

The evolution of general intelligence

Judith M. Burkart

Department of Anthropology, University of Zurich, CH-8125 Zurich, Switzerland

Judith.Burkart@aim.uzh.ch

<http://www.aim.uzh.ch/de/Members/seniorlecturers/judithburkart.html>

Michèle N. Schubiger

Department of Anthropology, University of Zurich, CH-8125 Zurich, Switzerland

michele.schubiger@aim.uzh.ch

<http://www.aim.uzh.ch/de/Members/phdstudents/micheleschubiger.html>

Carel P. van Schaik

Department of Anthropology, University of Zurich, CH-8125 Zurich, Switzerland

vschaik@aim.uzh.ch

<http://www.aim.uzh.ch/de/Members/profofinstitute/vanschaik.html>

Abstract: The presence of general intelligence poses a major evolutionary puzzle, which has led to increased interest in its presence in nonhuman animals. The aim of this review is to critically evaluate this question and to explore the implications for current theories about the evolution of cognition. We first review domain-general and domain-specific accounts of human cognition in order to situate attempts to identify general intelligence in nonhuman animals. Recent studies are consistent with the presence of general intelligence in mammals (rodents and primates). However, the interpretation of a psychometric *g* factor as general intelligence needs to be validated, in particular in primates, and we propose a range of such tests. We then evaluate the implications of general intelligence in nonhuman animals for current theories about its evolution and find support for the cultural intelligence approach, which stresses the critical importance of social inputs during the ontogenetic construction of survival-relevant skills. The presence of general intelligence in nonhumans implies that modular abilities can arise in two ways, primarily through automatic development with fixed content and secondarily through learning and automatization with more variable content. The currently best-supported model, for humans and nonhuman vertebrates alike, thus construes the mind as a mix of skills based on primary and secondary modules. The relative importance of these two components is expected to vary widely among species, and we formulate tests to quantify their strength.

Keywords: brain size evolution; comparative approach; cultural intelligence; evolution of intelligence; general intelligence; modularity; nonhuman primates; positive manifold; psychometric intelligence; rodents; social learning; species comparisons

1. Domain-general and domain-specific accounts of human cognition

“Animal behavior is driven by instincts, whereas human beings behave rationally.” Views like these are still commonly expressed and deeply anchored in the Western worldview (e.g., Pinker 2010). A modern version of this dichotomy construes animals as having domain-specific, modular cognitive adaptations, whereas humans have domain-general intelligence. However, we now know that in human cognition, domain-specific components are ubiquitous too (Cosmides & Tooby 2013), perhaps even in complex cognitive tasks such as logical inference (Cosmides et al. 2010) or solving Bayesian probability problems (Lesage et al. 2013). At the same time, much evidence has accumulated that nonhuman minds are not exclusively made up of domain-specific specializations, but that domain-general cognitive processes may also be widespread. These empirical findings have implications for contemporary theories of the evolution of general intelligence, highlighted in section 3, provided it is established that general intelligence in animals is both real and refers to the same construct as in humans.

JUDITH M. BURKART is a senior researcher at the Department of Anthropology of the University of Zurich. She leads the Evolutionary Cognition Group and is interested in the cognitive evolution of primates. A main focus of the group concerns the role of systematic allomaternal care, present in callitrichid monkeys and humans, in the evolution of social, motivational, and cognitive processes.

MICHÈLE N. SCHUBIGER is a Ph.D. student of the Evolutionary Cognition Group, University of Zurich, and investigates general intelligence in marmoset monkeys. Currently, she is also a fellow in psychology, primate cognition, at Abertay University, Dundee, studying cognitive abilities in gibbons.

CAREL P. VAN SCHAİK is Professor and Director of the Department of Anthropology, University of Zurich. His main interests are socioecology and social evolution in primates, especially the primate foundations of human culture and intelligence. He wrote *Among Orangutans: Red Apes and the Rise of Human Culture* (Belknap Press of Harvard University Press, 2004) and the recent textbook, *Primate Origins of Human Nature* (Wiley-Blackwell, 2016), and has co-edited various volumes on primate behavior and conservation.

The evolution of general intelligence poses a major puzzle. Because modular systems may readily evolve (Pavlicev & Wagner 2012; Schlosser & Wagner 2004; Shettleworth 2012b; but see Anderson & Finlay 2014; Lefebvre 2014), the evolution of the mind as a set of domain-specific adaptations or modules can easily be imagined. Indeed, a small set of dedicated modules, without any domain-general cognitive abilities, to which additional modules can be added as needed, may be the ancestral state of vertebrate cognition. This perspective is so convincing that it has led to accounts of massive modularity, not only for animal cognition, but also for human cognition as well (reviews: Barrett 2015; Frankenhuys & Ploeger 2007; Hufendiek & Wild 2015).

Evolutionary pathways leading to the emergence of domain-general cognitive processes, on the other hand, may appear less straightforward, because such open-content processes translate far less reliably into fitness-enhancing behavior, and because they may also require disproportionate amounts of energetically costly brain tissue compared to domain-specific specializations (van Schaik et al. 2012). Consequently, compared to the evolution of additional cheap and reliable, domain-specific, specialized cognitive solutions to specific problems, the evolution of general cognitive processes might pose greater obstacles to natural selection. Nonetheless, humans possess general intelligence, and if general intelligence can also be found in nonhuman animals, we can attempt to identify the evolutionary processes that can lead to its emergence, including the specific case of humans.

The aims of this review are (1) to critically evaluate the evidence for general intelligence in nonhuman animals, and (2) to explore the implications of its presence in nonhumans for current theories of cognitive evolution. To achieve these aims, we will review the theoretical background and evidence from a variety of research traditions, such as animal behavior and psychology, psychometrics and developmental psychology, and evolutionary psychology. Whereas all of these fields share an interest in understanding how the mind works, they are not well integrated, and attempts at integration have not yet produced consensus (e.g., Eraña 2012; Evans 2011; 2013; Toates 2005). In this target article, we will therefore selectively focus on those aspects that are necessary to integrate the findings from animal studies on general intelligence with what is known about humans. As non-experts in several of these fields, we are aware that we may not fully represent all of the relevant aspects of the respective theories, let alone solve current controversies in individual fields. Nevertheless, we hope that this article serves as a first step in achieving the much-needed integration across these disciplines at a more fine-grained level, which will eventually enable the development of a more unified theory of cognitive evolution.

This article is structured as follows. We first briefly review conceptualizations of both domain-general and domain-specificity of human cognition, and use this as background to situate current evidence for general intelligence in nonhuman animals, which is increasingly reported in various species based on factor-analytical approaches. We examine alternative explanations for these findings and develop a set of empirical criteria to investigate to what extent a statistically derived psychometric factor does indeed correspond to general intelligence as broadly defined. Such criteria are

increasingly met in rodent studies but are strikingly underexplored in primates or birds.

Next, we discuss different evolutionary theories that may explain why and how general intelligence can be widespread in nonhuman animals even though it is not immediately obvious how it can reliably produce fitness-enhancing behavior. We argue that the broad version of the cultural intelligence approach (Tomasello 1999; van Schaik & Burkart 2011; van Schaik et al. 2012) can best account for the current body of evidence. We end by proposing a model that construes the mind of both humans and nonhuman vertebrates as a mix of truly modular skills and seemingly modular skills that are ontogenetically constructed using general intelligence abilities. We refer to them as primary and secondary modules, respectively. Species differences are likely with regard to the importance of these components, and we formulate tests to quantify their strength.

1.1. The positive manifold and general intelligence

Intelligence in humans has been intensely studied for more than a century (e.g., reviewed in Deary et al. 2010; Nisbett et al. 2012). It is broadly defined as involving “the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience. It is thus not merely book learning, a narrow academic skill, or test-taking smarts. Rather it reflects a broader and deeper capability for comprehending our surroundings – ‘catching on,’ ‘making sense’ of things, or ‘figuring out what to do’” (Gottfredson 1997, p. 13). This definition has received broad acceptance (Nisbett et al. 2012). In animals, intelligence is thought to involve an individual’s ability to acquire new knowledge from interactions with the physical or social environment, use this knowledge to organize effective behavior in both familiar and novel contexts, and engage with and solve novel problems (Byrne 1994; Rumbaugh & Washburn 2003; Yoerg 2001). Thus, general intelligence, as defined in either humans or nonhuman animals, stresses reasoning ability and behavioral flexibility.

The concept of human general intelligence is built on one of the most replicated findings in differential psychology. In humans, performance across tasks of different cognitive domains is positively correlated: the positive manifold. Factor-analytical procedures applied to large data sets of individual performance across tasks consistently reveal a single factor that loads positively overall and can explain a significant amount of variation, often termed *g* for (psychometric) general intelligence. Within this psychometric, factor-analytical approach, an individual’s loading on this factor thus estimates its intelligence. Performance in specific cognitive tasks (e.g., Raven’s Progressive Matrices) or test batteries (e.g., Wechsler Adult Intelligence Scale [WAIS]) is highly correlated with *g*, and is in fact often used as a proxy measure for it, for instance in studies aimed at localizing *g* in the brain (Burgess et al. 2011; Colom et al. 2006; Gläscher et al. 2010). In this article, we will speak of *general intelligence* when referring to the broad definition of Gottfredson (1997) that stresses reasoning ability and behavioral flexibility, and of *psychometric intelligence* when referring to the entity estimated by the psychometric variable *g*. For humans, it is generally assumed that *g* estimates general intelligence, based on the strong empirical correlations between the two, as reviewed below.

Psychometric intelligence, estimated through g , typically explains around 40% of variance in test performance, whereas the rest is explained by group factors and variance unique to specific tasks (Plomin 2001). It has been found that g in humans has a clear genetic foundation (Davies et al. 2011), and in the absence of adverse environments that compromise the complete deployment of an individual's capacity, heritability can explain remarkably high proportions of variance (Joshi et al. 2015; Nisbett et al. 2012). Furthermore, g has robust correlates in brain structure and function, such as brain size, gray matter substance, cortical thickness, or processing efficiency (Deary et al. 2010; Jung & Haier 2007). However, rather than being localized in specific brain parts, it seems to be a system-level property of the brain (Pietschnig et al. 2015). Finally, g is also a good predictor for various measures of life outcome, including school achievement, the probability of being in professional careers, occupational attainment, job performance, social mobility, and even health and survival. In particular, it is better at predicting such variables than specific cognitive abilities on their own (reviewed in Deary et al. 2010; Reeve 2004).

1.1.1. The structure of cognition. The structure of human cognition continues to be debated (e.g., Ortiz 2015). Nonetheless, the presence of g is now widely accepted due to the pervasive evidence from Carroll's (1993) seminal meta-analysis of over 460 carefully selected data sets on human cognitive ability. An influential account is Horn and Cattell's fluid-crystallized gf - gc model (see also Major et al. 2012). Fluid intelligence gf refers to the capacity to think logically and solve problems in novel situations independently of previously acquired knowledge, and to identify patterns and relationships, whereas crystallized intelligence gc refers to the ability to use skills, knowledge, and experience and crucially relies on accessing information from long-term memory. An explicit causal link from gf to gc is provided by investment theory (Cattell 1987), which is the developmental version of the gf - gc model and finds considerable empirical support (Thorsen et al. 2014).

An integrated version, the so-called CHC (Cattell-Horn-Carroll) theory, has been supported by several studies and is a widely accepted consensus model (McGrew 2009). The CHC model is hierarchical, placing a general factor g at the top, which affects both gf and gc . Most current models involve some hierarchical structure involving a general factor, g , and fluid intelligence, gf (but see, for instance, Bartholomew et al. 2009; Major et al. 2012; van der Maas et al. 2006). In fact, some have argued that gf and g represent the same entity (Kan et al. 2011), and the previously mentioned definition of intelligence in a broad sense in fact emphasizes elements of both constructs.

Some models of general intelligence that do not involve g are also still being considered. Van der Maas et al. (2006), for instance, have presented a dynamic model of general intelligence that assumes independent cognitive processes early in ontogeny. Over the course of development, the positive manifold emerges because of mutually beneficial interactions between these initially independent processes. To the extent that one agrees to equate general intelligence with the positive manifold, the mutualism model may be viewed as a model of general intelligence for human and nonhuman animals in which variation between species would reflect the extent to which mutually beneficial

interactions between cognitive processes arise during development. Because, across species, bigger brains require more time to mature than smaller brains (Schuppli et al. 2012), and thus have more opportunities to develop such mutually beneficial interactions, such a scenario is compatible with an evolutionary perspective.

1.1.2. Executive functions and intelligence. Closely related to general intelligence are executive functions, or EFs (Barbey et al. 2012; Blair 2006). EFs refer to "general-purpose control mechanisms that modulate the operation of various cognitive subprocesses and thereby regulate the dynamics of human cognition" (Miyake et al. 2000, p. 50). In other words, they are "a family of top-down mental processes needed when you have to concentrate and pay attention, when going on automatic or relying on instinct or intuition would be ill-advised, insufficient, or impossible" (Diamond 2013, p. 136). Three core EFs can be distinguished, namely inhibitory control (behavioral inhibition, cognitive inhibition, and selective attention), working memory (Baddeley 2010), and cognitive flexibility.

Various measures of EFs have shown strong correlations with g/gf . Whereas the average correlation between working memory and g is 0.72, in some studies using latent variable analysis, it even reached identity (Colom et al. 2005; Nisbett et al. 2012), leading some authors to suggest that the two cannot be distinguished from each other (Royall & Palmer 2014). That g and EF are closely related is consistent with two further lines of evidence. First, working memory can be trained, and these training gains can translate into gains in general intelligence even though not all procedures are effective, and it is not always clear whether the training affects working memory per se or instead improves learning strategies (reviewed in Klingberg 2010; Morrison & Chein 2011; Nisbett et al. 2012; Shipstead et al. 2012). Second, growing up bilingually, which makes high demands on a variety of EFs on a routine basis, is associated with stronger EFs in non-linguistic contexts, and thus with g (Abutalebi & Clahsen 2015; Bialystok et al. 2012; Rabipour & Raz 2012). Nonetheless, because EFs do not provide the logical problem-solving functions and learning that are the hallmark of general intelligence (Embretson 1995), some aspects of general intelligence are independent of EFs.

In sum, evidence for domain-general intelligence in humans, estimated by the first factor derived in psychometric, factor-analytical approaches, is pervasive, and is backed up by neurobiological evidence and various correlates of life-outcome measures. The psychometrically derived g factor is thus consistent with the broad notion of general intelligence, which stresses reasoning ability and behavioral flexibility and invokes cognitive processes such as learning and remembering, planning, and executive functions. This conclusion raises the question of the evolutionary origin of general intelligence in humans, which we will address by reviewing recent developments in the nonhuman literature. To do so, we will review evidence for g in animals, and whether it is warranted to assume that g in animals is also consistent with a broader notion of general intelligence.

Intelligent behavior needs to be distinguished from behavior that may appear intelligent but lacks flexibility (Shettleworth 2012a). Intelligent behavior in animals is often referred to as behavior that shows some degree of flexibility and emanates from some kind of mental

representation rather than immediate perception only (Tomasello & Call 1997). For instance, when digging wasps are interrupted anywhere in the sequence of actions involved in measuring the size of a hole to place a larva together with a prey item into it, they must start again at the very beginning of the behavioral sequence (Wooldridge 1968). Thus, many behaviors that at first sight look like they are the product of reasoning or learning turn out to be inflexible adaptations or modules (Sherry 2006). A collection of such dedicated adaptations presumably represents the ancestral state (e.g., Shettleworth 2012a; 2012b), and thus the null model against which the hypothesis of general intelligence has to be tested. Before turning to nonhuman animals, we will therefore provide an overview of domain-specific, modular conceptions of the mind that have been put forward particularly, but not exclusively, by evolutionary psychologists.

