

Apes, feathered apes, and pigeons: differences and similarities

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Apes, corvids, and pigeons differ in their pallial/cortical neuron numbers, with apes ranking first and pigeons third. Do cognitive performances rank accordingly? If they would do, cognitive performance could be explained at a mechanistic level by computational capacity provided by neuron numbers. We discuss five areas of cognition (short-term memory, object permanence, abstract numerical competence, orthographic processing, self-recognition) in which apes, corvids, and pigeons have been tested with highly similar procedures. In all tests apes and corvids were on par, but also pigeons reached identical achievement levels in three tests. We suggest that higher neuron numbers are poor predictors of absolute cognitive ability, but better predict learning speed and the ability to flexibly transfer rules to novel situations.

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Introduction

The first scholars of comparative cognition firmly believed in a scala naturae, according to which humans represent the apex of cognitive evolution, while other animals scale down according to their evolutionary proximity to us [1]. Consequently, non-human primates were thought to occupy the second rung on this ‘intelligence’ ladder. This was bolstered by historical neuroanatomical studies demonstrating that apes had especially large brains, both in terms of total brain weight and when expressed as relative to body weight. Not surprisingly, birds were initially distant competitors; their brains are very small in absolute terms and they also lack a layered cortex and instead possess a pallium organized in a

nuclear fashion. Over the last three decades, however, researchers demonstrated that the non-layered avian pallium is a functional equivalent to the mammalian cortex [2–4,5**]. Further, corvids and parrots are now seen to be on par with apes in all cognitive processes studied [6]. This view is supported with novel neuroanatomical studies showing that pallial/cortical neuron numbers are higher than expected in birds [7**]. Interestingly, these insights have created a new avian ‘intelligence’ hierarchy with corvids, referred to recently as ‘feathered apes’, placed on the same rung as great apes and pigeons languishing at the bottom of the ladder [6]. What is the evidence for this cognitive hierarchy, both in terms of neuroanatomy and behavior? The last decade has brought completely new insights into this discussion. This paper is about these developments.

Comparing brains

Until very recently comparative neuroanatomists were mostly dealing with brain weights. Now, novel techniques allow us to precisely estimate neuron numbers and it appears that these may constitute a more relevant metric to evaluate species’ abilities [8]. For example, primates possess more neurons per unit of brain mass than any other mammalian order [9*]. Since humans and great apes have the highest brain weights among primates, they also have the most neurons [10]. This holds especially true for the cortex in which humans hold more neurons than the elephant, despite the elephant’s cortex being two-fold larger [8,11]. Very recently, similar data have been obtained for birds [7]. This study shows that in primates, parrots, and songbirds a doubling of brain weight goes along with a doubling of neuron numbers. In other mammalian orders, however, a doubling of brain weight is associated with a comparably smaller increase of neurons. However, there is one important difference: neuronal density in parrots and songbirds is drastically higher when compared to primates. Specifically, when compared to a comparably sized primate brain, parrots and songbirds hold more than double the number of neurons. In addition, while in primates approximately 19% of all neurons are cortical, in parrots and songbirds the corresponding numbers of pallial neurons are 55% and 61%, respectively [7**,9*]. For example, while rooks and marmosets have approximately the same absolute brain size, rooks have more than 3 times more pallial neurons. So, are rooks three times smarter than marmosets? We do not know but possibly neuron numbers may only help to define

functional boundary conditions but cannot be used as readout for cognitive prowess. This becomes salient when comparing parrots and corvids with apes [12]. While cognitive studies show these animals to be cognitively on par, their pallial neuron numbers are not (kea: 1.28 billion, raven: 1.2 billion, chimpanzee: 7.4 billion neurons; [7^{**},11,12]). Thus, cognitive abilities are similar while neuron numbers differ widely (Figure 1).

