

A new approach to comparing problem solving, flexibility and innovation

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Comparative cognition aims at unfolding the cognitive processes underlying animal behavior and their evolution, and is concerned with testing hypotheses about the evolution of the brain and intelligence in general. It is a developing field still challenged by conceptual and methodological issues. Systematic cross-species comparisons of cognitive abilities, taking both phylogeny and ecology into account are still scarce. One major reason for this is that it is very hard to find universally applicable paradigms that can be used to investigate the same cognitive ability or ‘general intelligence’ in several species. Many comparative paradigms have not paid sufficient attention to interspecific differences in anatomical, behavioral and perceptual features, besides psychological variables such as motivation, attentiveness or neophobia, thus potentially producing misrepresentative results. A new stance for future comparative research may be to establish behavioral and psychological profiles prior or alongside to comparing specific cognitive skills across species. Potentially revealing profiles could be obtained from examining species differences in how novel experimental (extractive foraging) tasks are explored and approached, how solutions are discovered and which ones are preferred, how flexibly multiple solutions are used and how much individual variation occurs, before proceeding to more detailed tests. Such new comparative approach is the Multi-Access-Box. It presents the animal with a novel problem that can be solved in several ways thus offering the possibility to examine species differences in all the above, and extract behavioral and perceptual determinants of their performance. Simultaneously, it is a suitable paradigm to collect comparative data about flexibility, innovativeness and problem solving ability, i.e., theoretical covariates of ‘general intelligence’, in a standardized manner.

Understanding the function, development and evolution of complex brain structures, remains a major scientific undertaking involving numerous disciplines and viewpoints.¹ The contemporary field of ‘comparative cognition’ is concerned with how different species acquire, process, store and use information from their environment and how in turn the environment has shaped these cognitive processes in the course of evolution.^{2,3} By

comparing cognitive adaptations to ecological and social environments in distantly and closely related species, comparative cognition may also permit the testing of hypotheses about convergent neural structure evolution in large brained animals.^{4,5}

Yet, such systematic cross-species comparisons taking both phylogeny and ecology into account (such, for example, as the studies by Balda and Kamil;⁶ Balda et al.;^{7,8} Bednekoff et al.;⁹ Clayton and Krebs;^{10,11} Olson et al.;¹² Tebbich et al.)⁵ are only in their early stages. Instead, comparisons of cognitive abilities across different species emerge in the literature typically either prompted by the discovery of hitherto uncharted abilities on certain taxa or through the expansion of an established paradigm to other species, often without consideration of the different ecological backgrounds. Thus, much of the published comparative work as yet consists of reports of specific cognitive abilities in different species in a yes/no tick list manner but without standardized testing procedures. Yet, unfolding the evolution of cognitive abilities through comparative research is not unjustly considered a notoriously complex and contentious topic. One major methodological issue is the difficulty of finding universally applicable paradigms that can be standardized and that are ecologically valid for the species to be compared.⁴ Additionally, the field is challenged by several other conceptual and methodological difficulties.

Conceptually, the comparison of cognitive abilities across species is a delicate topic, since cognitive abilities may be functionally related though mechanistically distinctive in different species, particularly if their brains anatomies have diverged. Furthermore, there are vast interspecific differences in perception, manipulatory skills, motivation, etc that are methodologically relevant.^{13,14} Research on cognitive abilities is typically focused on the outward manifestation of potentially complex inner cognitive processes that are to date not directly observable and quantifiable without MSR (which is so far impossible to administer in unrestrictedly moving animals) and that may vary considerably between species. They may consist of complex interplays of different brain regions that could differ between species. An even greater problematic applies to cross-species comparisons of ‘intelligence’, given that ‘intelligence’ ought to comprise flexible interaction and integration of not just one, but many cognitive abilities and associated processes. Accordingly, it is hard to pinpoint and target certain cognitive abilities in order to compare them across different species.

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Still more delicate and often neither meaningful nor revealing are comparisons based on a linear scale of ‘intelligence’.¹⁵ Different species are adapted to different environments, and thus, at the most, have been selected for qualitatively different forms of ‘intelligences’, which they employ in specific situations. This has also been termed domain-specific intelligence^{1,3,16-18} meaning that cognitive abilities can be restricted to specific contexts in which they occur.