1.2. Cognitive adaptations and domain specificity

A domain-general factor of intelligence can be contrasted with domain-specific cognitive mechanisms or adaptive specializations (Cosmides & Tooby 2002). The basic idea is that whenever a fitness-relevant cognitive problem arises repeatedly and predictably over long periods of time in a given species, natural selection favors a genetically based, developmentally canalized (“hardwired”) solution to this problem. For instance, natural selection may provide a species with a particularly strong spatial memory to retrieve stored food, without endowing it with more-powerful cognitive capacities in other contexts (Sherry 2006). Importantly, domain-specific mechanisms cannot be used in domains other than the ones for which they evolved, whereas domain-general mechanisms can be used to solve problems across domains.

Thus, the mind of animals, including humans, can be conceived of as a collection of adaptive specializations, often construed as modules, each of which evolved to solve a specific adaptive problem (Duchaine et al. 2001). Notice that a mind uniquely made up of these kinds of specific adaptations is arguably incompatible with standard accounts of intelligence, because virtually no learning and flexibility are involved. Similarly, none of these specific cognitive adaptations require the presence of the domain-general processes underlying intelligence such as executive functions.

1.2.1. Modularity and general intelligence. A modular organization of mind is particularly appealing to evolutionary thinking because modular systems allow parts to be removed, added, or modified without affecting the function of the structure as a whole. Therefore, modular systems may be more evolvable or even the only evolvable systems (Clune et al. 2013; Pavlicev & Wagner 2012; Ploeger & Galis 2011; Schlosser & Wagner 2004; Shettleworth 2012b). Thus, whenever conditions are sufficiently stable or at least predictable across generations, natural selection should favor solving recurrent fitness problems via modules rather than via general cognitive processes, because the former solve these problems on average quickly, effortlessly, and efficiently (Cosmides et al. 2010) and can presumably evolve more readily. General intelligence, in contrast, is thus expected to evolve under conditions of social or environmental unpredictability. Solutions to these evolutionarily novel problems have to

be acquired effortfully, via slow learning (e.g., Geary 2005; Geary & Huffman 2002).

The advantages of a modular solution to recurrent fitness problems, however, are not necessarily as straightforward. First, the fundamental assumption that a modular solution is indeed more evolvable can be questioned on both empirical and conceptual grounds (e.g., Anderson & Finlay 2014; Bolhuis et al. 2011; d’Souza & Karmiloff-Smith 2011; Lefebvre 2014). Empirical evidence for a direct mapping of specialized adaptive behavioral functions to specific modular neural units is actually rare, even for neural systems as simple as those of invertebrates. Novel adaptive functions seem mostly to be achieved via massive re-use of neural tissue rather than via the addition of encapsulated neuronal pools. Conceptually, the evolvability argument seems largely incompatible with what is known about short-term neuromodulation, brain plasticity over the life span, response to damage, and ontogenetic principles of brain development. The a priori evolvability argument, therefore, does not lead to an unambiguous conclusion as to the superiority of domain-specific over domain-general organization.

Second, the other advantage of modularity – fast, effortless, and ultimately efficient solving of evolutionarily recurrent fitness problems – may hold only for particular notions of modularity, such as Fodorian modules (Fodor 1983). These are thought to be domain-specific functional units that process distinctive input stimuli using distinctive mechanisms. In particular, a module is thought to exclusively process information from a specific domain and to produce a correspondingly specific output in the form of representations and/or a behavioral response. Fodor listed criteria that must – at least to “some interesting extent” (Fodor 1983, p. 37) – be fulfilled by a functional unit to qualify as modular. These criteria include domain specificity, mandatory processing, high speed, production of shallow outputs (i.e., not requiring extensive processing), limited accessibility, a characteristic ontogeny (reliable emergence without explicit learning), a fixed neural architecture, and informational encapsulation (meaning it is not affected by other cognitive processes, a criterion thought to be particularly important). Paradigmatic examples of Fodorian modules are optical illusions. Accordingly, the presence of modules involving the processing of sensory information is widely accepted, and that their speed and efficiency are beneficial is obvious. However, a modular organization has also been proposed for more higher-level cognitive processes including ones related to folk psychology (e.g., processing of faces and facial expressions, theory of mind, cheater detection), folk biology (e.g., animate-inanimate distinction, flora-fauna), or folk physics (e.g., movement trajectories, gravity biases, representation of space, solidity, and causality; summarized in Geary 2005). Indeed, massive modularity accounts hold that the mind is exclusively made up of modules (Barrett 2015; Carruthers 2005; Sperber 2001).

Massive modularity would appear to be irreconcilable with general intelligence (and therefore with the ability to solve evolutionarily novel problems), but much of the long-standing controversy about the massive modularity hypothesis of the human mind comes down to the use of different notions of modularity (see also Barrett & Kurzban 2006). Indeed, a variety of highly divergent notions have developed (Barrett 2015; Barrett & Kurzban 2012; Chiappe &

Gardner 2012; Coltheart 2011; Grossi 2014; Mahon & Cantlon 2011), and many of these are much broader than the Fodorian one (e.g., Sternberg 2011). Because they also encompass the possibility of overarching, central control processes (Carruthers 2011), they are entirely compatible with the coexistence of domain-general processes and general intelligence (Barrett 2015; Carruthers 2011). In fact, Carruthers (2011) argued that most modules are specialized learning systems. Such broad notions of modularity, however, arguably no longer support the original idea of automatically providing fast and frugal solutions to recurrent fitness problems.

Unlike many proponents of massive modularity in humans, comparative behavioral biologists and comparative psychologists typically refer to notions of modularity that hew closely to the classical Fodorian modules, that is, dedicated, inflexible cognitive adaptations that have evolved in response to specific recurrent fitness-relevant problems (e.g., Fernandes et al. 2014; Shettleworth 2012a; 2012b). Functional specialization here is mostly used in the biological, ultimate sense—that is, referring to the specific adaptive pressures that gave rise to the evolution of specific dedicated modules. This perspective is grounded in research traditions such as neuroecology (Sherry 2006) that have provided empirical evidence for the occurrence among animals of dedicated cognitive adaptations, such as spatio-temporal memory abilities in food-caching species, birds in particular (Brodin 2010; Pravosudov & Roth 2013). These cognitive adaptations typically do not generalize to problems for which they did not evolve.

A mind composed of such dedicated adaptations represents a plausible null model, and indeed a plausible ancestral state of vertebrate cognition. Dedicated adaptations and general intelligence can obviously coexist (e.g., Cosmides et al. 2010; Geary 2005)—for instance, when the output of modules serve as inputs for intelligent reasoning, which may be responsible for the fact that in humans general intelligence predicts reasoning ability even in evolutionarily familiar contexts (Kaufman et al. 2011). The key questions with respect to the evolution of general intelligence, therefore, are how central, domain-general processes could evolve on top of domain-specific adaptations, whether and to what extent they also exist in nonhuman animals, and what adaptive benefits drove their evolution.

1.2.2. Adaptive canalization beyond modularity. Strictly domain-general approaches that construe the mind as a general-purpose computer face several well-known problems (Cosmides & Tooby 1994; Cosmides et al. 2010; Frankenhuis & Ploeger 2007; Heyes 2003; Kolodny et al. 2015; see also Table 1). First, an agent has to efficiently identify relevant information and filter out irrelevant information in the process of problem solving, a challenge known as the frame problem. Second, once the relevant information has been identified, the agent has to decide what to do with it. To do so, she has to solve the problem of how to pick and combine correct, adaptive behavioral options or cognitive processes out of an exponentially growing number of possibilities (the problem of the combinatorial explosion) or to learn important associations and skills in a limited period of time despite dealing with relevant stimuli that occur at a low rate (the poverty of the stimulus problem). Third, correct responses have to be made quickly and efficiently (the urgency problem). And

fourth, while doing so, the agent has to find general, rather than only locally successful, solutions (the functionality problem). It is thus beyond doubt that some canalization of cognitive processes is necessary.

Evolved Fodorian modules (referred to as “cognitive adaptations” by behavioral biologists and neuroecologists) are clearly one way of solving the problems highlighted previously, in particular when they define the entire sequence from the acquisition of information to the adaptive behavioral response. However, they are not necessarily the only possible way, and natural selection may also overcome these problems in a different way that would allow domain-general abilities to evolve. A straightforward solution to this problem would be that domain-general abilities coevolve together with adaptive canalizing mechanisms that guide how general abilities are applied. Canalizing mechanisms can have a phylogenetic origin, such as a genetically predetermined preference for a certain category of stimuli: for example, the preference for faces in human infants (Shah et al. 2015). Alternatively, they can have an ontogenetic origin, such as the propensity of chimpanzees from tool-using communities to automatically perceive a stick as a potential tool, compared to genetically indistinguishable chimpanzees from non-tool-using communities who do not recognize this affordance (e.g., Gruber et al. 2011).

Table 1 summarizes the phylogenetic and ontogenetic canalizing mechanisms that ensure that domain-general cognition produces adaptive behavior despite the problems highlighted previously. Unlike Fodorian modules, these mechanisms do not define the entire sequence from signal detection to behavioral output, but may be deployed at different stages during information processing. We will now examine the evidence for such domain-general canalization processes.

The first problem an individual faces is what to attend to in the continuous stream of stimuli coming in from different sensory modalities. This can be solved by innate dispositions or data acquisition mechanisms (also referred to as phylogenetic inflection: Heyes 2003). Importantly here, innateness is not equivalent to inflexibility because innate dispositions to pay attention to one stimulus over another can be conditional. For instance, an animal foraging for berries may have an attentional bias to perceive small red entities, but the same animal when exposed to a raptor will be biased to perceive only potential hideouts. Alternatively, animals can learn ontogenetically which targets are particularly worth attending to (ontogenetic inflection). Here, social guidance of attention may play a particularly important role. Ontogenetic inflection automatically arises whenever immatures follow the mother and later other conspecifics, and is even more powerful in species that follow gaze (Shepherd 2010). In many species, including humans, immatures are particularly attracted to everything conspecifics are interacting with, and immatures of some species, such as aye-ayes (Krakauer 2005), marmoset monkeys (Voelkl et al. 2006), or orangutans (Forss et al. 2015) are highly neophobic toward stimuli they have not witnessed their mother or other familiar conspecifics interact with. Natural selection can, therefore, favor the disposition to preferentially use social information to decide which stimuli to attend to, and thus leave the specific target of attention largely unspecified.

In a second step, the individual has to “decide” what to do with the stimuli that have captured its attention,

Table 1. Overview of some specific problems that a domain-general cognitive apparatus has to overcome in order to produce ultimately adaptive behavior, as well as potential solutions – that is, adaptive canalization mechanisms. Note that these solutions may be very general themselves, such as a preference for social learning. See text for references.

Problem	Domain-General Canalization Processes	Examples
The frame problem: <i>What to attend to?</i>	Input filters (phylogenetic inflection)	Facilitated detection of small red entities (when hungry) or dark openings (when chased)
Problems of combinatorial explosion and poverty of stimulus <i>What to do with the information?</i>	Socially guided attention (ontogenetic inflection)	Immatures following mothers, or following mothers' gaze
	Direct triggering, prepared learning	Flight reactions, learning to be fearful of snakes but not flowers
The urgency problem: <i>How to reach a quick, efficient response?</i>	Socially guided learning Integration with core knowledge ¹	Copying how to extract food from a matrix Embedding the expectation that objects always fall down in a straight line (gravity bias) with knowledge of solidity
	Innate response tendencies	Evolved modules, evolved heuristics (primary modules)
The functionality problem: <i>How to find generally, not only locally, successful solutions?</i>	Acquired response tendencies (automatization, secondary modules)	Learned heuristics to solve algebraic equations (secondary modules)
	Innate goals	Innate template of a safe burrow, or of good food
	Socially acquired end-state preferences	Learning by following mother what a good sleeping place is; copying the goals of successful individuals, conformity biases

¹That is, evolved cognitive domains that are fleshed out with experience; for example, Gelman (1990).

because input mechanisms filter incoming stimuli but do not produce behavior. Subsequent processes are therefore required to determine what to do with these stimuli without being stymied by the problems of poverty of stimulus and the combinatorial explosion. First, in the case of phylogenetic inflection, coevolution of input mechanisms and response tendencies is frequent (Lotem & Halpern 2012), as when a moving stimulus in the sky automatically triggers a flight reaction, but also when individuals are more likely to associate a snake (but not a flower) with fear (Cook & Mineka 1989), or a taste (but not an auditory stimulus) with subsequent nausea (known as biologically prepared learning or the Garcia effect: Garcia & Koelling 1966). Second, in the case of ontogenetic inflection, social learning can also affect how the individual processes a stimulus that has come to its attention. Third, the stimuli that have attracted an individual's attention may be integrated with innate bodies of knowledge, so-called core knowledge (Gelman 1990; Spelke & Kinzler 2007) or psychological primitives (Samuels 2004), and so give rise to more elaborate skills and conceptual systems (Carey 2009).

A third problem for the individual is that decisions often have to be made under time pressure (the urgency problem). Evolved modules, heuristics, or direct and reflexive triggering of responses are particularly good at providing fast responses because they bypass central processes. But quick and efficient responses can also be achieved in evolutionarily novel contexts, such as solving algebraic equations or playing chess, if a learned heuristic approach becomes an automated subroutine and can be applied effortlessly (Bilalić et al. 2011; Chang 2014). Such problem solving

has similar surface properties to modular organization *sensu* Fodor. This fact has sometimes led to conceptual misunderstandings (see also section 1.2.3), and is relevant for approaches that try to identify domain-general processes in nonhuman animals (see also section 2.4.3).

A final potential problem is that developmentally acquired response tendencies may be successful in solving local problems, but nevertheless may not ultimately help an individual survive and reproduce (the functionality problem). Individuals, be they animals or humans, typically do not represent ultimate fitness goals in their everyday behavior. Rather, they pursue a set of innate psychological goals, which on average results in fitness-enhancing behaviors (Tinbergen 1963) but may become maladaptive in environments other than the one in which the goals evolved, as shown by our strong preferences for sweet, fatty, and salty foods. However, innate goals may be modified or supplemented by socially acquired end-state preferences. For immatures, who are most strongly affected by the canalization problems listed in Table 1, copying successful adult individuals is widespread and generally results in adaptive behavior because they are copying individuals who have survived until adulthood and managed to reproduce. Socially acquired end-state preferences and goals are particularly widespread in humans, who are highly susceptible to conformity and prestige biases (Dean et al. 2014; Richerson et al. 2016). Increasing evidence also suggests the existence of such biases in at least some nonhuman primates and birds (Aplin et al. 2015; Kendal et al. 2015; Lunz & Boesch 2014; van de Waal et al. 2013).