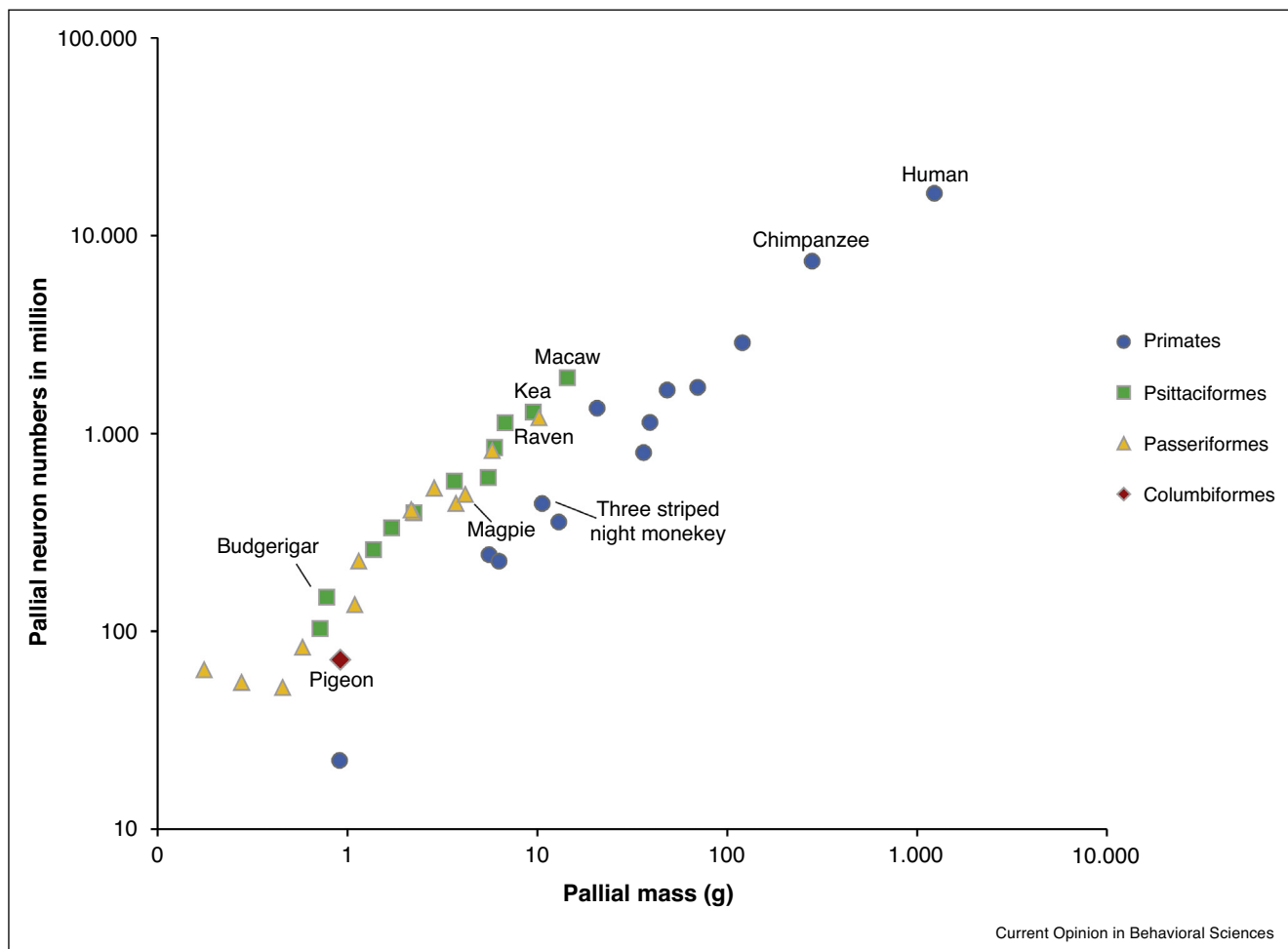
What about the humble pigeon? The pigeon telencephalic connectome is similar to that of monkeys and cats [2] but pallial neuron numbers in pigeons are 6, 11, and 17 times lower than those in magpies, rooks, and ravens, respectively [7^{**}]. Similarly, they are 27 times lower than in the Blue Macaw and even two times lower than in budgerigars [7^{**}]. While these neuronal metrics appear to justify the division between ‘feathered apes’ (parrots and corvids) and ‘bird brains’ (pigeons), does this division also