The notion of ‘(domain-) general’ or ‘overall’ intelligence’ in contrast suggests that cognitive abilities could also be expanded to several domains and may allow species to behave flexibly, innovate, solve novel problems and thus cope with changes to their environment.¹⁹⁻²² Recent demonstrations that species differ in behavioral flexibility and propensity to adopt novel foraging behaviors, have revived discussions of overall animal intelligence.^{23,24} The predominant approach to investigate this has been to take innovation rate as proxy for intelligence²⁵⁻²⁹ and indeed correlation of overall brain size and/or size of the forebrain and rate of innovation were found in several animal groups including birds.²³ Yet, these results should be interpreted with caution, given that that innovation rate was measured crudely^{3,30} that innovation does not necessarily involve intelligence (exploration patterns can be equally important-see discussion below) and that equating brain size with intelligence is too simplistic.^{3,24}

With these caveats in mind and relinquishing any ranking of intelligence, the question why and in how far species differ in their ability to innovate and solve novel problems (abilities commonly associated with general intelligence), and why these abilities correlate with brain size, is valid to ask. The unconfirmed hypothesis behind this, that also concerns the evolution of human intelligence is that innovativeness, problem solving ability and flexibility e.g., in extractive foraging, are selected for in certain, e.g., unpredictable or harsh environments, because such species would better adapt behaviorally and cope with the changing living conditions than less flexible and innovative ones.³⁰⁻³² This leads to the idea that increased flexibility, innovativeness and problem solving ability ultimately added up to what one might call a ‘general’ or ‘overall’ ‘intelligence’. Alternatively, this may be affected by a species’ mode of exploration and trial- and –error learning strategies; species that try more are clearly more likely to acquire new behavioral strategies through individual learning.^{13,33}

These questions can only be addressed by systematic comparative data on innovative problem solving and flexibility and a standardized paradigm ecologically valid for a range of species.

Comparing Problem Solving: Different Approaches

Apart from the correlation studies mentioned above, the ability to innovate and solve novel problems flexibly, proxies for flexible cognitive capacities and potentially for domain-general intelligence, have not been investigated comparatively. Few experimental studies have specifically focused on innovativeness, and flexible problem solving per se.^{5,13,29,34-36}

The majority of experiments in animal cognition, in both the physical and social domain, present animals with specific problems and investigate how the animals solve them in order to

examine specific cognitive abilities/processes. These can be physical tasks,³⁷ social situations³⁸⁻⁴⁰ or time related.^{41,42} Mostly, these tasks have been tailored to be ecologically valid for one particular species, or have focused on contexts/ questions so specific that they could not be reproduced in other species easily (e.g., dolphins⁴³ ; food-storing scrub jays¹¹).

Other problem solving tasks, particularly in physical cognition, have secondarily become comparative paradigms and have been established as so-called ‘benchmark tests’ for examining the existence of certain cognitive abilities in different species, e.g., the ‘trap-tube’⁴⁴ for examining an understanding of causality in terms of surface continuity, Povinelli’s³⁷ cane task and Heinrich’s⁴⁵ ‘string-pulling task’ for testing responsiveness to connectivity etc. Most of these typically started off from a single experiment designed for testing a particular species and some subsequently applied to other species, sometimes without paying sufficient attention to species differences in morphological (hand or beak), behavioral (e.g., object exploration, affordance learning) and perceptual features (e.g., field of vision), in addition to psychological variables (such as motivational, emotional or attentional states, inhibitory control or neophobia/neophilia). Yet all these factors can potentially have a big impact masking cognitive skills actually present in a species and producing misrepresentative results.

Another methodological problem of comparative cognition is that paradigms are applied to many species, but with slightly converted methodologies (better fitting the newly compared species’ demands), hence at a cost of comparability. If the methodology is not standardised, it is hard to interpret the findings of comparative studies, because any detected differences between species could be owing to the different procedures. An odd handicap for comparative cognition in this context appears to be that modification or ‘improvement’ of an already used comparative paradigm, instead of merely replicating it in a new species, may increase the chances of a study to become published. Often however, a direct comparison would have been scientifically more valuable than yet another improvement to an existing experimental paradigm. Recently, this has been acknowledged and several research groups have begun to run comparative studies with the exact same methods.⁴⁶⁻⁴⁸

The difficulty of comparative cognition therefore is to find comparative paradigms that are compatible with many different species (i.e., that are ecologically valid for all the species to be compared, and not influenced by potentially confounding species-specific variables), and that have a standardised methodology that can be applied to different species in exactly the same way.

Because of the potentially confounding impact of different methodologies, the same cognitive ability should be investigated with not just a single but several tests with slightly different angles in any given species.^{1,49} Recently, comparative studies carry out entire batteries in different species tests, e.g., those comparing cognitive abilities in the social and physical domain.^{46,50} Yet, what is missing is to have a battery of tests establishing species differences that might affect performance in different cognitive tests, such as object exploration, motivation, attentiveness and fear/neophobia.⁵¹

The Multi Access Box Approach

A new such comparative approach is the Multi-Access-Box (MAB), recently published in PLoS One (see Fig. 1¹³). It presents the animal with a novel problem that can be solved in four different ways, thus offering the possibility to examine species differences in how novel problems are perceived, explored and approached and in which order solution(s) are discovered. This provides several data that can be used for establishing a behavioral (e.g., object exploration,) and psychological profile (e.g., motivation, flexibility, impulsivity, persistence, inhibitory control) and hence extract behavioral and perceptual determinants of different species' performance in the tasks. Simultaneously, it is a suitable paradigm to collect data about problem solving ability, innovativeness and flexibility, i.e., theoretical covariates of 'general intelligence', across species in a standardized manner.

