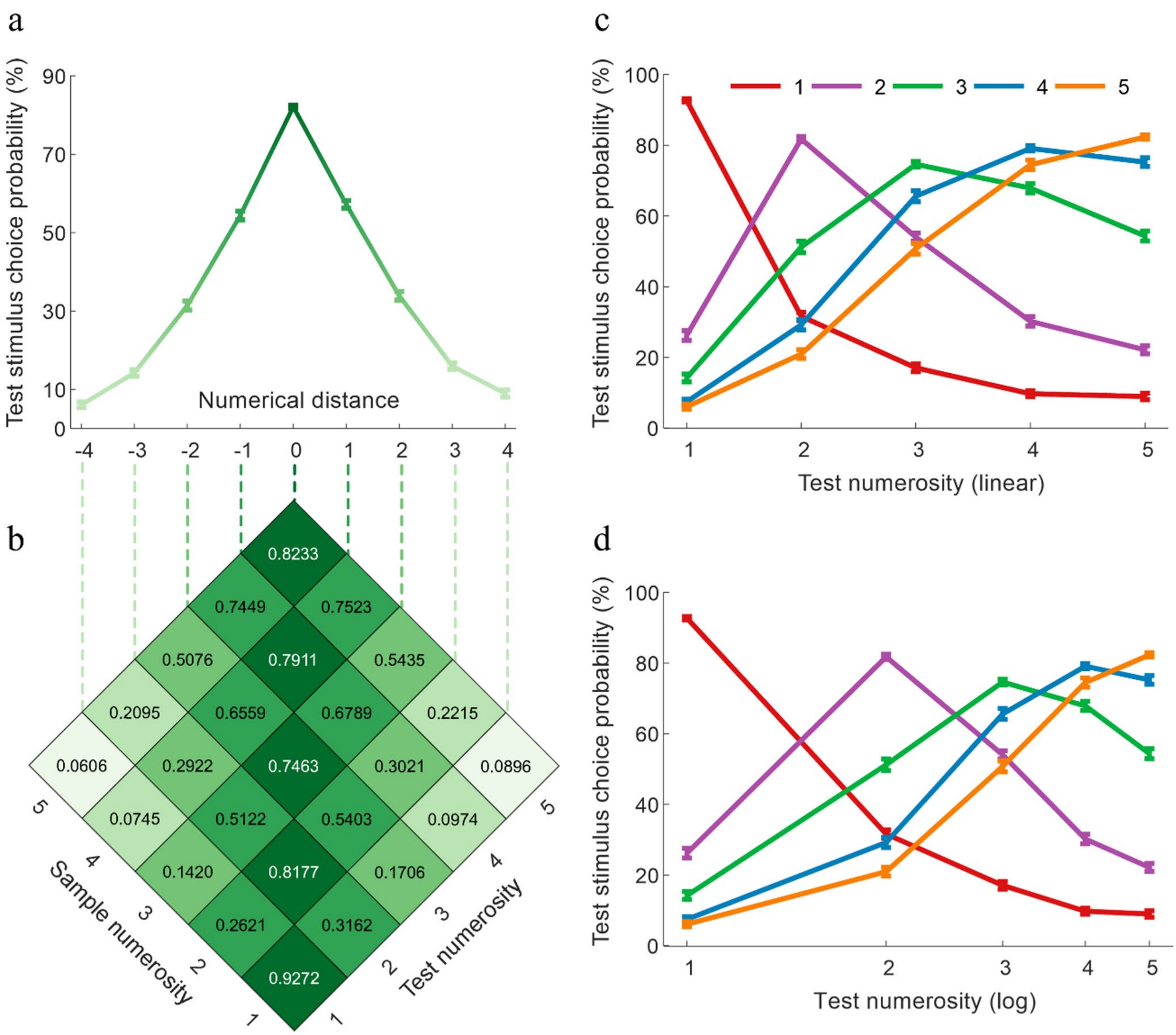

Fig. 4 Statistical analysis of behavioral data across all 114 sessions. (**a**) Correlation between numerical distance and behavioral performance. As the numerical distance increased, the probability that pigeons chose the test stimulus decreased. (**b**) Statistical results of behavioral data. The left axis represents the numerosity of the sample stimulus, while the right axis represents the numerosity of the test stimulus. The data correspond to the average probability of pigeons choosing the test stimulus. (**c**) Behavioral performance functions under a linear scale. (**d**) Behavioral performance functions under a logarithmic scale. Error bars correspond to SEM

Fig. 5d. The linear fit slopes for sigma on the linear scale, the power 0.5 scale, the power 0.33 scale, and the logarithmic scale were 0.262, 0.044, 0.018, and 0.008, respectively.