Despite being incomplete, Table 1 serves to highlight that adaptive canalization of cognition not involving Fodorian modules is possible, indeed potentially quite frequent. It also highlights the prominent reliance on social inputs to overcome the canalization problems inherent to domain-general mechanisms. Social learning is broadly defined in the animal literature – that is, learning influenced by observation of, or interaction with, another animal or its products (Heyes 1994; see also Box 1984). It is widespread in the animal kingdom, both in vertebrates and invertebrates, and ranges from processes as simple as social facilitation and enhancement learning to observational forms of social learning such as true imitation (e.g., Hoppitt & Laland 2013). Interestingly, it is increasingly assumed that many of the cognitive mechanisms involved in social learning are of a general nature rather than specialized, and are thus not specific to social learning (Behrens et al. 2008; Heyes 2012; 2016). Indeed, all forms of social learning also include a major element of individual learning. This is most evident in forms such as stimulus enhancement, where the attention of a naïve individual is drawn to stimuli other individuals are interacting with, which then releases individual exploration, play, and trial-and-error learning with this stimulus. Individual learning and practice, however, are also involved in the acquisition of skills through imitation learning, whereby it is typical that, after observation, a phase of individual practice is required (Galef 2015; Jaeggi et al. 2010; Schuppli et al. 2016). Thus, natural selection for social learning seems to automatically trigger selection on individual learning and general cognitive ability, suggesting that ontogenetic canalization through social learning may have contributed to enabling the evolution of domain-general cognition, an issue to which we return in section 3.3.

1.2.3. Primary and secondary modularization, and implications for general intelligence in nonhuman animals. Evolved Fodorian modules have specific surface properties: they work fast, effortlessly, and automatically, and they do not require significant amounts of executive

control and working memory. Nevertheless, identifying modules in animals based on these properties is problematic because skills, capabilities, and solutions to problems that are acquired through effortful problem solving and learning based on general cognitive processes may become automatized over time, a process we refer to as secondary modularization. After such secondary modularization, or automatization, these skills have many of the surface properties in common with primary, evolved Fodorian modules. Note that this distinction in primary and secondary modularization is analogous to the distinction in primary and secondary cognitive abilities by Geary (1995), but whereas the latter has been developed specifically for humans, the former is thought to apply to a broad array of animal species.

Despite the similarities in surface properties, primary and secondary modules differ fundamentally with regard to their origin (see Table 2): Primary modules are evolved adaptations with canalized, buffered development, whereas secondary modules represent ontogenetically acquired skills that were automatized during ontogeny. In fact, secondary modularization is particularly common during the immature period (d'Souza & Karmiloff-Smith 2011). A consequence of the different etiology of primary and secondary modules is that the latter are more variable in their content and distribution across individuals or populations of the same species. Because little is known about the ontogeny of many of the specialized cognitive modules postulated for humans (Geary 2005), we should also acknowledge the possibility that some or all of these are secondary rather than primary (Anderson & Finlay 2014) or at least subject to experiential influences. For instance, even some prototypical modules such as those involved in face perception depend on experience (Dahl et al. 2014).

The implication for the question of general intelligence in nonhuman animals is that it is no longer possible to uniquely rely on surface properties such as speed, effort, efficiency, and reliability to infer the presence of evolved domain-specific modules, because secondary modules have similar properties. Instead, a better diagnostic tool

Table 2. *Primary and secondary modules differ with regard to their etiology and development, which has implications for their content and distribution within a species or population*

Type of Module	Etiology	Development	Content of Skills	Distribution	Examples
Primary modules	Evolutionary; reflect natural selection for domain-specific cognitive adaptation	Skill matures, motor practice (experience-expectant ¹)	Preset, highly predictable	Uniformly present in a given species	Tendency of (young) felids to respond to small moving objects with behaviors from the hunting repertoire
Secondary modules	Ontogenetic; reflect behavioral flexibility and learning ability, acquisition often based on EFs	Skill is learned (experience-dependent ¹) and practiced to the point of automaticity	More variable, determined by nature of inputs	Variable among individuals, populations	Automatic perception of a stick as potential tool in some apes; learned algorithms to solve algebraic equations in humans

¹Greenough et al. (1987).

for the presence of general cognitive abilities is the presence of variable skill profiles across individuals and genetically similar populations due to secondary modularization (see section 2.4.3).

We have shown that human cognition involves elements of domain-specific and domain-general processes, but that the same can potentially be true for animals as well. Hence, animal minds need not be bundles of specialized cognitive adaptations. Having thus leveled the playing field, we first, in section 2, review recent evidence for whether a positive manifold (g) is present in nonhuman animals at all, and if so, how such a g factor is best explained. In particular, we will focus on the question whether such psychometric intelligence shows any of the features usually referred to as general intelligence. Even if we can be confident that this is the case in humans, whether the same applies to animals must be an empirical question (Galsworthy et al. 2014), and we highlight different research strategies that may prove to be fruitful in the future. In section 3, we then use this pattern of results to examine the ultimate evolutionary question of why general intelligence evolved, and which selection pressures may have favored it.

2. General intelligence in nonhuman animals?

Unless general intelligence is inextricably linked to language, considerations of evolutionary continuity suggest that nonhuman animals, especially our closest extant relatives, the great apes, may well possess it too, at least to some extent. The presence of evidence for executive functions in animals (Chudasama 2011) supports this contention, as does the overall flexibility of brains in animals, both during development and as response to experience, including the training of cognitive skills (Johansen-Berg 2007; Kolb & Gibb 2015; Matsunaga et al. 2015; Sale et al. 2014). According to most neurobiologists, such developmental plasticity is incompatible with purely domain-specific descriptions of cognitive abilities (Anderson & Finlay 2014; Prinz 2006; Quartz 2003). Nonetheless, evolutionary plausibility does not amount to empirical evidence, to which we turn now.

The question of whether general intelligence is unique to humans has typically been addressed by asking whether we find a positive manifold or psychometric intelligence, by following two complementary approaches: First, within a given species, in analogy to human studies, psychometric test batteries have been applied to many individuals. Second, broad comparative analyses (both experimental and meta-analytical) have been conducted across species to investigate whether species differ from each other in general intelligence, rather than in specific cognitive adaptations. In addition, some studies have simultaneously analyzed intraspecific and interspecific variation in cognitive performance. In the following subsections, we first give an overview of these studies. We refer to general factors extracted from intraspecific studies as g , and to those extracted from interspecific studies as G . We then critically assess to what extent alternative explanations may account for the findings, and formulate criteria for future studies that should help pin down to what extent a statistically derived g/G factor reflects general intelligence as broadly defined.

2.1. Intraspecific studies of psychometric intelligence: g

Interest in the question of whether general intelligence may be found in nonhuman animals briefly spiked in the 1930s and 1940s (Locurto & Scanlon 1998), after Spearman's g factor (Spearman 1927) had become widely known. These studies reported positive correlations across various types of tasks, but predominantly concerned mazes and mostly in non-primate species such as mice, rats, and chicks (Locurto 1997). Because the model of a hierarchical structure of human cognition and the methodological tools to detect it became widely available only in the late 1940s, the design of these early studies was often not suitable to detect g or any factor structure.

For the next half century, the question of animal general intelligence was largely ignored, with interest resurging only after the late 1990s, mainly focusing on mice and primates. Table 3 provides an overview of these studies that have assessed and analyzed correlated performance across three or more cognitive tasks within subjects of the same species, for rodents, primates, and other species (see also Bouchard 2014; Chabris 2007; Galsworthy et al. 2014; Matzel et al. 2013).

In rodents, robust evidence for g is available from a range of studies, mostly on mice, from test batteries including as many as eight different tasks and various regimes of principal component analysis (e.g., reviewed in Bouchard 2014; Galsworthy et al. 2014; Matzel et al. 2011b; but see Locurto et al. 2003; 2006). In general, g explains between 30% and 40% of variation in cognitive performance, and in rats, it is positively correlated with brain size (Anderson 1993). Moreover, heritability estimates of up to 40% have been reported (Galsworthy et al. 2005). Test batteries often include typical, rather basic learning tasks, such as associative fear conditioning, operant avoidance, path integration, odor discrimination, and spatial navigation. Nevertheless, as in humans, the derived g factors have been shown to covary with executive functions, such as selective attention (Kolata et al. 2007; Matzel et al. 2011a) and working memory (particularly working memory capacity: Kolata et al. 2005; Matzel et al. 2008; Sauce et al. 2014) as well as performance in tests of reasoning. For instance, g derived from a standard mouse test battery predicted performance in inductive (finding efficient search strategies in a complex maze) and deductive reasoning (inferring the meaning of a novel item by exclusion, i.e., “fast mapping”: Wass et al. 2012). Working memory training did increase g (Light et al. 2010; Matzel et al. 2011a), mainly through its positive effect on selective attention (Light et al. 2010; see also Sauce et al. 2014). Importantly, g did not simply capture fear and stress reactivity (Matzel et al. 2006), anxiety (Galsworthy et al. 2002), or other lower-level biological processes such as sensory or motor abilities (Matzel et al. 2006). In sum, for rodents, the finding of a first component in cognitive test batteries that corresponds to g is robust, and several implications of its presence have been confirmed.

In nonhuman primates, only a handful of studies on the consistency of individual-level differences in cognitive tasks are available. Herndon et al. (1997) were interested in classifying patterns of age-related cognitive decline in adult rhesus macaques, an Old World monkey species. They found a first PCA factor that explained 48% of the variance in cognitive performance and on which all six tasks loaded

Table 3. *Intraspecific studies that have assessed and analyzed correlated performance across at least three cognitive tasks within subjects of the same species, for rodents, primates, and other species*

	Species (n)	Test Battery	Key Findings and Conclusion	Reference
Rodents	Rats (22 + 20 ¹)	4 tasks: attention to novelty, speed, and accuracy of reasoning (8-arm radial maze), response flexibility (detour problem)	Evidence for <i>g</i> in both samples; <i>g</i> was correlated with brain weight (second sample).	Anderson (1993)
	Mice (two strains: 34 + 41)	5 water escape tasks: route learning (Hebb-Williams maze), use of spatial navigational cues (Morris water maze), spatial reversal learning and visual reversal learning (T-maze), place learning (4-arm maze); <i>plus</i> activity control task	Evidence for <i>g</i> in both strains (explaining 61% and 55% of variance in the latency measures, and 28% and 37% in the error measures); authors stress limited implication for <i>g</i> because mainly spatial tasks were used; activity loads on first factor in strain A but not in strain B.	Locurto and Scanlon (1998)
	Mice (40)	6 tasks: curiosity (spontaneous alternation in T-maze), route learning (Hebb-Williams maze), use of spatial navigational cues (Morris water maze), detour problem (burrowing task), contextual memory, plug puzzle; <i>plus</i> anxiety in new environments (open field)	Evidence for <i>g</i> (explaining 31% of variance); <i>g</i> was independent of anxiety.	Galsworthy et al. (2002)
	Mice (60)	6 tasks: route learning (Hebb-Williams), place learning (plus maze), and a set of detour problems; 3 working memory tasks (8-arm radial maze, 4 × 4 radial maze, visual non-matching to sample), <i>plus</i> 3 activity and stress control tasks	No evidence for <i>g</i> (first factor explains 19.4% of variance, control tasks included in PCA).	Locurto et al. (2003)
	Mice (56)	Standard mouse battery of 5 tasks: associative fear conditioning, operant avoidance, path integration (Lashley III maze), odor discrimination, and spatial navigation (spatial water maze) <i>plus</i> open field exploration task	Evidence for <i>g</i> (explaining 38% of variance); exploration propensity related to individual learning ability.	Matzel et al. (2003)
	Mice (21)	Variant of standard mouse battery <i>plus</i> exploration task (open field), long-term retention (retest in Lashley III maze after 30 days) and working memory task (simultaneous performance in two 8-arm radial mazes)	Evidence for <i>g</i> (explaining 43% of variance); <i>g</i> covaried with exploration and working memory capacity but not with long-term retention.	Kolata et al. (2005)
	Mice (84 unrelated, ¹ and 167 siblings)	Tasks from Galsworthy et al. (2002) <i>plus</i> object exploration and 2nd problem-solving task	Evidence for <i>g</i> (explaining 23%–41% of variance); <i>g</i> showed sibling correlations of 0.17–0.21 and an estimated heritability of 40% (upper limit).	Galsworthy et al. (2005)
	Mice (47 + 51)	Exp. 1: 5 tasks: detour, win-shift, olfactory discrimination, fear conditioning, and operant acquisition; <i>plus</i> open field and light-dark control tasks Exp. 2: similar but optimized task battery (same detour and fear conditioning but 3 new tasks, including working memory); same control tasks	Evidence for <i>g</i> (explaining 28%–34% of variance) but only after removing control procedures from the analysis; <i>g</i> was stronger in the second experiment.	Locurto et al. (2006)
	Mice (43)	Standard mouse battery; <i>plus</i> 21 tests of exploratory behavior, sensory/motor function (e.g., running and swimming speed, balance tasks, grip strength) and fitness, emotionality, and hormonal and behavioral stress reactivity	Evidence for <i>g</i> (explaining 32% of variance); open field exploration and 7 other explorative behaviors also loaded on this first factor, but <i>g</i> was not correlated with general activity, sensory/motor function, physical characteristics, or direct measures of fear; lower-level biological properties loaded weakly and inconsistently on <i>g</i> .	Matzel et al. (2006)

(continued)

Table 3 (Continued)

Species (<i>n</i>)	Test Battery	Key Findings and Conclusion	Reference
Mice (27)	Standard mouse battery; <i>plus</i> selective attention (complex discrimination), short-term memory capacity (nonspatial radial arm maze), short-term memory duration (delayed reinforced alternation)	Evidence for <i>g</i> (explaining 44% of variance); <i>g</i> was most strongly correlated with selective attention, followed by simple memory capacity and only weakly with short-term memory duration.	Kolata et al. (2007)
Balb/C Mice (56)	Standard mouse battery <i>plus</i> working memory span and capacity, and 12 non-cognitive tests of unlearned behaviors and fitness	Evidence for <i>g</i> (explaining 31% of variance); old subjects (19–21 months of age) had lower <i>g</i> than young ones (3–5 months of age) but also showed higher variability. Working memory capacity and duration explained variance in <i>g</i> , and particularly so in old mice. Old mice with age-related cognitive decline had increased body weight and decreased activity. Some non-cognitive variables were also correlated with <i>g</i> .	Matzel et al. (2008)
Mice (69)	Standard mouse battery as adults; <i>plus</i> extensive exposure to 12 novel environments prior to testing	Evidence for <i>g</i> (explaining 27% of variance); exposure to novelty as juveniles (from 39 days of age) and young adults (from 61 days of age) increased exploration but did not affect <i>g</i> compared to control groups when tested as adults (from 79 days of age).	Light et al. (2008)
Mice (241)	Standard mouse battery; subsample of 78 subjects also tested with 2 additional spatial tasks (win-stay and reinforced alternation)	Evidence for <i>g</i> (explaining 38% of variation); identification of an additional domain-specific factor for tasks that depended on hippocampal/spatial processing in subsample.	Kolata et al. (2008)
Mice (60)	Standard mouse battery; <i>plus</i> prefrontal cortex gene expression profiles	Evidence for <i>g</i> (explaining 41%–42% of variance); dopaminergic genes plus one vascular gene significantly correlated with <i>g</i> ; D1-mediated dopamine signaling in the prefrontal cortex was predictive of <i>g</i> , arguably through its modulation of working memory.	Kolata et al. (2010)
Mice (29)	Standard mouse battery; <i>plus</i> extensive training on short-term memory duration and working memory capacity, and a selective attention task (Mouse-Stroop)	Evidence for <i>g</i> (explaining 30% of variance); working memory training promoted <i>g</i> , largely but not exclusively via increased selective attention; effects were smaller when selective attention load of training task was reduced.	Light et al. (2010)
Mice (42)	Standard mouse battery; <i>plus</i> 2 exploration tasks (open field and novel environments)	Evidence for <i>g</i> (explaining 40% of variance); link between <i>g</i> and exploration propensity was mediated by different rates of habituation in high vs. low <i>g</i> subjects.	Light et al. (2011), experiment 2
Mice (26)	5 tasks: acquisition of three learning tasks (passive avoidance, shuttle avoidance, reinforced alternation), reversal learning, and selective attention; <i>plus</i> longitudinal working memory training (radial arm maze task with overlapping cues, various regimes) and four non-cognitive variables	Evidence for <i>g</i> (explaining 26%–37% of variance); longitudinal working memory training prevented age-related decline of attention, learning abilities, and cognitive flexibility; non-cognitive variables loaded moderately to weakly on <i>g</i> and in a non-consistent manner; old (from 18 months of age); young (from 5 months of age).	Matzel et al. (2011a; 2011b)