The MAB approach comprises not just one but several solutions to an extractive foraging problem at the same time (food out of reach in the center of a transparent box), i.e. it consists of a battery of alternative tasks that all lead to the same goal. Two solutions (opening a window and pulling a string) could be discovered by haptic exploration (touching the box at particular sites), while the other two additionally required the handling of objects, either wooden sticks or marbles, as tools (inserting a ball or a stick tool into specific openings).

The other important feature of the MAB is that subjects were forced to continue exploring alternative solutions, once they had successfully discovered and consistently used one particular solution, by blocking the one in use. This creates an order system which allows to detect species differences in which tasks are approached and explored first and how, how many solutions are discovered and how fast, whether and how quickly the subjects switch between options or whether they focus or settle on particular ones, as well as which tasks are problematic and why. In this manner we can detect not only species differences in problem solving performance, but also learn about the various underlying non-cognitive factors that may affect it. Although designed for large scale comparisons of different closely- and distantly related species from different ecological backgrounds, the initial MAB study compared just two avian species from different families, a corvid, the New Caledonian crow (NCC; *Corvus moneduloides*) and a parrot, the kea (*Nestor notabilis*) (see Fig. 2). Both species are known for their large brains, their innovativeness and problem solving skills, but NCCs are naturally tool-using species while kea have not been observed to use tools in the wild, but are famous for their neophilia. Subjects were exposed to the transparent MAB with the food reward in the center, which could be extracted by the four different methods corresponding to the four walls of the box. Once a method was mastered, it was blocked and the bird's performance