The higher the R^2 values, the better the fit of the Gaussian functions. Therefore, under the logarithmically compressed scale, the behavioral performance functions were closest to symmetrical Gaussian bell curves ($p<0.001$, Wilcoxon signed-rank test, $n=114$). The closer the linear fit slope for sigma is to zero, the smaller the variation in the widths of the Gaussian fitted curves. Thus, the performance functions for numerosities of different magnitudes exhibited the highest stability under the logarithmic scale. These findings indicate that the performance functions of pigeons are best described by a logarithmic number scale, consistent with the Weber–Fechner law.

Discussion

The results indicated that the pigeons relied on the number of items rather than covarying low-level visual features such as average density, total area, and total perimeter to complete the delayed match-to-sample task. Further analysis revealed that under the linear scale, the pigeons' behavioral

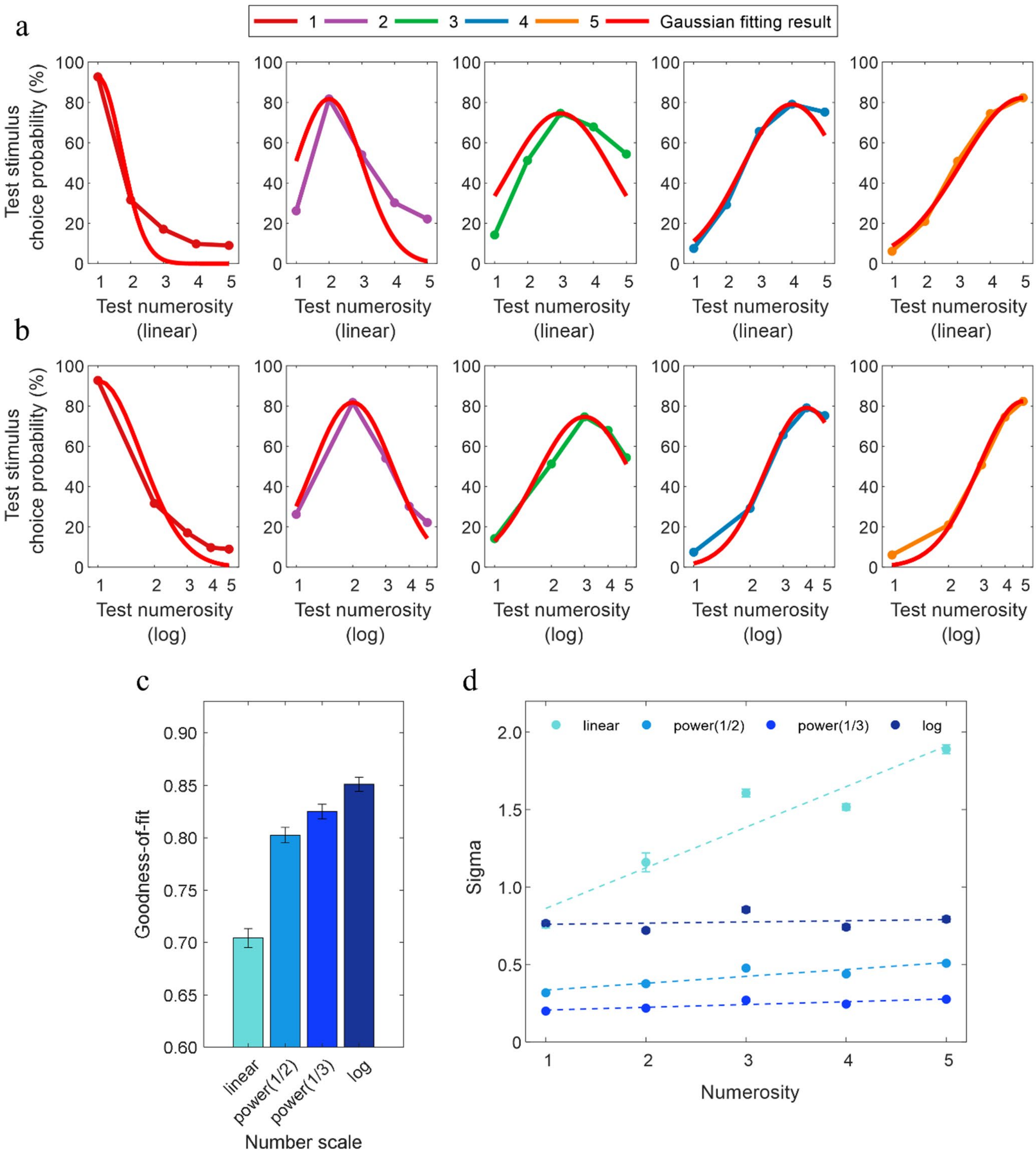

Fig. 5 The symmetry and stability of behavioral performance functions. (**a**) Examples of Gaussian fitting results under a linear scale. The red curves represent the fitting results. (**b**) Examples of Gaussian fitting results under a logarithmic scale. (**c**) The mean goodness-of-fit values under four different scales. The higher the goodness-of-fit values, the closer the performance functions are to Gaussian bell curves. (**d**) The linear fitting results of sigma under four different scales. Sigma represents the width of the Gaussian fitted curve. The closer the linear fit slope for sigma is to zero, the smaller the variation in the widths of the Gaussian fitted curves, meaning that there is higher stability across the performance functions. Error bars correspond to SEM

performance functions gradually widened as the numerosity increased, exhibiting the numerical magnitude effect. When the linear scale was compressed into a logarithmic scale, this magnitude effect was offset, with similar response characteristics observed across different numerosities. The Gaussian fitting results also indicated that, on the logarithmically compressed scale, the pigeons' behavioral performance functions exhibited the best symmetry and stability. This finding suggests that the mental number line of pigeons is logarithmic, consistent with the Weber–Fechner law.

Logarithmic mental number line