	Mice (47)	Standard mouse battery; <i>plus</i> deductive reasoning (inferring by exclusion: fast mapping) and inductive reasoning (efficient search strategy)	Evidence for <i>g</i> (explaining 27%–32% of variance); <i>g</i> correlated with inductive and deductive reasoning performance.	Wass et al. (2012)
	Mice (26)	4 learning tasks: odor discrimination, reinforced alternation, fear conditioning, radial arm maze <i>plus</i> attention battery consisting of 4 tasks: Mouse-Stroop (conflicting visual and olfactory cues), T-maze reversal, coupled latent inhibition, and dual radial arm maze	Evidence for <i>g</i> (explaining 37% of variance); different types of attention (external: selective attention; internal: inhibition) contributed independently to variation in <i>g</i> .	Sauce et al. (2014)
Primates	Rhesus macaques (30+23)	6 non-social tasks ($n = 30$): delayed non-matching to sample (acquisition time and performance after 120 sec delay), delayed recognition span task (spatial and color condition), and reversal learning task (spatial and object condition) Subset of the 6 tasks above ($n = 53$): acquisition and 120" performance in delayed non-matching to sample, spatial delayed recognition span	Evidence for <i>g</i> (explaining 48% of variance), <i>g</i> but none of the other two extracted factors declined with age. Age groups (age in years): young adults (<15), early-aged (19–23), advanced aged (24–28), and oldest aged (≥ 29). Evidence for <i>g</i> (explaining 62% of variance); <i>g</i> declined with age and was strongly correlated with <i>g</i> extracted from the full test battery.	Herndon et al. (1997)
	Cotton-top tamarins (22)	11 mostly non-social tasks ³ : 10 from the physical domain, 1 from the social domain	Evidence for <i>g</i> (Bayesian latent variable approach) but no additional group factors (domains).	Banerjee et al. (2009)
	Chimpanzees (106), 2-year old children (105)	15 of the 16 tasks of the PCTB ⁴ from the physical and social domain (tool use excluded)	Confirmatory factor analysis revealed different factor structures for chimpanzees (factor 1: spatial tasks; factor 2: some physical and some socio-cognitive tasks) and children (factor 1: spatial tasks; factor 2: some physical tasks; factor 3: 6 social tasks); Inconclusive regarding <i>g</i> for both human children and chimpanzees because of inclusion of social domain and low variability in performance in some of the tasks.	Herrmann et al. (2010b)
	Chimpanzees (99)	13 of the 16 tasks of the PCTB ⁴ from the physical and social domain (without the number addition, social learning, and intention task)	Evidence for <i>g</i> (Parallel analysis); <i>g</i> was heritable (heritability $h^2 = 0.525$, $p = 0.008$). Individual differences in cognitive performance and heritability remained stable in a retest after two years ($n = 86$). Evidence for <i>g</i> (loadings of tasks on first factor range from 0.048–0.607). Subtests with higher <i>g</i> loadings were more heritable, and performance in these subtests was more variable between individuals.	Hopkins et al. (2014)
Other species	Dogs (13)	3 tasks: response latencies in discrimination, reversal learning, and visuo-spatial memory (3 delayed non-matching to sample conditions)	Highly significant correlations of performance across all 3 tasks.	Nippak and Milgram (2005)
	Dogs (68 border collies)	6 tasks: four detour tasks, human point following, and numerical discrimination	Evidence for <i>g</i> ; confirmatory factor analysis on 8 variables (4 detour performance plus speed and choice in point and discrimination task), with latent factors navigation speed, choice speed, and choice accuracy, best fit for hierarchical model with <i>g</i> explaining 17% of variation.	Arden and Adams (2016)

(continued)

Table 3 (Continued)

Species (<i>n</i>)	Test Battery	Key Findings and Conclusion	Reference
Bowerbirds (21)	6 ecologically relevant tasks (2 problem solving, 1 mimetic repertoire, and 3 bower building tasks)	Weak evidence for <i>g</i> (explaining 27.5% of variance), but <i>g</i> as well as separate performance in 4 tasks was correlated with mating success.	Keagy et al. (2011)
Bowerbirds (11)	6 cognitive tasks (an ecologically relevant bower maintenance task, 2 discrimination tasks, and a reversal learning, a spatial memory, and a novel motor task)	Evidence for <i>g</i> (explaining 44% of variance), but no correlation between <i>g</i> or separate performance in any task with mating success.	Isden et al. (2013)
New Zealand Robins (16)	6 ecologically relevant tasks (1 motor task, color and shape discrimination, reversal learning, spatial memory, and inhibitory control); <i>plus</i> motivation (sitting on an electronic scale and eating a mealworm) and neophobia (latency to touch the new apparatus)	Evidence for <i>g</i> (explaining 34% of variance). Consistent pattern of results after removing the spatial memory task or/and subjects with a color preference. Even stronger evidence for <i>g</i> (45%) when removing both the motor task and subjects with a color preference from the PCA.	Shaw et al. (2015)

¹ In the second sample, variation in brain size was induced by prenatal exposure to methyl-azoxymethanol, which induces microcephaly

² Data for 40 subjects were taken from Galsworthy et al. (2002)

³ Inhibition (occluded reach, A-not-B error, reversal learning), perceptual speed (targeted reach), exploration, numerical discrimination, acoustic discrimination, inspection time (objects and social), memory (hidden reward retrieval), food extraction puzzle

⁴ The PCTB (Primate Cognition Test Battery, Herrmann et al. 2007) consists of 16 tasks from the physical domain (space: spatial memory, object permanence, rotation, transposition; quantities: relative numbers, addition numbers; causality: noise, shape, tool use, tool properties) and the social domain (social learning; communication: comprehension, pointing cups, attentional state; theory of mind: gaze following, intentions)

positively. This factor, based on 30 subjects, was highly correlated with a factor derived from a subset of only three of these tasks (all of which, again, loaded positively on it) in an overlapping sample of 53 subjects. Furthermore, this putative *g* declined linearly with increasing age of the monkeys.

Banerjee et al. (2009) found evidence for *g* in a New World monkey species, the cotton-top tamarin (*Saguinus oedipus*). They tested 22 subjects with a battery consisting of 11 tasks that assess a range of cognitive abilities such as inhibitory control, quantity discrimination, and memory. Owing to the relatively high number of missing individual test scores, they used Bayesian analysis and found a *g* factor but no group factors that would have corresponded to more specialized cognitive domains (although the a priori classification of domains is inevitably tenuous without extensive validation; see also section 2.4).

Among great apes, evidence for *g* is more mixed. Herrmann et al. (2007) developed the Primate Cognitive Test Battery (PCTB) consisting of 16 tasks from the physical and the social domain, a priori placed into six categories (i.e., space, quantities, causality, social learning, communication, and theory of mind) and applied it to 106 chimpanzees, 32 orangutans, and 105 two-year old human children. Chimpanzees and human children performed equally well (and better than orangutans) in tasks from the physical domain, but the children outperformed both ape species in the social domain. These results were not consistent with *g* in any of the species, including human children. To explicitly address the structure of individual differences, Herrmann et al. (2010b) re-analyzed the data from the chimpanzees and children in 15 of the 16 PCTB tasks (tool use was not included) using a confirmatory PCA (see sect. 2.4.1 for further discussion). They found a different structure of cognitive abilities for chimpanzees (2 factors) and children (3 factors). In addition to a “Spatial” factor in both species, only one additional “Physical-Social” factor emerged in chimpanzees, whereas two additional factors, a “Physical” and a “Social” one, emerged in children. The authors thus did not find evidence for *g* in either chimpanzees or humans. However, human test batteries typically do not include subtests assessing social cognition. In fact, the relationship between general cognitive processes and socio-cognitive processes is currently poorly understood in humans (Korman et al. 2015). This problem, however, does not explain the presence of two other factors rather than a single *g* in human children.

More recently, Hopkins et al. (2014) tested 99 chimpanzees with a reduced and slightly modified version of the PCTB consisting of 13 of the 16 tasks (including tool use but excluding one of two quantity tasks, the social learning task, and one theory of mind task). They report a *g* factor derived from a non-rotated PCA and used quantitative genetic analyses to estimate its heritability (h^2), which was found to be 53% and highly significant. Furthermore, the results remained stable when 86 of the 99 chimpanzees were retested with the same test battery after two years, and were confirmed with parallel analysis. Woodley of Menie et al. (2015) further analyzed the data set and concluded that the more *g*-loaded a task is, the higher its heritability and phenotypical variability, as also found in humans. The more *g*-loaded tasks also had higher coefficients of additive genetic variance, suggesting that cognitive abilities with higher *g* loadings have been subject to stronger recent selection.

Taken together, then, the psychometric studies in specific rodent and primate species lend increasing support to the notion that the positive manifold is not unique to humans but also present in nonhuman animals. Studies on other lineages such as dogs (Arden & Adams 2016; Nippak & Milgram 2005) and birds (Keagy et al. 2011; Isden et al. 2013; Shaw et al. 2015) are also beginning to provide evidence. However, a serious limitation of psychometric studies in nonhuman animals is that they tend to lack power with respect to sample size, the diversity of cognitive tasks, or both. We discuss these limitations in section 2.4. Fortunately, there is a complementary approach, which examines interspecific variation and is particularly powerful to reveal evolutionary trends.

2.2. Interspecific studies of psychometric intelligence: G

In comparative approaches, the fundamental question is whether some species systematically outperform others across an array of distinct cognitive tasks, consistent with the notion of psychometric and perhaps general intelligence,

or whether species differences are instead characterized by independent variation in performance across tasks and domains, consistent with higher domain specificity. Comparative studies thus investigate whether what evolves are specialized skills or rather general intelligence. This approach (Table 4) has predominantly been applied to primates but also to birds and involves both meta-analyses and targeted experimental comparisons.

For primates, Deaner et al. (2006) conducted a meta-analytical study that compared the performance of 24 primate taxa tested with nine experimental physical-cognition paradigms using Bayesian hierarchical modeling (Johnson et al. 2002). They found strong evidence for *G*, which correctly predicted 85% of the species rankings (but note that caution is needed when comparing the proportion of explained variance between standard PCA and Bayesian analyses). Moreover, in a follow-up study, *G* was strongly correlated with brain size (Deaner et al. 2007).

In another set of studies, Reader and Laland (2002) collected data from the literature on the incidence of innovation, social learning, and tool use in 116 species of

Table 4. Interspecific, comparative studies that have assessed correlated cognitive performance across species

Species (<i>n</i>)	Type of Study	Key Finding	Reference
Primate species (116)	Correlation of ecologically relevant cognitive abilities (innovation, tool use and social learning) and volume measures of the executive brain (neocortex and striatum) and brainstem (mesencephalon and medulla oblongata)	The 3 measures were correlated across nonhuman primate species and with both absolute and relative executive brain volumes; results consistent with <i>G</i>	Reader and Laland (2002)
Primate taxa (24) (3 great ape species, 1 lesser ape, and 7 catarrhine, 6 platyrrhine, & 7 prosimian genera)	Meta-analysis of 9 experimental paradigms (detour problems, patterned-string problems, invisible displacement, tool use, object discrimination learning set, reversal learning, oddity learning, sorting, and delayed response) of captive subjects using hierarchical Bayesian latent variable analysis (Johnson et al. 2002)	Species- <i>G</i> explained 85% of variance; great apes (<i>Gorilla</i> , <i>Pan</i> , <i>Pongo</i>) outperformed all other genera; <i>G</i> was positively correlated with various measures of brain size	Deaner et al. (2006; 2007)
Primate species (62) (including apes, catarrhine and platyrrhine monkeys, & prosimians)	Meta-analysis on ecologically relevant tasks: behavioral innovation, social learning, tool use, extractive foraging (expanded data set from Reader & Laland 2002), and tactical deception (data from Byrne & Whiten 1990) using principal component, factor, and phylogenetic analyses	Species- <i>G</i> explained 65% of the variance in cognitive performance and covaried with brain size. <i>G</i> also covaried with results from captive subjects: that is, the species- <i>G</i> from Deaner et al. 2006 and learning performance from Riddell & Corl 1977)	Reader et al. (2011)
Primate species (69) (including apes, catarrhine and platyrrhine monkeys, & prosimians)	Meta-analysis of data sets from Reader et al. (2011, innovation, tool use, social learning, and extractive foraging) and Byrne and Whiten (1990, tactical deception) using principal axis factor analysis and unit weighted factor analysis	Differences in cognitive abilities among primates were concentrated on <i>G</i> (explaining almost 62% of variance), and this effect was particularly pronounced in catarrhines (i.e., apes and Old World monkeys)	Fernandes et al. (2014)

nonhuman primates, both in captivity and in the wild, and found that across species, all three measures were correlated with each other (r^2 values around 0.4), as well as with brain size. In a follow-up study involving 62 primate species (Reader et al. 2011), they found evidence for general intelligence on the interspecific level (G) in principal component and factor analyses explaining 65% of the variance, based on measures of innovation, social learning, and tool use, as well as extractive foraging and tactical deception. As in Reader and Laland's (2002) earlier study, G was correlated with brain size, but also with a combined measure of performance across several learning tasks, with learning set performance (both taken from Riddell & Corl 1977), and the G measure of Deane et al. (2006).

More recently, Fernandes et al. (2014) compiled published data from five cognitive domains (innovation, tool use, social learning, extractive foraging, and tactical deception) across 62 primate species (data sets from Reader & Laland 2002; and Byrne & Whiten 1990). Fernandes et al. found that a single factor G explained almost 62% of the total variance. Furthermore, they reported that cognitive abilities that load more strongly on G show bigger interspecific variation, weaker phylogenetic signals, and faster rates of evolution. These results are consistent with the idea that G has been subjected to selection pressure stronger than narrow, more domain-specific abilities and that G is thus the principal locus of selection in the evolution of primate intelligence (but see also section 2.5).

The only other taxon to which comparative approaches have been applied are birds. As in primates, significant positive correlations across species were found between

innovation rates, tool use, and learning performance. These studies also found positive correlations between innovation rates and brain size as well as colonization success (Ducatez et al. 2015; Lefebvre 2013; Lefebvre et al. 2004; Sol et al. 2005).

2.3. Mixed studies combining intraspecific and interspecific variation

Some studies have pursued a mixed approach by applying test batteries to multiple individuals from several species (see Table 5). For instance, Herrmann and Call (2012) analyzed data of 23 individuals from all four nonhuman great ape species, which were studied in a range of tasks from the physical domain, and found no support for the existence of g . Nevertheless, some subjects performed particularly well (or poorly) across tasks, both in the sample of 23 great apes and in the 106 chimpanzees mentioned previously (Herrmann et al. 2010b), indicating that there was some consistency in individual performance.

In another mixed study, Amici et al. (2012) found no evidence for G or g when re-analyzing data from seven primate species (all four great ape species, long-tailed macaques, spider monkeys, and capuchin monkeys, totaling 99 individuals) from 17 cognitive tasks. In the Bayesian approach used to analyze the data (see also Barney et al. 2015), the 17 tasks were a priori attributed to the domains of inhibition, memory, transposition, and support, similar to Herrmann et al. (2010b).

