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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

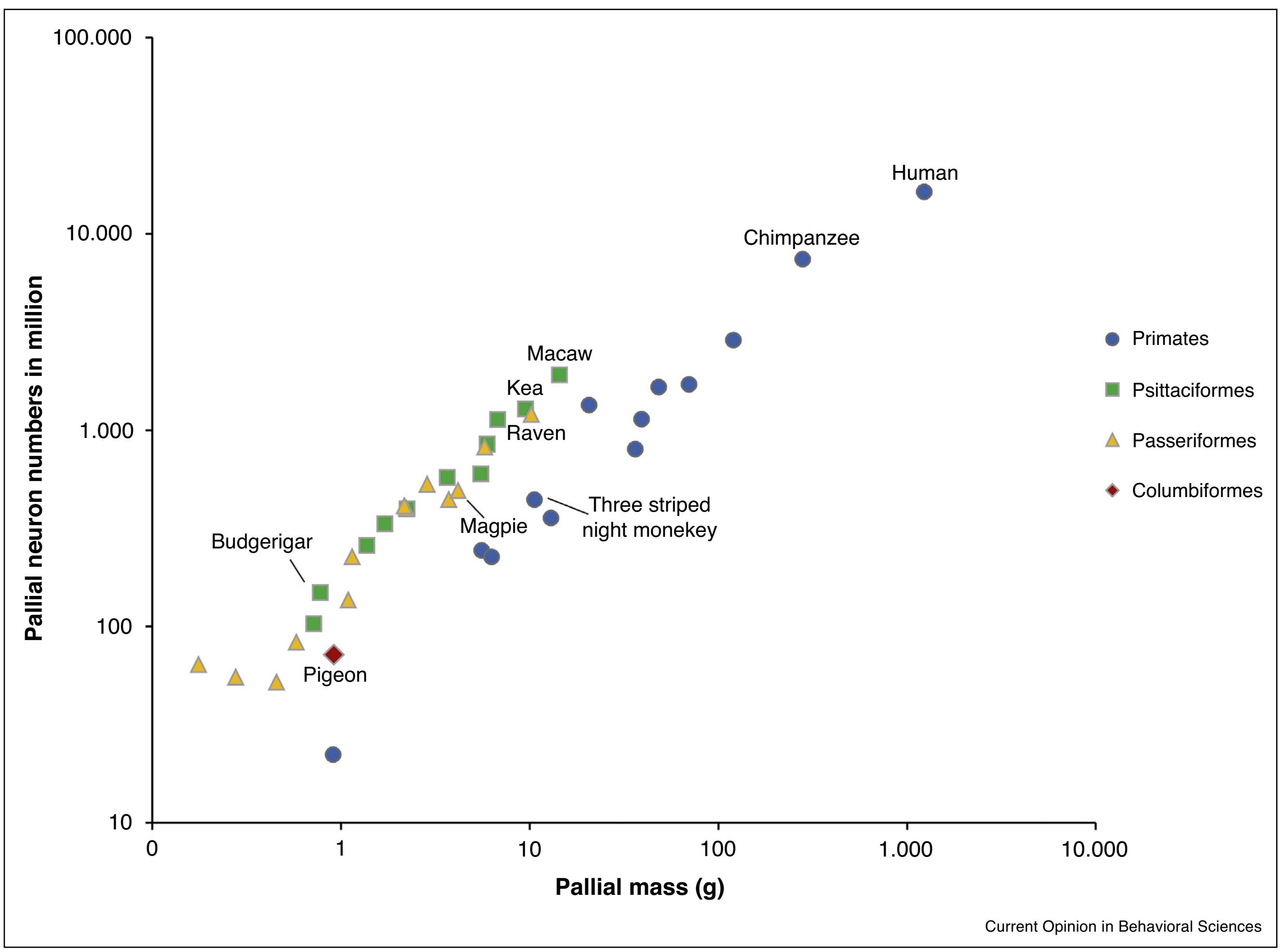
Until very recently comparative neuroanatomists were mostly dealing with brain weights. Now, novel techniques allow us to precisely estimate neuron numbers and it appears that these may constitute a more relevant metric to evaluate species' abilities [8]. For example, primates possess more neurons per 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].