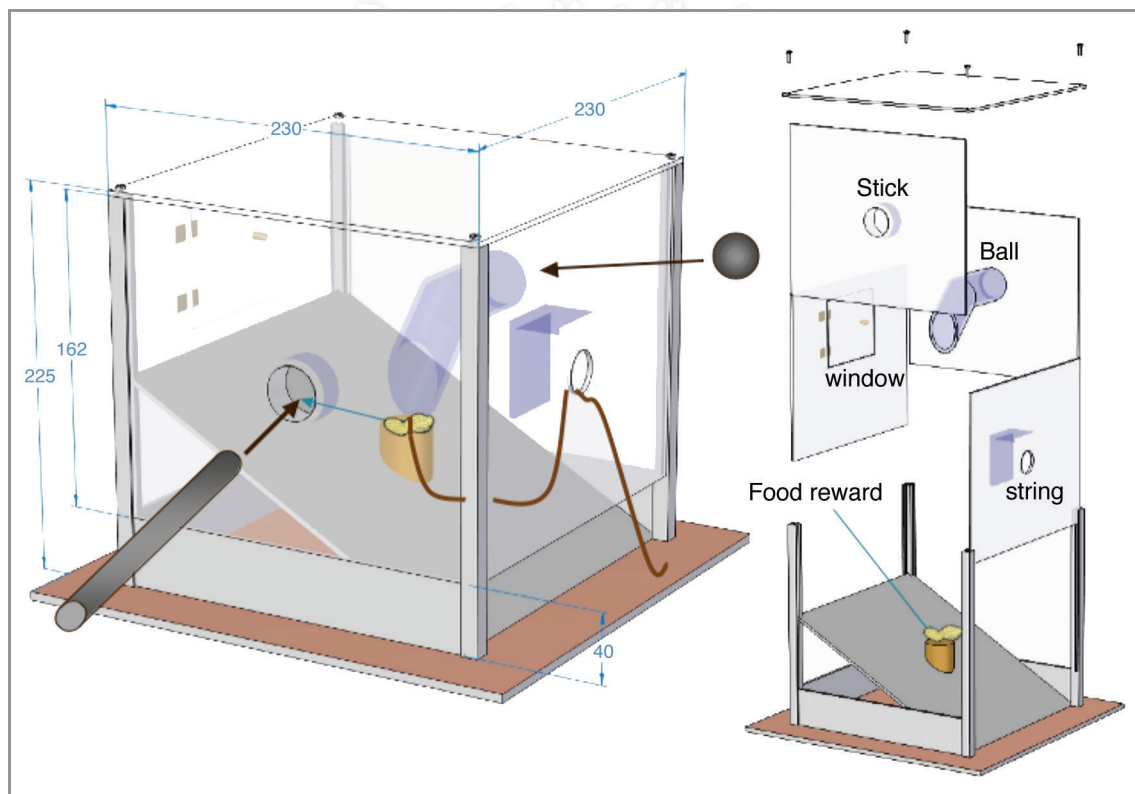


Figure 1. Multi Access Box (MAB) (as in PLoS ONE,¹³ Copyright 2011 by the Public Library of Science. Reprinted with permission of the author). A food reward presented in the center of a transparent box can be retrieved by one of four possible methods, which are built in the four walls of the MAB: opening a window, pulling a string, inserting a ball or inserting a stick tool. The walls can be replaced with blocked non-functional versions.



Figure 2. Kea and New Caledonian crow using the stick (left) and the ball-shaped (right) tool on the Multi Access Box.

in reaching criterion in any of the others was recorded until all four methods had been discovered.

Auersperg et al.¹³ found that one kea and one NCC detected all four solutions, demonstrating that the solutions offered were within both species' capacity. The kea were much quicker in discovering multiple solutions than the habitually tool-using NCCs and showed more individual variation. The keas were also more flexible once openings were blocked, switching to other solutions much quicker than the NCC.

Innovation rate as well as performance in this paradigm were strongly impacted by differences in exploration technique and neophilia rather than by cognitive discrepancies. The highly neophilic kea explored the apparatus more in a haptic than in a visual manner. They found its functional properties, while manipulating the affordances^{31,52} of the MAB they perceived as most salient. In contrast to the kea and probably due to their more visually guided exploration technique, the NC crows had problems solving the window solution. The window mechanism could not be deduced by visual inspection alone (without knowledge of hinge-mechanisms), but could be readily discovered by haptic exploration. Another difference was that the NC crows tended to persist with the first option that worked, whereas the kea, owing to their higher level of neophilia, switched between solutions.

Differences in beak morphology also affected the birds' performance: the kea had problems maneuvering the stick tool because of their beak curvature, whereas the crows with their straight beaks had a good grip of the tools. Yet, the NC crows used their straight beak more for pecking than tearing actions, which would have been advantageous in detecting the MAB apparatus's affordances in case of the window option (grasping and pulling the window crank).

An important new tool that could be incorporated in the MAB procedure and that could be revealing in comparisons of flexible problem solving may be 'reversal learning'.^{5,53-55} Species with different ecological backgrounds may have been selected for different strategies in trial and error learning and problem solving. In terms of energy pay-off it may, under certain circumstances, be advantageous to persist (e.g., in the case of NCCs fishing for particularly nutritious wood-boring beetle larvae in rotten wood as, which can take considerable time but has a high potential return).⁵⁶ In other contexts it may save energy to give up if something does not work and try something else instead. Reversal learning tasks reflect differences in flexibility and are informative of how fast animals can adjust their behavior to new external feedback, let go of previously reinforced behavioral patterns, but at the same time they offer a measure of persistence.

To illustrate how reversal learning could be implemented, we present some data not published in the original Auersperg et al.¹³ paper. Once a subject had discovered all solutions, we incorporated a reversal learning task for the two solutions incorporating a tool (see Fig. 2). For the two successful subjects, Uék, a NCC and Kermit, a kea, the last used tool option was blocked and the previous tool option was reopened. The results are presented in Table 1. As can be seen the crow required a similar amount of trials to relearn the previous option as the kea, although of course data on more individuals would be desirable.

The outcomes of Auersperg et al.¹³ illustrate how even diminutive differences in non-cognitive behavioral components such as neophilia or morphology can mask and/or interfere with the respective cognition involved and impact on the species' performance. It highlights how different performance in problem solving task are not always symptomatic of species differences in cognitive ability or general intelligence. It highlights in particular, what major impact differences in object exploration (haptic or visual exploration mode) and affordance learning, which have only recently become a topic in animal cognition,

Table 1. Reversal sessions for the two subjects (Uék = NCC; Kermit = Kea), which reached in all solutions of the Multi Access box. Session number in which reversal took place. Number of trials to reach criterion (9/10 correct)

Subject		Reversal trials		
		From Ball to Stick	From Stick to Ball	From Window to Stick
Uék	Session No.	15	14	13
	No. of trial to criterion	14	20	12
Kermit	Session No.	12	11	-
	No. of trial to criterion	20	13	-

can have on performance in artificial experimental tasks, and hence how this affects the comparability of two species in the same task.

In future comparative research, establishing behavioral and psychological profiles of the species to be compared ought to precede comparative tests of specific cognitive skills or general intelligence. This may help to identify problem solving tasks that are equivalently applicable to the target species and hence achieve a high degree of 'comparability' of the obtained data.

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