In contrast to intraspecific and interspecific studies, mixed studies thus provide less support for psychometric intelligence. Here, we offer a tentative suggestion to

Table 5. Mixed studies that have simultaneously analyzed correlated performance within and between species

Species (n)	Type of Study	Key Finding	Reference
Chimpanzees (106) Orangutans (32) 2.5-year-old human children (105)	Psychometric study using the Primate Cognitive Test Battery (PCTB) consisting of 16 tasks from the physical domain (space: spatial memory, object permanence, rotation, transposition; quantities: relative numbers, addition numbers; causality: noise, shape, tool use, tool properties) and the social domain (social learning; communication: comprehension, pointing cups, attentional state; theory of mind: gaze following, intentions) using analysis of variance	Chimpanzees and human children performed equally well (and better than orangutans) in the physical domain, but the children outperformed both ape species in the social domain; results not consistent with G	Herrmann et al. (2007)
Bonobos, chimpanzees, gorillas, and orangutans (23)	8 non-social tasks from various studies: spatial knowledge (i.e., delayed response, inhibition, A-not-B, rotations, transpositions and object permanence), tool use (4 tests), inferential reasoning by exclusion, quantity discrimination, causal reasoning and color, size and shape discrimination learning	No evidence for g ; but some individuals performed consistently well across tasks	Herrmann and Call (2012)
Chimpanzees (19), orangutans (10), bonobos (5), gorillas (8), long-tailed macaques (12), spider monkeys (18), capuchin monkeys (27)	Re-analysis of data obtained from two psychometric studies resulting in 17 tasks from four physical domains (inhibition from Amici et al. [2008; 2010], and memory, transposition, and support from Herrmann et al. [2007]) with captive subjects using a hierarchical Bayesian modeling approach	Most variance explained by species and cognitive domain; results not consistent with G	Amici et al. (2012); Barney et al. (2015)

explain this absence of evidence for psychometric intelligence in mixed studies that will need to be examined in more detail in future work. First, despite including a large number of individuals overall, the effective sample size to identify g remains the number of individuals within each species, and to identify G is the number of species. This may strongly influence the outcome because in mixed studies the detection of G is not based on average species-specific performance as is done in interspecific studies, but is instead based on individual values, which are more susceptible to noise. A recent memory task illustrates the superiority of species averages in estimating abilities at the species level. In this study, both marmoset and squirrel monkeys as a group provided results fitting the Ebbinghaus forgetting curve, but at the individual level, several individuals did not, indicating that the performance of these individuals was strongly affected by noise (Schubiger et al. 2016). Such noise may overshadow G , especially in species that are very close in G .

A second issue is that in a sample of species with similar G (e.g., according to Deaner et al. 2006), and thus both the great ape study by Herrmann and Call (2012) and the study by Amici et al. (2012), species-specific predispositions linked to domain-specific adaptations may mask a G effect. Thus, chimpanzees and orangutans are more extraction-oriented than bonobos or gorillas (van Schaik 2016), as expressed, for instance, in species differences in tendencies to handle objects (Koops et al. 2015), or to solve social problems (Herrmann et al. 2010a). Such variation is bound to produce species differences in mean performance on some but not on other tasks, reducing the correlation across tasks in the overall data set. Intraspecific comparisons obviously are not affected by this problem, whereas the effect on interspecific comparisons is reduced the broader the comparison in terms of G are, because major interspecific differences in G lessen the effects of species differences in domain-specific predispositions.

More generally, we can ask, if in a given lineage, a robust G is found, whether this implies that all species in the comparison *must* have g , and vice versa. Several combinations of evidence for g and G are possible, in particular in mixed studies, as summarized in Table 6, and we discuss likely explanations for these combinations.

The interpretation is straightforward whenever evidence for g and G point in the same direction (see entries I and IV in Table 6), and where it is positive for both, can be externally validated separately at both the level of g and G (see

also section 2.5). One potentially conflicting constellation is when positive evidence for g but no evidence for G is available (as for entry II in Table 6). Such a result can arise if g is present in only a few of the species involved in the comparison, which might occur when distantly related lineages are compared. The other conflicting constellation (entry III in Table 6) is that comparative studies provide evidence for G , but there is no evidence for g within the species involved in the comparison. This was the case in some primate studies. In principle, it is possible that we are dealing with cumulative modularity and that by chance the distribution of modules across the species included in the sample is hierarchically nested. In this scenario, no correlation between G and EFs or, arguably, brain size is expected, which is inconsistent with current findings. The most likely cause of constellation III, therefore, is lack of power of animal studies to reliably detect the absence of g , due to the small sample sizes and difficulties to construct a suitable test battery, which make animal psychometric g studies prone to Type II errors (see also section 2.4.1).

Taken together, there is increasing evidence for g in non-human animals, particularly in mice and primates, for which positive evidence is available for New World monkeys, Old World monkeys, and chimpanzees (but see Herrmann et al. 2010b). At the interspecific level based on comparative analyses across species, studies of primates and birds provide a robust pattern consistent with G . Finally, mixed studies in primates that simultaneously analyze within- and between-species variation yield a more ambiguous pattern.

2.4. Facts or artifacts?

A legitimate concern is whether a presumptive g/G factor can arise as an artifact, and a legitimate question is to what, exactly, it corresponds. We now review why statistical or methodological artifacts may produce false positives, whereas secondary modularization may lead to false negatives, and formulate criteria for future directions that may be used to evaluate whether g/G corresponds to general intelligence broadly defined.

2.4.1. Statistical issues. The use of PCAs or related procedures involves a suite of decisions, including whether exploratory or confirmatory analyses are applied, whether non-rotated or rotated factors are considered, and whether oblique or orthogonal rotations are used. A

Table 6. Summary of the potential combinations of evidence for g and G , and under what conditions apparently conflicting findings can be reconciled

	No Evidence for g	Evidence for g
No evidence for G	I: domain-specific cognitive abilities	II: g is present in only a few of the species involved in the comparative approach; or the involved species are very close in G and evidence for it is masked by variation in species-specific predispositions
Evidence for G	III: largely cumulative modularity; or artifact due to lack of power of animal psychometric studies	IV: general intelligence, in particular if supported by external validation of both g and G

detailed discussion of factor-analytical procedures is far beyond the scope of this review, and we refer readers to the specialized literature (e.g., Barney et al. 2015; Garson 2013; Stevens 2012). However, because these decisions may critically affect the conclusions of animal studies, we must highlight some issues that appear relevant to the empirical results summarized previously.

First, the use of confirmatory analyses requires an a priori decision of what a domain is, and which tasks are associated with the respective domains (this also applies to Bayesian approaches that likewise categorize tasks a priori to hypothesized domains: Amici et al. 2012; Barney et al. 2015). The identification of domains of animal cognition, however, is not straightforward. For instance, some classify spatial reversal learning tasks as spatial cognition (e.g., Locurto & Scanlon 1998) whereas others stress their inhibition component (Tapp et al. 2003). In reality, of course, subjects may recruit several specific abilities to solve a particular task, and in fact different subjects may even recruit a different mix. Accordingly, Hopkins et al. (2014) found that their exploratory PCA findings were not entirely consistent with the a priori structure of the PCTB originally proposed by Herrmann et al. (2007; 2010b). An a priori allocation of tasks to domains is thus not straightforward; in fact, the structure of a species' cognition is an empirical question (see also sect. 1.1.1 for corresponding efforts in human intelligence research). Accordingly, the use of confirmatory techniques may lead to diverging results compared to analytical approaches that are a priori agnostic with regard to factor structure.

Second, studies vary with regard to whether they present rotated or non-rotated solutions. Because rotations are designed to make the pattern of factor loadings more pronounced, it is generally recommended to use non-rotated solutions in *g* studies (Galsworthy et al. 2014; Jensen & Weng 1994; Locurto et al. 2003; Plomin 2001; Woodley of Menie et al. 2015). Rotated and non-rotated solutions from the same data set are presented in Hopkins et al. (2014) and Woodley of Menie et al. (2015). Whereas the varimax-rotated solution (Hopkins et al. 2014, Table 1) appeared to suggest that a general factor *g* was lacking, the results of non-rotated solutions, verified by parallel analysis, demonstrated it was in fact present.

Third, a common intuition in general intelligence studies on animals is to compare the amount of variance explained by a first factor, and to conclude that the higher the amount of explained variance, the stronger the evidence for *g*. In human studies, the first non-rotated factor typically accounts for about 40% of variance (Plomin 2001), which is in fact similar to what has been reported for mice (see Table 3). However, an exclusive focus on the amount of explained variance is problematic for empirical and conceptual reasons. Empirically, the proportion of explained variance not only depends on the statistical issues discussed previously, but also on the heterogeneity of the subjects in the sample: the more heterogeneous, the higher the proportion of variance explained. In interspecific investigations, for instance, this means that studies that involve species that vary widely in general intelligence and brain size (e.g., 20 species of primates ranging from great apes to prosimians) will find higher proportions of explained variance than studies with a similar sample size, but where the species are all relatively similar (e.g., 20 different species from the same genus or taxonomic family). Conceptually,

to the extent that the mind is a combination of both specialized cognitive adaptations and domain-general processes (see also sect. 4.1), very small proportions of explained variance may still be indicative of a real *g*. Likewise, a first factor with high loadings of some tasks but not others may reflect the absence of general intelligence, but may also reflect the co-occurrence of a general factor and one or several additional, more specialized domains (e.g., for spatial orientation, see Herrmann et al. 2007; see also first PCA factor in Hopkins et al. 2014).

Last but not least, the most severe statistical restriction of nonhuman psychometric studies is that they critically lack power due to their small sample sizes. Reaching a near-consensus about the structure of human intelligence required meta-analyses involving thousands of subjects (Carroll 1993). Obtaining sample sizes comparable to human studies is unrealistic for most nonhuman animal species, in particular for nonhuman primates (albeit less so for rodents). However, replicating studies is feasible, and if this reveals the same factorial solution in a different set of subjects, and if combining such data sets also increases the fit of the solution, we can be increasingly confident that we are not dealing with statistical artifacts. Unfortunately, although this approach minimizes Type I errors, it suffers from very limited power to avoid Type II errors. In other words, if successful, we can be confident that we have obtained a real result, but if it fails, this may reflect either the absence of a general factor or too low a number of subjects. This shortcoming highlights the need to use external validation for psychometric *g/G* studies, as discussed below in section 2.5.

2.4.2. Methodological issues. We now turn to the possibility that a *g/G* factor may arise as a methodological artifact, because the results reflect variation in underlying variables other than general intelligence (see also Macphail's [1982] contextual variables) or because the tasks mainly tap into problems of the same domain.

Some individuals, or some species, may systematically outperform others not because they are more intelligent, but because they are less fearful and better habituated to testing, are more motivated to participate in tasks, have sharper senses, or are simply more active than others (Macphail 1982). Ideally, such confounds are directly quantified, as for instance in Matzel et al. (2006). In a sample of 43 mice individuals, they examined to what extent the general learning ability *g* extracted via PCA from a test battery of six cognitive tasks was correlated with 21 measures of exploratory behavior, sensory/motor function (e.g., running and swimming speed, balance tasks), activity, or fear/stress sensitivity. They found that *g* was not explained by general activity, sensory/motor function, physical characteristics, or direct measures of fear, but was correlated with several exploratory behaviors. Follow-up studies suggested that this link is caused by variation in habituation rates when exposed to potentially stressful situations (Light et al. 2011) rather than by fearfulness influencing both exploration and task performance: Treatment with anxiolytic drugs did increase exploratory behaviors but did not improve performance in individual tasks or *g* (Grossman et al. 2007). Likewise, temporary environmental enrichment resulting in increased exploration tendency did not improve performance on the cognitive test battery (Light et al. 2008). Thus, exploration and *g* may covary

because more exploratory individuals are more likely to encounter contingencies in the environment that promote learning and problem solving, which over time leads to greater experience. The correlation between exploration and g may thus reflect a long-term, cumulative effect of experience on g . This is in line with investment theory (Cattell 1987), and with findings in human infants, where the preference for novelty and habituation is positively correlated with later performance in IQ tests (Teubert et al. 2011), but also with apes, where individuals more likely to approach novel objects and a human stranger performed better in physical-cognition tasks (Herrmann et al. 2007). Thus, the rodent studies support the idea that g is not an artifact of confounding factors.

Another non-cognitive factor that may explain variation in cognitive performance is motivation to participate. Female callitrichid monkeys have been reported to outperform males in problem-solving tasks (Brown et al. 2010; Yamamoto et al. 2004). However, female callitrichids are typically also more food-motivated, whereas males are more vigilant than females (Koenig 1998). Accordingly, males are less interested in participating in experimental tasks and more easily emotionally aroused during testing. But if male performance is controlled for the presence of attention to the test stimuli, their performance is no longer inferior to that of females (Schubiger et al. 2015). The sexes thus do not differ in cognitive ability, but in their motivation to participate in experimental tasks.

The problem that we may never be sure if species differences in cognitive performance are the result of differences in cognitive ability or differences in contextual variables (Macphail 1982) remains an ongoing challenge for any species comparison. Nevertheless, not all tasks are affected by this problem to the same extent. Reversal learning tasks, for instance, are arguably less affected, because individuals first have to reach a criterion of making an initial discrimination. Differences in sensory-motor abilities and so on may well influence how difficult it is for a species to learn a particular discrimination. However, the crucial test is applied only once a specific criterion has been reached, and at least in marmosets, the time needed to achieve this criterion does not predict performance in the reversal trials (Strasser & Burkart 2012). Furthermore, it is reassuring that the strongest association between a specific task and G in Deaner et al. (2006) was the one between reversal learning and G .

A second fundamental methodological issue refers to the task selection and battery development. With respect to task design, it is increasingly recognized that small differences in methodological details can strongly influence task performance, which has to be taken into account when performing species comparisons. For instance, memory performance strongly depends on task format in both marmosets and squirrel monkeys. Tests of memory often rely on a two-option choice task (e.g., Banerjee et al. 2009), but many individuals are then happy to follow a random choice, which yields a 50% reward rate. When the choice involves many more options, subjects will be more motivated to remember the location of the food items and provide more-accurate estimates of their ability to memorize the location of the food item (Schubiger et al. 2016). Regarding battery design, if all tasks in the test battery are drawn from the same domain (i.e., a lower-order group factor), rather than from a variety of

domains, the positive correlations will reflect a domain-specific ability rather than a more general underlying cognitive factor (g/G). For instance, a positive manifold across a number of maze tasks is consistent with a spatial factor, but not informative with regard to g . The issue of task selection is thus closely linked to the identification of domains in animal cognition, which in fact is part of the empirical question that needs to be addressed in intelligence research in animals in general, by using batteries as diverse as possible and statistical procedures that are a priori agnostic to the underlying factor structure.

2.4.3. False negatives as a result of secondary modularization. Task selection may also bias the result and potentially produce false negatives if tasks prone to secondary modularization are included. Secondary modularization refers to the process that during ontogeny, individuals may specialize on a specific set of problems in a particular domain (Table 2). Problem solving in this domain becomes automatized and thus acquires many features commonly associated with modules rather than domain-general reasoning, particularly fast and frugal information processing, which is independent of reasoning. Thus, despite the presence of g in a given species, performance among individuals across domains need not be correlated whenever heterogeneous developmental inputs prevail that lead different individuals to specialize in different tasks (see Fig. 1c). This applies in particular to the small samples typical for nonhuman primate studies.