In this study, we trained two pigeons to perform a delayed match-to-numerosity task. Despite the relatively small sample size, we strictly controlled the number of food pellets given in each correct trial, which enabled us to collect a large number of experimental trials for each pigeon (Pigeon B5: 29,338 trials; Pigeon C3: 35,127 trials). This facilitated a comprehensive and precise assessment of pigeons' numerical cognition, ensuring the reliability of the results. The experimental results also indicate a high degree of consistency in their behavioral performance functions (Fig. 3 and Fig. S3), suggesting that the observed numerical cognition pattern is robust. Further analysis results indicate that pigeons' numerical cognition conforms to the Weber–Fechner law, consistent with findings observed in monkeys and corvids.

Monkeys and corvids represent some of the most evolutionarily advanced species within their respective phylogenetic groups, both possessing an enlarged pallial telencephalon and advanced intelligence (Güntürkün et al. 2021; Nieder et al. 2020). In contrast, pigeons, representing a more basal bird lineage, show significant differences from them in both the number of pallial neurons and certain aspects of cognitive abilities (Emery and Clayton 2005; Olkowicz et al. 2016). Species with such vast evolutionary differences employ the same strategy to represent numerical information, suggesting that this encoding strategy offers advantages in biological computation. The essence of this encoding strategy is higher precision for smaller numerosities and lower precision for larger numerosities. For larger numerosities, biological brains reduce computational load by sacrificing encoding precision, thereby exhibiting the numerical magnitude effect. Meanwhile, the inherent scaling effect of the logarithmic number line counteracts this magnitude effect, resulting in similar representational characteristics for numerosities of different magnitudes. This encoding strategy may represent the optimal outcome of the trade-off between computational precision and computational load in biological brains. Similarly, in terminal devices with limited computational resources and engineering applications that require real-time processing, there is often a need to balance computational precision and computational load. The aforementioned encoding strategy provides a biological reference for addressing this challenge.