hold in terms of cognition? Here, we review five areas of cognition in which studies with similar procedures were employed with pigeons, corvids, and primates. As we will make clear, while the neuronal metrics may justify the division between feathered apes and bird brains, the cognitive abilities of these species are much more similar than one may expect.

Short-term memory

Short-term memory is a core component of higher cognition and there are hardly any cognitive abilities that do not rely on it. Short-term memory capacity closely correlates with fluid intelligence in humans [13] and may define limits of ongoing cognitive performance [14]. Humans have a visual short-term memory capacity of 4–5 items [15]. When trained to remember arrays of 2–6 colored squares and detect which of two squares had changed color, this range is reduced to 2–4 items [15–17]. When

Figure 1



Pallial neuron numbers per pallial mass in Primates, Psittaciformes (parrots), Passeriformes (songbirds) and Columbiformes (pigeon). Note that parrots and songbirds are shifted towards higher neuron numbers per pallial mass, while pigeons are about on the primate regression. Specified data points are examples mentioned in the main text. Figure is based on data from [7^{**},10,11,50].

this design is used identically on humans, macaques, and pigeons, humans reach a memory capacity of 2.5 items and outperform monkeys and pigeons by 27.3% and 15.4%, respectively [18]. Pigeons require extensive training, but then display a slightly higher short-term memory capacity than monkeys. The results of humans, monkeys, and pigeons were all characterized by an inverse power-law function fit to d' values for the display sizes. Thus, visual short-term memory declines with memory load with highly similar functional relationships, making it likely that similar underlying processes operate across these three species. A recent study [19] conducted a similar procedure with carrion crows and discovered an identical capacity to that of monkeys [20]. Taken together, short-term memory capacity in pigeons, carrion crows, and monkeys is largely on par, while humans are at least one item ahead [21].

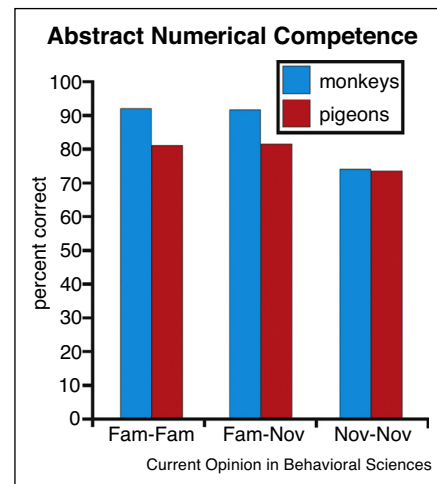
Object permanence

Object permanence refers to the ability to understand that items that are temporary out of view do not cease to exist. In children, this ability develops in a staggered manner across the first 2 years of life, advancing from stage 1 (*i.e.*, not searching for an object that disappeared out of sight) to stage 6 (*i.e.*, tracking disappeared objects through sequential invisible displacements). Great apes pass these tests [22], as do corvids and parrots [5**]. Ring doves, close relatives of pigeons, only reach stage 4 [23]. That is, they can find a hidden object after its disappearance but are unable to solve a sequential object displacement. Typical for stage 4, the doves committed the so-called A-not-B error, searching for the object where they had previously found it even when the object had been visibly hidden in another location.