Prima facie, this situation (Fig. 1c) may seem incompatible with the positive manifold, which is well documented in humans and perhaps other animals. It is important to keep in mind, however, that psychometric studies in humans are typically performed on subject pools with a rather uniform cultural background (the same is also true for the rodent studies performed on lab animals with virtually identical rearing conditions). If, in human studies, the cultural backgrounds of subjects were more diverse (e.g., ranging from Western-industrialized to a variety of hunter-gatherer societies), and only a small number of subjects tested, such an outcome (as in Fig. 1c) is quite likely (see also Reyes-García et al. 2016). The notorious difficulty of devising culture-free or at least culture-fair intelligence tests is a direct consequence of this problem (Saklofske et al. 2014).

The prime example for secondary modularization in nonhuman primates is tool use, which is part of many test batteries typically used with nonhuman primates (e.g., Herrmann et al. 2007; Reader et al. 2011). Nonhuman primates vary considerably with regard to tool use, with great apes typically outperforming monkeys. But differences also occur within a species, both between wild and captive animals and among wild populations. Individuals of the same species show much higher propensities to use tools in captivity compared to their counterparts in the wild (Meulman et al. 2012; van Schaik et al. 1999). Once proficient, individuals show tool use with high degrees of automatization and efficiency. Wild populations, too, vary significantly with regard to their propensity to use tools and solve tool-related problems (e.g., chimpanzees, Gruber et al. 2011; orangutans, van Schaik et al. 2003; or capuchin monkeys, Cardoso 2013), arguably because they have ontogenetically acquired systematically different affordances of sticks or stones, which are perceived as

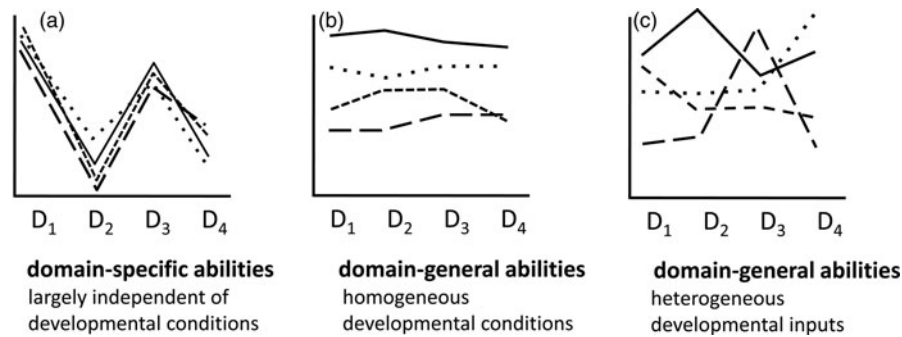


Figure 1. Performance across different cognitive domains (D₁-D₄). Each line represents the performance of an individual (or, in highly cultural species, of a population). (a) Performance is driven by domain-specific abilities; all individuals perform well in some domains but worse in others, but individual differences across domains are random; (b) performance is driven by domain-general abilities and individuals experience homogeneous developmental conditions, which leads to correlated performance between individuals across domains; (c) performance is driven by domain-general abilities but heterogeneous developmental conditions lead to specialization and secondary modularization of individuals in different domains. As a result, performance between individuals across domains is not correlated despite the presence of *g*.

potential tools in habitual tool users but not in non-tool users.

False negatives resulting from secondary modularization (see Fig. 1c) can be minimized if subjects with comparable rearing conditions are selected for the tests, but also if tasks prone to secondary modularization are excluded from test batteries. Thus, instead of naturalistic tasks that test for ontogenetically constructed skills that are likely to become automatized, such as tool use, or the ability to point and understand pointing, or even to use human language systems (Savage-Rumbaugh et al. 2005), it is preferable to include tasks testing for more elementary cognitive abilities, such as reversal learning, mental rotation, or quantity discrimination. Likewise, tests should avoid reliance on experience and knowledge of affordances that may differ among individuals depending on their biographies.

Although it is important to identify tasks and abilities prone to secondary modularization, it is not always easy to identify them. One way to do so is to examine the ontogeny of skills that are suspected to be the result of secondary modularization. Such skills should be acquired by developing immatures after a period of learning (perhaps following alternating series of instances of social learning and practice: Meulman et al. 2013; Schuppli et al. 2016), and could also potentially show high variation among adults. The increasing evidence for a major amount of skill learning by immature primates (e.g., Schuppli et al. 2016) and mammals and birds more generally (van Schaik et al. 2016) suggests a greater prevalence of secondary modularization in nonhumans than revealed by the size of cultural repertoires (Whiten & van Schaik 2007). Because in wild populations, social and ecological problems tend to be very uniform for all individuals, variation of skill profiles (see Fig. 1) between populations (that live under similar, wild or captive, conditions), rather than among individuals of the same population, provides an additional heuristic tool to distinguish between genuine primary and secondary modularity. This criterion would work for primate tool use, for instance. Most powerful to disentangle primary from secondary modularity, finally, are cross-fostering experiments. When cross-fostered individuals exhibit species-typical behavior from the foster species rather

than their own species, these behaviors clearly cannot result from primary modules. If the same procedure works within a species at the level of populations, it is similarly evidence for secondary, and thus learned, modules.

2.5. Psychometric or general intelligence? Future directions for animal studies

A crucial question that remains unanswered so far is to what extent a reliably identified *g/G* actually captures general intelligence in a broad sense: that is, reasoning ability and behavioral flexibility (Byrne 1994; Gottfredson 1997; Rumbaugh & Washburn 2003; Yoerg 2001; see also sect. 1.1). If it indeed does so, the processes underlying general intelligence (see also sects. 1.1.2 and 1.2.3) in animals should be broadly similar to those found in humans, with the obvious exception of language, and general intelligence should be correlated with independent measures of reasoning ability and behavioral flexibility (see also Bailey et al. 2007). If it is not, the statistically derived psychometric factors may reflect cumulative modularity: that is, the coexistence of separate, but coevolved modules.

These two possibilities can be teased apart empirically: If *g/G* represents intelligence in a broad sense, it must be possible to independently assess its validity, for instance, by showing that *g/G* is correlated with the domain-general EFs, as has been shown for humans. In principle, an association at a higher hierarchical level (e.g., between-species *G*) may be absent within the subgroups comprising it (e.g., within-species *g*), a phenomenon known as Simpson's paradox (Kievit et al. 2013). In the present case, we may thus find a correlation between *G* and EFs but not between *g* and EFs, which would suggest that *g* and *G* were not aspects of the same phenomenon: that is, general intelligence. Thus, to ensure that *g* and *G* are related to the same phenomenon, one must validate both of them independently.

Intraspecific studies of primates have so far largely neglected the approach to validate *g*, but this approach has provided fruitful insights in rodent studies. In rodents, individual levels of *g* have been shown to correlate with executive functions such as working memory. Matzel

et al. (2008; 2011b) have compared performance on standardized test batteries that reliably quantify g in mice with several measures of working memory, including short-term memory duration (how long can the mouse remember which arms of a maze it has already visited?), simple memory span (how many symbols associated with food can the mouse remember?), and selective attention (an adapted version of the STROOP task, in which the subject has to focus on one dimension of the task while suppressing a second dimension that provides conflicting information). As in human studies, they found that g was most strongly correlated with selective attention, followed by simple memory span and only weakly with short-term memory duration (Matzel et al. 2008; 2011b; Kolata et al. 2007). Moreover, they showed that training working memory capacity, but not simple working memory span, promotes selective attention and g (Light et al. 2010). Future validation tests could also examine the correlation between g and conduction speed or the ability to ignore irrelevant, distracting information, which are known correlates of g in humans (Melnick et al. 2013; Sheppard & Vernon 2008).

The corresponding validation of psychometrically derived g -scores in other species, particularly in nonhuman primates, would be highly desirable. Nonetheless, some evidence consistent with g representing domain-general cognitive mechanisms is already available from nonhuman primates. Within chimpanzees, heritability was strongest for overall cognitive performance g rather than for distinct aptitudes (Hopkins et al. 2014), as expected when the latter are due to secondary modularization rather than reflect specific adaptations. As a result, cognitive abilities that load higher on g in chimpanzees are more heritable, phenotypically variable, and presumably the result of recent natural selection (Woodley of Menie et al. 2015).

The independent evolution of large numbers of modules instead of general intelligence is particularly difficult to reconcile with interspecific findings of G . If we are dealing with independent modules, each species would be expected to possess a different repertoire of primary modules, according to the specific adaptive problems it faces. Importantly, across species, this should not result in a stable G factor. Studies providing evidence for G , however, suggest that particular species generally perform better or more poorly across all tested domains. This is also consistent with the empirical findings suggesting that differences in cognitive abilities among primates are concentrated on G (Fernandes et al. 2014). Furthermore, because specific skills, even if complex, can be performed with a very modest amount of brain tissue (e.g., Chittka & Niven 2009; Holekamp et al. 2015; Patton & Braithwaite 2015), one would not necessarily expect that G as a reflection of a large number of dedicated modules would correlate with brain size. The well-documented positive correlations between G and brain size thus further suggests that G reflects general intelligence, as does the finding that across primate species G was the principal locus of selection in the macroevolution of intelligence (Fernandes et al. 2014).

Empirical data also support a link between interspecific G and executive functions: Across primate species, brain size is not only correlated with G , but also with self (inhibitory) control (MacLean et al. 2014). This measure of self-control is directly correlated, in addition (Fig. 2), with G as

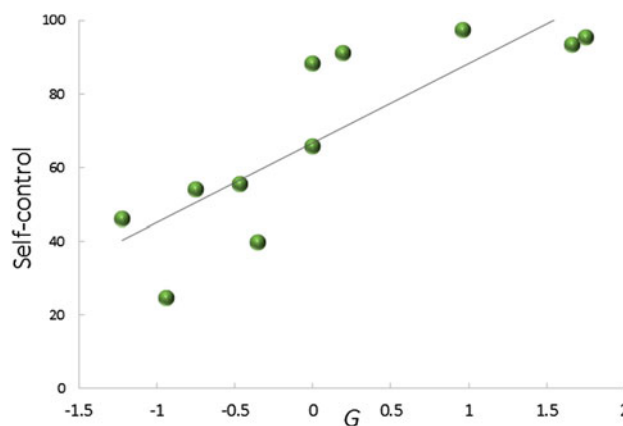


Figure 2. Positive correlation between the composite self-control measure of MacLean et al. (2014) and G (Deaner et al. 2006). Adjusted $r^2 = 0.66$, $F_{(1,9)} = 20.75$, $p = 0.001$ based on PGLS (phylogenetic generalized least squares) analyses. The same results are also found when the inhibitory control tasks included in the composite measure are analyzed separately (Cylinder task: adjusted $r^2 = 0.58$, $F_{(1,11)} = 20.75$, $p = 0.002$; A-not-B error: adjusted $r^2 = 0.41$, $F_{(1,12)} = 10.03$, $p = 0.008$).

established by Deaner et al. (2006), which has been derived from a completely independent data set.

A particularly powerful, but likewise underexplored, approach to construct validation consists in training individuals to solve a task in one domain and test to what extent they are able to apply their solution in a different domain. Intraspecific variation in this kind of cognitive flexibility (which is consistent with broad notions of general intelligence as applied by comparative scientists) should be correlated with psychometrically derived measures of individual g . Such a pattern would confirm that g is indeed a proxy of animal intelligence broadly defined.

Equally promising is to focus on unusually difficult problems relative to individual performance (i.e., problems that cannot be solved in a routine way). For instance, performance in difficult problems such as fast mapping or inductive reasoning was correlated with independently assessed g in mice (Wass et al. 2012). Particularly strong evidence would include the demonstration that individuals recruit the same basic cognitive processes for such difficult problems that are also strongly correlated with g , such as selective attention or working memory capacity (Matzel et al. 2013; Geary 2009).

Finally, particularly rigorous validation would be based on extra-domain assays. Just as human g correlates with academic success, workplace success, health, and even happiness (for references, see section 1), one could in principle ask whether g in animals is correlated with outcomes such as the size of cultural repertoires in nature, the ability to rise in social dominance, or to find food during periods of scarcity, and thus survival and even fitness. Unfortunately, this approach is difficult to achieve because it requires both reliably quantifying g and the various real-life outcomes in animals under natural conditions. More importantly, g may not necessarily predict basic fitness measures such as reproductive success, because of possible tradeoffs between investment into improving general intelligence and other vital activities, such as vigilance or social monitoring.

Table 7 summarizes the issues we have discussed in the form of criteria that may be fruitful to guide future studies.

3. Implications for the evolution of general intelligence

Taken together, although more validation remains to be done, especially in primates, the body of evidence is currently more consistent with the presence of domain-general cognitive abilities in primates and mice, reflected in g and G , than with the exclusive presence of independent, domain-specific cognitive adaptations. If general intelligence is not limited to humans, this inevitably leads to the question of the conditions favoring the evolution of general intelligence, to which we now turn. Whereas the evolution of Fodorian, specific, dedicated cognitive adaptations in response to recurrent fitness-relevant problems is seemingly straightforward (but see sect. 1.2.1), the evolution of general intelligence poses a puzzle. Domain-specific cognitive adaptations can be instantiated with modest amounts of neural tissue (Chittka & Niven 2009; Holekamp

et al. 2015; Patton & Braithwaite 2015) and directly bring about fitness-relevant benefits. Domain-general cognitive ability, however, seems to require substantial amounts of additional expensive brain tissue (Deaner et al. 2007; Reader et al. 2011), and is not automatically linked to fitness-relevant benefits because survival-relevant skills have to be ontogenetically constructed during a process of learning (van Schaik & Burkart 2011). This ontogenetic construction may be more successful in individuals with higher cognitive ability, as posited by investment theory (Cattell 1987), but additional factors also come into play, which renders the link between cognitive ability and fitness-relevant skills more fragile. For instance, whether a survival-relevant skill is acquired may also depend on pure chance (van Schaik & Burkart 2011; van Schaik et al. 2016). Furthermore, in order to more reliably translate general cognitive ability into fitness-relevant skills, some mechanisms for adaptive canalizations (as highlighted in sect. 1.2.2, Table 1) remain necessary, which have to coevolve or, if already present, be linked to the evolving domain-general cognitive processes. We are, therefore, faced with the puzzle that domain-general cognitive ability apparently

Table 7. Criteria that may be useful in guiding future efforts to (a) reliably identify g/G in nonhuman animals and (b) evaluate whether a statistically identified g/G captures intelligence in a broad sense: that is, reasoning ability and behavioral flexibility. The last two columns indicate to what extent corresponding criteria have been applied in rodents and primates. See text for details (the relevant sections are indicated in italics).

Criteria for Future Studies	Already Applied in	
	Rodents? (g)	Primates?
(a) To avoid statistical and methodological artifacts:		
• Use of large samples and diverse tasks, and analytical routines that do not require an a priori categorization of tasks into domains (2.4.1)	mostly (least for task diversity)	partly
• Replication of results in independent samples (particularly when large samples are not available, 2.4.1)	yes	g : partly ¹ G : yes
• Empirical control for confounds such as motivation, anxiety, or lower-level biological properties (2.4.2)	yes	no
• Avoidance of tasks prone to secondary modularization (2.4.3)	yes	No
(b) To explore whether an empirical finding of g/G captures intelligence as broadly defined (2.5):		
• Is g/G correlated with independently assessed executive functions?	yes	g : no G : yes
• Does executive function training, in contrast to a non-cognitive control training, increase g ?	yes	no
• Is g/G correlated with brain size?	yes	g : no G : yes
• Is there evidence that g/G has been selected for?	no	yes
• Is g/G correlated with the ability to transfer solutions across domains (i.e., cognitive flexibility)?	no	no
• Does g predict performance in very difficult tasks?	yes	no
• Does g predict success in real life?	no	no

¹ But not successfully: see Herrmann et al. (2010b); Hopkins et al. (2014); Woodley of Menie et al. (2015)

evolved in at least some lineages, or perhaps even in birds and mammals in general, even though its evolution has had to overcome more obstacles compared to the emergence of domain-specific cognitive adaptations. Hence, the goal of this section is to delineate the conditions favoring the evolution of general intelligence.