Approximate number system

The object file system (OFS) and the approximate number system (ANS) are two distinct non-symbolic numerical representation systems, originally proposed within the field of human cognitive and developmental psychology (Kahneman et al. 1992; Xu and Spelke 2000). They have been extensively studied in infants (Feigenson et al. 2002; Xu 2003), children (Bugden and Ansari 2016; Kwon and Kim 2023), and adults (Barth et al. 2003; Siegler and Opfer 2003), and have also been extended to non-human animals, including monkeys and corvids (Ditz and Nieder 2016; Kirschhock and Nieder 2023; Nieder and Miller 2004), offering valuable insights into numerical cognition across species (Feigenson et al. 2004; Seguin and Gerlai 2017). Of these two systems, the OFS provides precise numerical representations by assigning markers to individual items in a set, but it has a strict capacity limit, typically representing up to four items. In contrast, the ANS does not have a fixed upper limit and derives numerical information through approximate estimation; therefore, accuracy decreases as the number of items increases. We explored the numerical cognition of pigeons within the range from one to five. The results indicated that on a linear scale, the widths of the behavioral performance functions gradually increased with numerosity, meaning that at the same numerical distance, the larger the numerosity, the lower the discrimination accuracy. Additionally, when the linear scale was compressed into a logarithmic scale, the width of the performance function for numerosity five remained consistent with the widths for numerosities one to four (Fig. 5d), indicating that pigeons exhibited similar band-pass filtering performance for numerosity five and numerosities one to four under this scale. Thus, we infer that the ANS underlies pigeons' numerical representation.

It remains to be seen whether the mental number line of pigeons remains logarithmic across a larger numerical range (e.g., 1–30). Previous research has demonstrated that both monkeys and corvids represent numerical magnitudes in a manner consistent with the ANS, and they exhibit a similar numerical cognition pattern across numerical ranges of different magnitudes (Ditz and Nieder 2015, 2016; Kirschhock and Nieder 2023; Nieder and Merten 2007; Nieder and Miller 2003). Since the ANS is not constrained by set size, we infer that pigeons' numerical cognition pattern is likely unaffected by numerical range.

Advantages of fully automated training apparatus

Training pigeons to complete the delayed match-to-numerosity task according to predefined rules is challenging; it requires prolonged and extensive effort. Conventional training apparatuses require manual assistance to replace experimental animals. This process not only consumes the experimenters' energy but also causes stress and fear in the animals, which could potentially affect the experimental results. Moreover, compared to species like crows and monkeys, pigeons require a significantly smaller total amount of food intake. Therefore, to ensure that pigeons complete enough trials in each session, the amount of food reward given in each trial must be strictly controlled. In light of these challenges, we specifically designed a fully automated training apparatus for pigeons, which automatically activated and deactivated each day, automatically trained the experimental animals to complete the behavioral task, and automatically replaced experimental animals according to preset conditions, all without the need for any involvement from the experimenters. It not only significantly reduced the experimenters' workload but also avoided causing stress and fear in the pigeons, thereby eliminating the potential impact of these factors on the experimental results. Additionally, the apparatus, through the precise coordination of its components, accurately dispensed a single food pellet as a reward whenever a pigeon made the correct choice. This design not only significantly increased the number of trials completed, thereby accelerating the task learning process, but also ensured the collection of sufficient experimental data in each session, allowing for a more comprehensive and precise analysis of the pigeons' numerical cognitive abilities.

The fully automated training apparatus is also well-suited for investigating pigeons' cognitive abilities in other domains, such as working memory (Diekamp et al. 2002), category discrimination (Asen and Cook 2012), stimulus ordering (Johnston et al. 2020), global versus local feature encoding (Clark and Colombo 2022), and causal mechanisms (Taylor et al. 2012). Additionally, it may provide valuable insights for exploring the cognitive abilities of other animals.

Conclusions

In this study, we developed a fully automated training apparatus tailored for pigeons and used it to investigate their numerical cognitive abilities. The results suggest that the mental number line of pigeons is logarithmic rather than linear, consistent with the Weber–Fechner law. As representatives of a basal bird lineage, pigeons employ the same strategy as monkeys and corvids in representing numerical information, indicating that this representational strategy offers advantages in biological computation. This may be the optimal outcome that biological brains have achieved through long-term evolution, and it can provide biological insights into balancing the trade-off between computational precision and computational load in relevant engineering fields.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10071-025-01957-y.