Abstract numerical competence

Numerical competence encompasses the nonverbal concepts of quantity and rank [24]. Indeed, several species are known for their advanced numerical competences, incl. corvids [25*]. With respect to quantity, Brannon and Terrace [26] were the first to demonstrate that non-human primates' abilities also extend into more abstract representations of number. Specifically, they demonstrated that monkeys trained to order stimuli containing one, two, three, and four elements in ascending order, could correctly order stimuli containing numbers of elements well outside the training range (*e.g.*, seven and nine). Scarf *et al.* [27] replicated this experiment with pigeons with nearly identical experimental procedures. While pigeons required significantly more trials to learn the task relative to the monkeys, they displayed an identical level of competence when tested on quantities outside the training range (Figure 2). Behavioral traits suggest a shared number representation between monkeys and pigeons. For example, pigeon's responses were not only constrained by Weber's law, with discrimination performance dependent on the ratio between

Figure 2



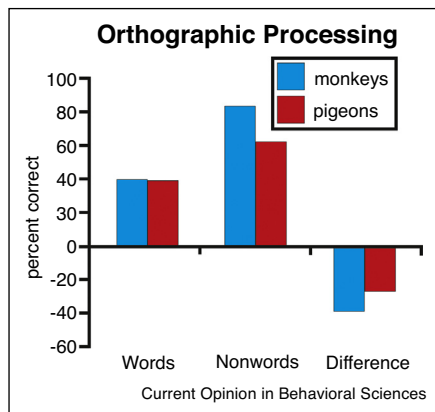
The performance of monkeys and pigeons discriminating between pairs of numerosities involving two familiar numerosities (Fam-Fam), a familiar and a novel numerosity (Fam-Nov), and two novel numerosities (Nov-Nov).

numerosities, their Weber fraction is with 0.36 also on par with monkeys [28], but not at the level of chimpanzees (0.17) [29].

Orthographic processing: parallels to human word learning

Animals may never be able to acquire human language, but this does not preclude them from informing us about the mechanisms that underlie the early stages of human word learning. For example, we can investigate their ability to acquire an orthographic code (*i.e.*, the statistical code that defines words). Grainger *et al.* [30] trained monkeys to discriminate between written four-letter strings that were either words (*e.g.*, DONE) or gibberish (*e.g.*, TOCT). Not only did their monkeys easily acquire a large vocabulary of words but, when transferred to novel words, they were able to classify them as words from the very first trial. Astonishingly, using virtually the same procedure, pigeons are on par with primates when it comes to orthographic processing [31**], also displaying the ability to correctly classify written novel words they have never seen before (Figure 3). Critically, the pigeon's similarity with the monkeys goes beyond simply their success with novel words. To borrow from those working with apes [32] and corvids [33], the study of Scarf *et al.* [31**] also meets the criteria for the signature-testing approach, with pigeons displaying the same biases and errors in their word classifications as primates. For example, just like for the monkeys, the pigeon's ability to classify nonwords correctly was related to the nonwords' orthographic similarity to words as measured in the Levenshtein distance. Indeed, if anything, the tendency of pigeons to mis-categorize transposed words [31**] was

Figure 3



The percentage of trials on which monkeys and pigeons classified 50 novel words as nonwords. The negative difference value for both groups reflects the fact that compared to actual nonwords, they were less likely to classify a novel word as a nonword.

even more similar to that of humans [34] than the performance of the monkeys [30].

Mirror self-recognition

In 1970, Gordon Gallup marked chimps with dye on their face such that they could only see it with a reflective surface [35]. When presented with a mirror, chimps spontaneously started touching the mark. This result is often seen as evidence for awareness about one's physical appearance [35]. Many species have now been studied with this deceptively simple test and only a few have passed. Within primates, chimpanzees and orangutans pass, gorillas rarely do, while gibbons and monkeys fail [36]. Monkeys, however, can be trained to succeed. Chang *et al.* [37] rewarded monkeys for touching spots on their body that were highlighted with a laser beam and that they could only see in a mirror. The monkeys learned to do so and then spontaneously started to use mirrors to look at hardly visible parts of their body. Thus, training seemed to induce the notion of self-recognition, suggesting that self-awareness may be a graded mental condition [38].