3.1. General intelligence as response to domain-specific selection pressures

The most common approach to explain variation in cognition across species, which has a long and venerable tradition, is to look for specific cognitive challenges in the social or ecological environment and investigate to what extent species facing these challenges have evolved bigger brains (Dunbar & Shultz 2007a; 2007b; Holekamp et al. 2015; Humphrey 1976; Jolly 1966; Parker 2015; Parker & Gibson 1977). Comparative analyses, particularly in primates, have shown that brain size is indeed correlated across species with various social and ecological variables, such as social complexity based on bonded relationships (Dunbar 1992; Dunbar & Shultz 2007b) and tactical deception (Byrne & Corp 2004), or extractive foraging (Parker 2015), manipulative complexity (Heldstab et al. 2016), and perceived seasonality (van Woerden et al. 2014; 2010; 2012). Shultz and Dunbar (2006) presented similar analyses for ungulates, with similar conclusions.

Nonetheless, much variation in brain size across species remains unexplained by domain-specific pressures (Holekamp 2007; van Schaik et al. 2012). Furthermore, not all species that excel in socio-cognitive tasks, most likely because of their complex social environment, also excel in non-social tasks and evolve big brains. Socio-cognitive abilities in hyenas, for instance, are on a par with those of the larger anthropoid primates, but there is no evidence that as in primates, this would be correlated with particularly powerful cognitive abilities outside of this domain (Holekamp et al. 2015). Likewise, callitrichid monkeys outperform their sister lineage, capuchin and squirrel monkeys, in socio-cognitive abilities, but the latter have superior physical cognition (Burkart & van Schaik 2010; 2016a; 2016b). For additional examples of how specific sophisticated cognitive skills can be achieved with very small brains, see Chittka and Niven (2009) for insects or Patton and Braithwaite (2015) for fish.

The crucial question thus is: Under what conditions do specific cognitive challenges result in an increase in general intelligence (and thus brain size) rather than in domain-specific cognitive solutions that do not require large amounts of brain tissue and do not translate into benefits in other domains too?

3.2. Direct selection on general intelligence

Some have argued that general cognitive ability is not the result of a domain-specific challenge but that it is directly selected so as to help animals cope with novel or unpredictable environments and overcome unusual or complex ecological challenges. According to this *cognitive buffer hypothesis*, large brains facilitate the construction of novel behavioral patterns through domain-general cognitive processes such as innovation and learning (Lefebvre et al. 2013; Sol 2009a). In support of this hypothesis, more innovative species tend to indeed have bigger brains – in birds

(Lefebvre et al. 1997) and primates (Reader & Laland 2002) – and innovation rates in the wild are correlated with *G* across primate species (Reader et al. 2011). Furthermore, innovation rates and brain size, and thus presumably *G*, predict colonization success in birds (Sol et al. 2005), mammals (Sol et al. 2008), amphibians and reptiles (Amiel et al. 2011), and in fishes (Shumway 2008; but see Drake 2007). Furthermore, large-brained birds use more successful learned strategies to avoid collision with human vehicles on roads (Husby & Husby 2014). Finally, anthropoid primates (but not lemurs, rodents, and omnivorous carnivores) cognitively buffer environmental seasonality (S. Graber et al. in prep.; van Woerden et al. 2014). Taken together, this work convincingly demonstrates that big brains are associated with greater behavioral flexibility and higher innovation rates under naturalistic settings, and that these in turn can be beneficial for a range of species when they face novel and unpredictable environments.

What remains to be answered in light of these obvious benefits, then, is why not all species evolved bigger and more-powerful brains. It is self-evident that all extant species are clearly smart enough for their current niche, but it is equally evident that a slightly better understanding that traces of a predator actually mark its presence, a better memory for which food sources already have been visited, or better object permanence to better keep track of a disappearing prey would convey a fitness benefit relative to conspecifics. We suggest that it is unlikely that focusing exclusively on potential benefits resulting from gains in brain size will further advance our understanding of the conditions under which domain-specific pressures lead to increased general intelligence. Rather, answering this question requires a focus not only on the benefits, but also on the costs of evolving a bigger brain.

3.3. Who can afford to evolve general intelligence? Cultural intelligence

Some species have larger brains than others, which, at least in primates, is associated with higher *G*. Why did these species respond to domain-specific selection pressures with an increase in general intelligence (see also sect. 3.1), or cope with environmental unpredictability by increasing their brain and intelligence, rather than opting for alternative, domain-specific adaptations (see also sect. 3.2)?

To answer these questions, it is important to keep in mind that the conditions under which large brains can evolve are to a substantial degree restricted by their costs (Isler & van Schaik 2014). Brains are energy-hungry organs that consume a large proportion of the energy available to an organism, particularly in growing immatures (Kuzawa et al. 2014). Thus, natural selection more readily favors an increase in brain size when this leads to an increase in net energy intake, a reduction in its variance, or ideally both. Furthermore, a big brain slows down the organism's development, which means that a species' ability to slow down its life history is a fundamental precondition for its opportunity to evolve larger brain size. Accordingly, the life-history filter approach (van Schaik et al. 2012) shows that slowing down life history, and thus evolving a larger brain, is only possible for species that can increase adult survival and are not subject to unavoidable extrinsic mortality, such as high predation pressure. Isler and van

Schaik (2014) have shown that such a cost perspective can explain a substantial amount of variation in brain size across primates, and that allomaternal care plays an important role in accommodating the costs associated with bigger brains (in particular, because food subsidies by allomothers help pay for the energetic costs of the growing immatures, and because of life-history consequences; see also Burkart 2017).

Natural selection thus evaluates the net fitness benefit of a bigger brain, which also takes the costs into account. The balance of benefits and costs is critically influenced by how efficiently an individual can translate brain tissue (or general cognitive potential) into survival-increasing innovations – that is, knowledge and skills. The cultural intelligence approach stresses that species that rely more systematically on social learning are more efficient in ontogenetically constructing survival-relevant skills (Herrmann et al. 2007; van Schaik & Burkart 2011; van Schaik et al. 2012; Whiten & van Schaik 2007) because social influences are very powerful domain-general canalization processes (as highlighted in Table 1). Whereas in the human literature, many approaches stress the importance of social inputs in the development of intelligence (e.g., Moll & Tomasello 2007; Tomasello 1999), the evolutionary version of this approach that suggests that social learning also plays a crucial role for the evolution of intelligence and brain size has received far less attention. Importantly, it builds on a broad notion of social learning (Heyes 1994, Box 1984; see also van Schaik et al. [2017], for a classification of social learning particularly suitable to test the predictions of the evolutionary dimension of the cultural intelligence hypothesis).

Consistent with the cultural intelligence approach, empirical results show that innovation rates in birds and primates are not only correlated with brain size or G , but also with the efficiency of social learning (Reader 2003; Reader et al. 2011). According to the cultural intelligence hypothesis, this is the case because, for species engaging systematically in social learning, additional brain tissue translates more reliably in survival-relevant skills, which lowers the threshold for evolution to favor an increase in brain size and general cognitive ability compared with species that do not rely on social learning. The frequency of opportunities for social learning is thus part of the answer why some lineages did evolve bigger brains, whereas others did not, even though they would all benefit from being more intelligent (van Schaik & Burkart 2011). Put in other words, we can use the pattern of solutions to the canalization problem (outlined in Table 1) to better understand under what conditions a species responds to a domain-specific selection pressure with a domain-general adaptation rather than with a narrow, domain-specific modular adaptation. The core message (to be derived from Table 1) was that all identified canalization problems can readily be overcome by social learning, and, therefore, species able to rely more on social learning should be more likely to be able to evolve domain-general cognitive adaptations. In sum, the cultural intelligence approach seems to best accommodate the findings of general intelligence as reviewed previously. For a more detailed comparison and discussion of the different approaches, see van Schaik et al. (2012) and Burkart (2017).

The cultural intelligence hypothesis was originally developed to explain why humans have evolved far bigger brains

and far greater intelligence than other great apes. Tomasello (1999; see also Herrmann et al. 2007) stressed that humans have evolved a set of species-specific socio-cognitive skills that facilitate social transmission, by allowing us to participate and exchange knowledge in cultural groups from an early age on. In other words, humans have become specialized in making use of social inputs to ontogenetically construct their skills, and rather than having evolved predominantly into a “cognitive niche” (Pinker 2010), they have evolved into a “cultural niche” (Boyd et al. 2011). Our extreme dependence on the socially guided ontogenetic construction of skills can also explain why the intraspecific link between g and brain size within humans is relatively weak (Muthukrishna & Henrich 2016; Pietschnig et al. 2015).

Humans can thus be seen as a special case of cultural intelligence, due to the active involvement of caretakers and the improved imitative abilities of our species. This view is consistent with approaches to human cognitive evolution that stress the role of allomaternal care, which not only results in energy subsidies to growing immatures but also increases the scope of social learning through the availability of more, and more tolerant, role models, who eventually also engage in teaching (Burkart & van Schaik 2016a; 2016b; Burkart et al. 2009; Hrdy 2009; Isler & van Schaik 2014; Kline 2015).

4. Discussion

4.1. Preliminary synthesis

The current body of evidence reviewed in this article is arguably most consistent with general intelligence not being unique to humans but also present in other species, even though much validation remains to be done, as outlined in sections 2.4 and 2.5. At present, the best-supported model for both animals and humans therefore views the ecological and social cognitive skills that can be measured in a species as the result of two pathways (indicated in Fig. 3).

In the downward pathway, cognitive skills result from general intelligence, which shows strong empirical correlations with brain size and executive functions. These skills correspond to Cattell’s (1963) crystallized intelligence and Geary’s (2005) secondary learning. In this case, the cognitive skills are ontogenetically constructed, facilitated by mechanisms of adaptive canalization beyond Fodorian modularity (summarized in Table 1) and eventually may become automatized (secondary modularization, which makes these skills particularly difficult to identify). As stressed by the cultural intelligence approach, social learning is a particularly efficient mechanism of ontogenetic canalization, particularly in large-brained animals. In the upward pathway, cognitive skills directly emerge as a result of dedicated, Fodorian cognitive modules that are independent of general intelligence, executive functions (Firestone & Scholl 2015), or brain size.

These two pathways to cognitive skills can coexist, and in fact almost certainly do. This situation has major implications. First, closely related, big-brained species that rely to some significant extent on the downward pathway and thus general intelligence may nevertheless exhibit rather distinct social and ecological skill sets. Some of their

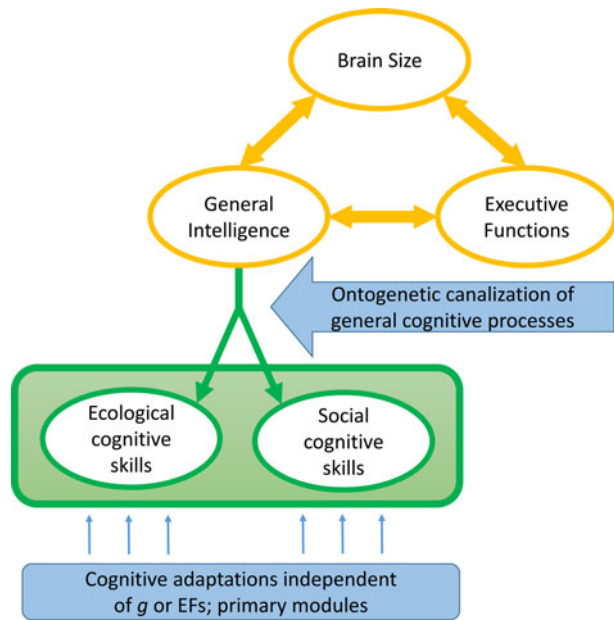


Figure 3. The origin of cognitive skills. Green: Ecological and social cognitive skills that can be measured in animals and that are visible to natural selection because they can result in fitness benefits. Yellow: Empirical interrelations between brain size, general intelligence, and executive functions. The latter two entities are only visible to selection to the extent that they are translated into fitness-enhancing cognitive skills. Blue: Adaptive canalizations that either guide the ontogenetic construction of cognitive skills from general intelligence (see Table 1 for details) or represent fully fledged Fodorian, modular adaptations that are independent of the domain-general (yellow) nexus.

species-specific ontogenetic canalization mechanisms can result in species differences in performance in specific domains, such as extractive foraging and tool use. Second, species may not primarily vary with regard to whether they have g , but with regard to the relative importance of these two pathways in building their skill sets, consistent with the increasing evidence for g in several nonhuman species. Approaches like cultural intelligence and the expensive brain framework delineate the conditions under which one or the other is more likely to evolve. This model is thus consistent with the broad pattern of results summarized in this review, including the results of mixed-species studies (sect. 2.3), and also with the idea of evolutionary continuity.

This preliminary synthesis suggests there is an alternative way of estimating the importance of general intelligence in a given species. Rather than exclusively relying on comparing the percentage of variance in performance explained by g (which in fact may be misleading, under the conditions outlined in sect. 2.4.1), one may attempt to estimate the importance of one pathway over the other in constructing an individual's skill set. To do so, it is crucial to be able to distinguish the origin of the skills in the green box (see Fig. 3), whether they result from the upward or the downward pathway. This is particularly difficult because eventually, skills constructed via the upper pathway may become automatized, and thus difficult to distinguish from primary modules (see also Table 2 in sect. 1.2.3). To identify them, one needs to show that they critically rely on EFs

(see also Table 6b) and show signs of being effortfully learned (see also Meulman et al. 2013; Schuppli et al. 2016). This is most feasible when the learning is social, either by directly recording the socially induced patterns of attention and practice (e.g., Jaeggi et al. 2010) or by interspecific cross-fostering (see section 2.4.3) where this is feasible. This alternative way of estimating the importance of general intelligence in a given species may turn out to be a promising complement to the alternatives pursued in nonhuman intelligence research so far.

4.2. Conclusions

Overall, the body of evidence from comparative studies lends increasing support to the notion that general intelligence is not unique to humans but also present in nonhuman animals and thus is not as tied up with language as some have suggested. Intraspecific evidence for g is particularly strong in rodents, whereas interspecific evidence (G) finds most support from primate and bird studies. Nevertheless, the rather young field of research into animal general intelligence still needs to mature just as work on human intelligence has taken decades to mature.

This enterprise can obviously profit from better integrating knowledge accumulated in the longstanding tradition of human psychometrics, not only with respect to the methodological aspects highlighted previously, but also to conceptual issues. For instance, obvious parallels exist between investment theory (Cattell 1987) and cultural intelligence approaches; pursuing them further may lead to novel insights. In other domains, however, superficial similarities are misleading. Modern massive modularity, for instance, based on very broad notions of modularity and inspired by evolutionary biology (Barrett 2015), hardly informs the debate about whether general intelligence exists in nonhuman animals. Among nonhuman animals, the ancestral state most likely corresponds to animal minds being made up entirely of dedicated modular adaptations (Shettleworth 2012a; 2012b). Among extant species, the question is, which behaviors are (still) regulated this way?