Acknowledgements We thank Jiangtao Wang for helping design and construct the fully automated training apparatus. We also thank Guanlei Feng and Hu Wang for their assistance in the care of the experimental animals.

Author contributions P.W.: Writing - original draft, Conceptualization, Investigation, Formal analysis, Visualization. J.Z.: Methodology, Software, Formal analysis. Q.H.: Methodology, Investigation, Visualization. Z.W.: Writing - review & editing, Conceptualization, Methodology, Investigation, Funding acquisition. L.S.: Writing - review & editing, Conceptualization, Software, Methodology, Resources.

Data availability The data are available on the Open Science Framework (OSF) repository at https://osf.io/zpqf9/?view_only=8bdea188028747d6a1bd67302f84cbc2.

Declarations

Ethics approval and consent to participate All experiments and procedures were conducted in accordance with the Regulations on the Administration of Laboratory Animals and were approved by the Life Science Ethical Review Committee of Zhengzhou University (No. SYXK 2019-002).

Competing interests The authors declare no competing interests.

References

Asen Y, Cook RG (2012) Discrimination and categorization of actions by pigeons. Psychol Sci 23:617–624. https://doi.org/10.1177/0956797611433333

Balakhonov D, Rose J (2017) Crows rival monkeys in cognitive capacity. Sci Rep 7:8809. https://doi.org/10.1038/s41598-017-09400-0
Balestrieri A, Gazzola A, Pellitteri-Rosa D, Vallortigara G (2019) Discrimination of group numerousness under predation risk in Anuran tadpoles. Anim Cogn 22:223–230. https://doi.org/10.1007/s10071-019-01238-5
Barth H, Kanwisher N, Spelke E (2003) The construction of large number representations in adults. Cognition 86:201–221. https://doi.org/10.1016/s0010-0277(02)00178-6
Bengochea M, Sitt JD, Izard V, Preat T, Cohen L et al (2023) Numerical discrimination in Drosophila melanogaster. Cell Rep 42:112772. https://doi.org/10.1016/j.celrep.2023.112772
Benson-Amram S, Gilfillan G, McComb K (2017) Numerical assessment in the wild: insights from social carnivores. Philos Trans R Soc Lond B Biol Sci 373. https://doi.org/10.1098/rstb.2016.0508
Bugden S, Ansari D (2016) Probing the nature of deficits in the 'approximate number system' in children with persistent developmental dyscalculia. Dev Sci 19:817–833. https://doi.org/10.1111/desc.12324
Call J (2010) Three ingredients for becoming a creative tool user. Tool Use Anim Cognition Ecol 3–20. https://doi.org/10.1017/CBO9780511894800.002
Clark W, Colombo M (2022) Seeing the forest for the trees, and the ground below my Beak: global and local processing in the Pigeon's visual system. Front Psychol 13:888528. https://doi.org/10.3389/fpsyg.2022.888528
Clayton NS, Emery NJ (2015) Avian models for human cognitive neuroscience: A proposal. Neuron 86:1330–1342. https://doi.org/10.1016/j.neuron.2015.04.024
Dicke U, Roth G (2016) Neuronal factors determining high intelligence. Philos Trans R Soc Lond B Biol Sci 371:20150180. https://doi.org/10.1098/rstb.2015.0180
Diekamp B, Kalt T, Güntürkün O (2002) Working memory neurons in pigeons. J Neurosci 22. https://doi.org/10.1523/JNEUROSCI.22-04-j0002.2002. Rc210
Ditz HM, Nieder A (2015) Neurons selective to the number of visual items in the Corvid Songbird endbrain. Proc Natl Acad Sci U S A 112:7827–7832. https://doi.org/10.1073/pnas.1504245112
Ditz HM, Nieder A (2016) Numerosity representations in crows obey the Weber-Fechner law. Proc Biol Sci 283:20160083. https://doi.org/10.1098/rspb.2016.0083
Emery NJ (2006) Cognitive ornithology: the evolution of avian intelligence. Philos Trans R Soc Lond B Biol Sci 361:23–43. https://doi.org/10.1098/rstb.2005.1736
Emery NJ, Clayton NS (2004) The mentality of crows: convergent evolution of intelligence in Corvids and apes. Science 306:1903–1907. https://doi.org/10.1126/science.1098410
Emery NJ, Clayton NS (2005) Evolution of the avian brain and intelligence. Curr Biol 15:R946–950. https://doi.org/10.1016/j.cub.2005.11.029
Fechner GT (1860) Elemente der psychophysik. Breitkopf und Härtel
Feigenson L, Carey S, Hauser M (2002) The representations underlying infants' choice of more: object files versus analog magnitudes. Psychol Sci 13:150–156. https://doi.org/10.1111/1467-9280.00427