Gallup's procedure has also been employed with birds and, at least initially, all but one species failed [39]: Prior *et al.* [40] marked magpies below their beak with either small black or brightly colored stickers and tested the birds with or without a mirror. Black stickers were hardly visible against the black plumage while colored stickers showed high contrast. Two out of the five tested magpies scratched off the colored stickers only when a mirror was present, clearly demonstrating evidence for mirror self-recognition. More recently, Soler *et al.* [41] failed to find similar evidence of self-recognition in jackdaws and suggested Prior *et al.*'s [40] successful magpies may have simply passed the task by feeling the stickers on their

plumage. This, however, is unlikely since the magpies had worn stickers in *all* trials, but only demonstrated self-recognition when colored stickers were used and the mirror was present. Finally, Clark and Kelly [42] tested Clark's nutcrackers with several procedures incl. that employed by Prior *et al.* [40]. One individual nutcracker passed all tests of mirror self-recognition.

Epstein *et al.* [43] and later Uchino and Watanabe [44] successfully trained pigeons to peck at a spot on their bodies that they could only see in a mirror in order to receive food. In neither study, however, were the pigeons reported to subsequently use the mirrors in a similar manner to the monkeys in Chang *et al.*'s [37] experiment. Thus, when the mark-and-mirror test is applied to primates, only humans, chimps, and orangutans succeed. In birds, two corvid species are successful. Monkeys fail, as do pigeons, but both can be trained to display the behavioral sequences that some apes and corvids spontaneously show. After which, monkeys begin to spontaneously use the mirror while pigeons do not. Overall, these data speaks for a graded representation of self-awareness, with pigeons being located at the lower end. However, it is also possible, that monkeys have the capacity for self-recognition but just need training to use a mirror to express it.

Conclusions

In summary, recent neuroanatomical studies show that pallial neuron numbers in corvids are about 2–6 times lower than in large monkeys and apes but 6–17 times higher than in pigeons. These numbers suggest a very clear cognitive hierarchy with apes being at the top, followed by corvids and pigeons. Our review of five areas of cognition, in which highly similar tests were employed across primates, corvids, and pigeons, presents a much more diverse and nuanced pattern. Not only are corvids on par with apes, but also pigeons fare much better than expected. In fact, on three of the five tasks (short-term memory, abstract numerical competence, and orthographic processing) pigeons are also on par with primates, while they seem to fall short on two (mirror-self recognition and object permanence). In essence, this suggests there is no such clear dividing line between 'feathered apes' and their bird brained cousins. When facing such a pattern, we have to consider that we might be asking the wrong questions when comparing cognition in animals.

We inherently assume that cognitive differences should produce dichotomous result (*i.e.*, 'fail' vs. 'success') while ignoring the fact that many tasks can be learned and performed in a number of different ways. As outlined above, pigeons can learn extremely complex tasks, a testament to their complex cognitive abilities. However, while their terminal level of performance may be comparable to that of primates, other differences become visible. For example, while pigeons perform equally to monkeys on change detection tasks, they do not transfer

easily to other kinds of stimuli [45], and other delay lengths [46]. Pigeons also discount more steeply in delay tasks [47], experience more interference when moving from one stimulus set to another [17], acquire demanding cognitive tasks much slower [27], and, different from corvids [48], require more exemplars to learn an abstract rule [17,49]. It is important to emphasize that, in all of these tasks, pigeons match primates or corvids in both their terminal level performance during training and in the principle mechanisms with which they process task contingencies [17]. Thus, by focusing on final test results only, we neglect more subtle species-typical differences of cognition. Our more nuanced view enables us to formulate much more specific hypotheses regarding the added value of higher neuron numbers. This extra dosage of neuronal power might not necessarily be needed to possess a certain cognitive ability, since this is in principle already possible with smaller brains. But, this neuronal surplus may translate into faster and more flexible learning, making the acquisition of certain abstract abilities a much easier task.

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