Feigenson L, Dehaene S, Spelke E (2004) Core systems of number. Trends Cogn Sci 8:307–314. https://doi.org/10.1016/j.tics.2004.05.002
Gómez-Laplaza LM, Gerlai R (2011) Can angelfish (Pterophyllum scalare) count? Discrimination between different shoal sizes follows Weber's law. Anim Cogn 14:1–9. https://doi.org/10.1007/s10071-010-0337-6
Güntürkün O, Ströckens F, Scarf D, Colombo M (2017) Apes, feathered apes, and pigeons: differences and similarities. Curr Opin Behav Sci 16:35–40. https://doi.org/10.1016/j.cobeha.2017.03.003
Güntürkün O, von Eugen K, Packheiser J, Pusch R (2021) Avian pallial circuits and cognition: A comparison to mammals. Curr Opin Neurobiol 71:29–36. https://doi.org/10.1016/j.conb.2021.08.007
Herculano-Houzel S (2017) Numbers of neurons as biological correlates of cognitive capability. Curr Opin Behav Sci 16:1–7. https://doi.org/10.1016/j.cobeha.2017.02.004
Jamadar SD, Behler A, Deery H, Breakspear M (2025) The metabolic costs of cognition. Trends Cogn Sci. https://doi.org/10.1016/j.tics.2024.11.010
Johnston M, Porter B, Colombo M (2020) Nidopallium caudolaterale neuronal responses during serial-order behaviour in pigeons. Behav Brain Res 378:112269. https://doi.org/10.1016/j.bbr.2019.112269
Kahneman D, Treisman A, Gibbs BJ (1992) The reviewing of object files: object-specific integration of information. Cogn Psychol 24:175–219. https://doi.org/10.1016/0010-0285(92)90007-o
Kirschhock ME, Nieder A (2023) Numerical representation for action in crows obeys the Weber-Fechner law. Psychol Sci 34:1322–1335. https://doi.org/10.1177/09567976231201624
Kobylkov D, Mayer U, Zanon M, Vallortigara G (2022) Number neurons in the nidopallium of young domestic chicks. Proc Natl Acad Sci U S A 119:e2201039119. https://doi.org/10.1073/pnas.2201039119
Kwon N, Kim SY (2023) Effects of intelligence and approximate number system on the non-symbolic division ability in preschoolers. Front Psychol 14:961140. https://doi.org/10.3389/fpsyg.2023.961140
Lennie P (2003) The cost of cortical computation. Curr Biol 13:493–497. https://doi.org/10.1016/s0960-9822(03)00135-0
Lyon BE (2003) Egg recognition and counting reduce costs of avian conspecific brood parasitism. Nature 422:495–499. https://doi.org/10.1038/nature01505
Nieder A (2016) The neuronal code for number. Nat Rev Neurosci 17:366–382. https://doi.org/10.1038/nrn.2016.40
Nieder A (2017) Evolution of cognitive and neural solutions enabling numerosity judgements: lessons from primates and Corvids. Philos Trans R Soc Lond B Biol Sci 373. https://doi.org/10.1098/rstb.2016.0514
Nieder A (2020) The adaptive value of numerical competence. Trends Ecol Evol 35:605–617. https://doi.org/10.1016/j.tree.2020.02.009
Nieder A, Merten K (2007) A labeled-line code for small and large numerosities in the monkey prefrontal cortex. J Neurosci 27:5986–5993. https://doi.org/10.1523/jneurosci.1056-07.2007
Nieder A, Miller EK (2003) Coding of cognitive magnitude: compressed scaling of numerical information in the primate prefrontal cortex. Neuron 37:149–157. https://doi.org/10.1016/s0896-6273(02)01144-3
Nieder A, Miller EK (2004) Analog numerical representations in rhesus monkeys: evidence for parallel processing. J Cogn Neurosci 16:889–901. https://doi.org/10.1162/089892904970807
Nieder A, Freedman DJ, Miller EK (2002) Representation of the quantity of visual items in the primate prefrontal cortex. Science 297:1708–1711. https://doi.org/10.1126/science.1072493
Nieder A, Wagener L, Rinnert P (2020) A neural correlate of sensory consciousness in a Corvid bird. Science 369:1626–1629. https://doi.org/10.1126/science.abb1447
Olkowicz S, Kocourek M, Lučan RK, Porteš M, Fitch WT et al (2016) Birds have primate-like numbers of neurons in the forebrain. Proc Natl Acad Sci U S A 113:7255–7260. https://doi.org/10.1073/pnas.1517131113
Scarf D, Hayne H, Colombo M (2011) Pigeons on par with primates in numerical competence. Science 334:1664. https://doi.org/10.1126/science.1213357
Seguin D, Gerlai R (2017) Zebrafish prefer larger to smaller shoals: analysis of quantity Estimation in a genetically tractable model

organism. Anim Cogn 20:813–821. https://doi.org/10.1007/s10071-017-1102-x
Sengupta B, Stemmler MB (2014) Power consumption during neuronal computation. Proceedings of the IEEE, 102, 738–750. https://doi.org/10.1109/JPROC.2014.2307755
Siegler RS, Opfer JE (2003) The development of numerical estimation: evidence for multiple representations of numerical quantity. Psychol Sci 14:237–243. https://doi.org/10.1111/1467-9280.02438
Stevens SS (1961) To honor Fechner and repeal his law: A power function, not a log function, describes the operating characteristic of a sensory system. Science 133:80–86. https://doi.org/10.1126/science.133.3446.80
Ströckens F, Neves K, Kirchem S, Schwab C, Herculano-Houzel S et al (2022) High associative neuron numbers could drive cognitive performance in Corvid species. J Comp Neurol 530:1588–1605. https://doi.org/10.1002/cne.25298
Taylor AH, Miller R, Gray RD (2012) New Caledonian crows reason about hidden causal agents. Proc Natl Acad Sci U S A 109:16389–16391. https://doi.org/10.1073/pnas.1208724109
Viswanathan P, Nieder A (2013) Neuronal correlates of a visual sense of number in primate parietal and prefrontal cortices. Proc Natl Acad Sci U S A 110:11187–11192. https://doi.org/10.1073/pnas.1308141110
von Eugen K, Tabrik S, Güntürkün O, Ströckens F (2020) A comparative analysis of the dopaminergic innervation of the executive caudal nidopallium in pigeon, chicken, zebra Finch, and carrion crow. J Comp Neurol 528:2929–2955. https://doi.org/10.1002/cne.24878
Wang L, Yang C, He G, Liang W, Møller AP (2020) Cuckoos use host egg number to choose host nests for parasitism. Proc Biol Sci 287:20200343. https://doi.org/10.1098/rspb.2020.0343
Wilson B, Mackintosh NJ, Boakes RA (1985) Transfer of relational rules in matching and oddity learning by pigeons and Corvids. Q J Experimental Psychol Sect B 37:313–332. https://doi.org/10.1080/14640748508401173
Wright AA, Magnotti JF, Katz JS, Leonard K, Vernouillet A et al (2017) Corvids outperform pigeons and Primates in learning a basic concept. Psychol Sci 28:437–444. https://doi.org/10.1177/0956797616685871
Xu F (2003) Numerosity discrimination in infants: evidence for two systems of representations. Cognition 89:B15–25. https://doi.org/10.1016/s0010-0277(03)00050-7
Xu F, Spelke ES (2000) Large number discrimination in 6-month-old infants. Cognition 74. https://doi.org/10.1016/s0010-0277(99)00066-9. B1-b11

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.