It is worth emphasizing that fruitful inputs can flow in the other direction too. For instance, the availability of valid animal models of general intelligence increasingly allows studying the underlying neurobiological and genetic mechanisms in ways that would not be possible in human studies (reviewed in Galsworthy et al. 2014; Matzel et al. 2013; Plomin 2001). Furthermore, via animal studies we can experimentally address the role of factors such as exploration tendency, known to be linked to g in mice (Grossman et al. 2007; Light et al. 2008), most likely via mechanisms stressed by investment theory (Cattell 1987). Finally, comparative studies are indispensable in addressing the broader question of where, why, and how g evolved. Among the most promising evolutionary explanations for general intelligence is the cultural intelligence approach, which predicts the coevolution of social learning and general intelligence. This perspective is strongly supported by interspecific studies where social learning, but also other social abilities such as deception, are strongly correlated with G across species (e.g., Reader et al. 2011) and where brain size is linked to opportunities for social learning during development (van Schaik et al. 2012).

A final issue concerns both animal and human studies. In most intraspecific studies, socio-cognitive tasks were not

part of the test battery, but where they were, the results were inconclusive. Thus, whereas Hopkins et al. (2014; Woodley of Menie et al. 2015) found socio-cognitive abilities loading on *g* in chimpanzees, Herrmann et al. (2010b) did not, neither in chimpanzees nor children. This may be because the intraspecific measures of socio-cognitive abilities used so far are less suitable than interspecific ones, for instance, because they sometimes produce ceiling or floor effects. However, human test batteries typically also do not include social cognition, and the relationship between general intelligence and socio-cognitive abilities in humans therefore remains poorly understood (Korman et al. 2015). Investigating the link between socio-cognitive abilities and general intelligence within humans thus is an important research priority.

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Open Peer Commentary

Coexistence of general intelligence and specialized modules

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Federica Amici,^{a,c} Josep Call,^{d,e} and Filippo Aureli^{f,g}

^aInstitute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, 04103 Leipzig, Germany; ^bDepartment of Primatology, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany; ^cDepartment of Psychology, University of Bern, 3012 Bern, Switzerland; ^dDepartment of Comparative and Developmental Psychology, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany; ^eSchool of Psychology and Neuroscience, University of St Andrews, St Andrews Fife KY16 9JP, United Kingdom; ^fInstituto de Neuroetología, Universidad Veracruzana, 91190 Xalapa, Veracruz, Mexico; ^gResearch Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, Liverpool L3 3AF, United Kingdom.

amici@eva.mpg.de <http://www.eva.mpg.de/pks/staff/amici/index.html>
 f.aureli@ljamu.ac.uk <https://www.ljamu.ac.uk/about-us/staff-profiles/faculty-of-science/natural-sciences-and-psychology/filippo-aureli>
 call@eva.mpg.de <http://www.eva.mpg.de/psycho/staff/josep-call/index.html>

Abstract: Here, we specifically discuss why and to what extent we agree with Burkart et al. about the coexistence of general intelligence and modular cognitive adaptations, and why we believe that the distinction between primary and secondary modules they propose is indeed essential.

We agree with Burkart et al. that general intelligence and specialized modules likely coexist in nonhuman animals. In mammals, similar cognitive skills have evolved independently in different phylogenetic lineages (Barton & Harvey 2000; de Winter & Oxnard 2001), suggesting the existence of independently evolving modules. These specialized modules likely reflect fitness-enhancing adaptations to specific socioecological challenges (Shettleworth 2010b). However, as Burkart et al. correctly argue, nonhuman

animals also solve problems flexibly across domains – something impossible for a strictly modular brain. Therefore, general intelligence and specialized modules likely coexist, at least in mammals: Although cognitive modules are the response to domain-specific socioecological challenges (Shettleworth 2010b), general intelligence may allow behavioural flexibility across domains – something especially useful in novel or unpredictable environments (Lefebvre et al. 2013; Sol 2009a).

From a neurological perspective, general intelligence and independent domain-specific cognitive skills compatibly coexist. Some properties of the human brain (e.g., amount of grey matter, neuronal speed of transmission) affect multiple brain regions, so that performance in different domains may correlate even if cognitive processes are localized in discrete regions (e.g., Jensen 1993; Lee 2007; Pennington et al. 2000). In our view, specific cognitive processes may be localized in specific brain regions also in other mammals, whereas other properties are intercorrelated across brain regions and affect all cognitive domains. Lee (2007), for instance, proposed that more synaptic connections might enhance the overall processing power of the brain, regardless of the brain regions involved. Therefore, having specific cognitive modules and more synaptic connections are two different brain characteristics that likely coexist.

In our view, Burkart et al. downplayed the importance of multifactor (as opposed to *g*-based) approaches in human intelligence (e.g., Kaufman 1979; Sternberg 1988; Gardner 1993). The concept of *g*, originally postulated by Spearman (1927), has been challenged on countless occasions and its current use in human IQ assessment is marginal at best, having been largely replaced by multifactor theories (see Kaufman 2009). An excessive reliance on *g* prevented Burkart et al. from considering multifactor approaches that may better capture interspecific cognitive diversity without necessarily invoking modularity. Several studies in nonhuman mammals have failed to find *g* and instead support a multifactor view of intelligence (e.g., Amici et al. 2012; Herrmann et al. 2007, 2010b; Herrmann & Call, 2012; Kolata et al. 2008; Schmitt et al. 2012). We suspect that the attractiveness of *g* stems from its simplicity and its use as a bastion against radical modularity. However, a multifactor view of intelligence should not be conflated with a modular view of the mind, at least not the kind of modularity defended by some evolutionary psychologists (e.g., Cosmides & Tooby, 2002). The multifactor view is general in spirit, as its factors subserve multiple cognitive problems, but each factor is specialized in particular operations (e.g., inference) or capacities (e.g., working memory). We think that a substantial portion of interspecific (and interindividual) variation in cognition can be captured by a multifactor theory without invoking modules, and as such, the multifactor approach is more germane with the notion of *g* than that of radical modularity.

We agree with Burkart et al. that different experimental and statistical approaches may lead to different results. Thus, finding *g* may, at least partly, depend on which data are included and how they are analysed. In particular, Herrmann and Call (2012) argued that task selection may inflate the relative importance of general intelligence (a point that Burkart et al. also made) by, for instance, selecting tasks that share a key feature (e.g., associative learning). Burkart et al. also argued that the allocation of tasks to specific domains (as done in confirmatory analyses and some Bayesian approaches) may be problematic, although it is possible to limit the drawbacks of a priori allocation by selecting multiple basic tasks with low cognitive demands (see Amici et al. 2012). Meta-analyses based on large data sets are especially useful for large-scale interspecific comparisons, but they often entail missing information (e.g., no interindividual variation), rely on data that are not evenly distributed across species, and disregard potentially important methodological differences across studies. These problems remain a challenge for future research, also because it is not easy to conceive tasks in which single cognitive skills are required.

We thought that the distinction between primary and secondary modules was useful. Burkart et al. argue that, through ontogeny, individuals may specialize in a certain domain, learning specific skills that become automatized and therefore appear to be domain-specific, even if they are not. The experimental distinction between primary and secondary modules is not easy, and relates to the more general problem of disentangling the relative contribution of evolutionary forces and developmental experience to cognition. Although the epigenesis of cognitive skills in nonhuman mammals is still largely unexplored, cross-fostering experiments would be a powerful tool to differentiate between evolutionarily selected and developmentally acquired behaviour. Experimental studies have shown that young macaques change their reconciliation tendencies (which are usually considered species-specific) depending on the social context in which they are raised (de Waal & Johanowicz 1993). Evolutionary forces and developmental experience are intertwined in complex ways: Differentiating between primary modules and ontogenetically acquired skills is an essential point that future research will need to address.

Finally, concerning the relative contribution of general intelligence and primary modules across taxa, there are various hypotheses as to how they should vary. On the one hand, an ecologically oriented approach suggests that taxa living in more unpredictable environments could especially benefit from behavioural flexibility across domains, and thus more strongly rely on general intelligence (Lefebvre et al. 2013; Sol 2009a). On the other hand, a more socially oriented approach suggests that taxa showing social learning can more efficiently acquire relevant skills through ontogeny without having to mainly rely on cognitive modules for their survival (Herrmann et al. 2007; van Schaik & Burkart 2011; van Schaik et al. 2012). Future research will need to find creative ways to contrast these hypotheses, while controlling for the existence of secondary modules.

An all-positive correlation matrix is not evidence of domain-general intelligence

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Rosalind Arden^a and Brendan P. Zietsch^b

^aLondon School of Economics & Political Science, London, WC2A 2AE, United Kingdom; ^bUniversity of Queensland, Brisbane, QLD 4072 Australia.

r.arden@lse.ac.uk zietsch@psy.uq.edu.au

Abstract: We welcome the cross-disciplinary approach taken by Burkart et al. to probe the evolution of intelligence. We note several concerns: the uses of g and G , rank-ordering species on cognitive ability, and the meaning of general intelligence. This subject demands insights from several fields, and we look forward to cross-disciplinary collaborations.

Burkart et al. make a substantial contribution to the literature on the evolution of intelligence. We agree with the implicit view of the authors that fostering connections between contiguous fields is essential in working towards a comprehensive understanding of intelligence. The shared goal includes identifying, at least, the selection pressures that shaped cognitive abilities in different species; the structure of cognitive abilities within different species; outcomes associated with intelligence; and the genetic architecture of intelligence. The target article helpfully reaches out to engage with scholars, questions, and methods emerging from several fields including comparative and differential psychology. We value highly this drawing together of disciplines. Here we raise some points arising from Burkart et al.'s work.

First, we do not find compelling the authors' argument that positive correlations among different cognitive abilities – and the resulting latent variable g – reflect domain-general intelligence. (“[E]vidence for domain-general intelligence in humans, estimated by the first factor derived in psychometric, factor-analytical

approaches, is pervasive ...” [sect. 1.1.2, para. 3].) By contrast, our empirically testable prediction is that positive correlations among cognitive abilities, and the resulting g factor, will be found within most animal species, whether the species exhibit domain-general intelligence. We expect this because random alterations to a complex system usually degrade its function; genetic mutations that affect multiple cognitive abilities will tend to affect them in the same direction (i.e., deleteriously). Such directional pleiotropy would cause positive correlations among cognitive abilities (even within species that do not exhibit domain-general intelligence). This conjecture is supported by the finding that lower scores on cognitive tests are linked with a greater proportion of the genome in runs of homozygosity (a measure of the extent to which recessive alleles are expressed) (Howrigan et al. 2016).

Likewise, G – a latent variable arising from factorial analysis of task scores *between* species – need not reflect domain-general intelligence. In the absence of domain-general intelligence, between-species differences in brain size, neural integrity, complexity, or myelination, for example, could affect different cognitive abilities in the same direction, leading to G . Therefore, neither g nor G is evidence for domain-general intelligence. Further, the causes of g and G may be unrelated; g might be caused by directional pleiotropy, but G could not be. We agree that existing within-species psychometric studies are few, small, and underpowered. The cure is larger studies.

Another important point is that, because latent variables are by definition unobservable, neither g nor G can itself be a direct target of selection – contrary to Burkart et al.'s suggestion that “ G is thus the principal locus of selection in the evolution of primate intelligence” (sect. 2.2, para. 4); g or G may reflect a real trait that is visible to selection (Borsboom & Dolan 2006), but we know of no conclusive evidence on this. Identifying biological or cognitive correlates of g and G is a useful approach to this question, but correlation is not causation, and so the cause(s) of g and G remain unclear. An additional note on the topic of selection is that, contrary to the target article (and Woodley et al. 2015), greater heritability does not indicate stronger recent selection – in fact, all else being equal, the opposite is true (Fisher 1930).

A linked issue is that the nature and cause(s) of g and G , and their relation to natural selection, depend on the tasks that are used to derive the factors. For example, interspecies differences in performance on behavioural tasks may depend on the match of the tasks to the species' typical environments and physical abilities as well as to their cognitive abilities (Barrett 2011) – in which case, the cause(s) of G could have environmental, physical, or cognitive sources.

Also, probing G does not answer the question “why are some species better at ‘catching on’ more generally than others?”; the answer to that lies in the recurrent problems posed by different ecologies and the costs and benefits of solving them. The costs of “generalising” make relatively more domain-general brains a better deal in some settings than in others. We should be cautious in rank-ordering intelligence between species, especially in the absence of comprehensive descriptions of cognitive abilities at the within-species level. Although it is manifestly true that some species are generalisers more than others (compare, for example, koalas with raccoons), it is also the case that a smart elephant makes a lousy bat.

It should be noted that even human intelligence, which has been shaped by selection, is not completely general; it is better described as under-specified. For example, although we may inhabit a 10-dimensional universe (Green & Schwarz 1984), we are unable to form a mental image of higher dimensional figures because our minds have evolved in a space containing relevant objects of only three or fewer dimensions.

We note that we can learn much about the evolution of intelligence from genetic analyses of cognitively well-characterised populations including parameters such as heritabilities, genetic correlations (among mental traits and biological substrates within species), and coefficients of genetic variation. Genetic

studies will allow us to test relations among any observed *g* factors and other fitness-related traits, and to explore evolutionary questions concerning convergence and homologies of cognitive abilities, or mechanisms that contribute to them, across species.

Last, we urge upon us all, conscious perspective-taking of those in other fields. We are all “cursed with knowledge” (Pinker 2014, p. 11). Unpalatable phrases like “positive manifold” (e.g., sect. 1.1.1, para. 3) and “phylogenetic inflection” (sect. 1.2.2, para. 4) act as caltrops impeding the free flow of knowledge and scholarship across disciplines. Reviewers and journals can help by emphasizing writing clarity. In saying this, we are not criticising the target article but celebrating and promoting the shared mission to help scholars talk to one another effectively. The focal problem, understanding the evolution of intelligence, is hard; maximising bandwidth across fields is essential.

Negative results are needed to show the specific value of a cultural explanation for *g*

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Ruben C. Arslan,^{a,b} Christoph J. von Borell,^{a,b,e} Julia Ostner,^{b,c,d} and Lars Penke^{a,b}

^aDepartment of Biological Personality Psychology, Georg Elias Müller Institute of Psychology, Georg August University Göttingen, 37073 Göttingen, Germany; ^bLeibniz ScienceCampus Primate Cognition, 37077 Göttingen, Germany; ^cGerman Primate Center Leibniz Institute for Primate Research, 37077 Göttingen, Germany; ^dDepartment of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, Georg August University Göttingen, 37073 Göttingen, Germany; ^eResearch Training Group 2070 – Understanding Social Relationships, Georg August University Göttingen, 37073 Göttingen, Germany.

ruben.arslan@gmail.com

<https://www.psych.uni-goettingen.de/en/arslan>

christoph.borell@psych.uni-goettingen.de

<https://www.psych.uni-goettingen.de/en/biopers/team/borell>

julia.ostner@biologie.uni-goettingen.de

<https://www.uni-goettingen.de/en/164051.html>

lpenke@uni-goettingen.de

<https://www.psych.uni-goettingen.de/en/biopers/team/penke>

Abstract: Burkart et al. suggest that social learning can explain the cognitive positive manifold for social animals, including humans. We caution that simpler explanations of positive trait intercorrelations exist, such as genetic load. To test the suggested explanation’s specificity, we also need to examine non-social species and traits, such as health, that are distal to cognitive abilities.

We commend Burkart et al. for writing a clear review of the available data on intraspecies *g* and interspecies *G*. Although data on individual differences on nonhuman animals are scarce, mapping out the potentially far-ranging implications will, we hope, encourage more high-quality nonhuman individual differences research. The authors’ effort to establish clearer and cross-species terms in the modularity debate and to highlight the existence of secondary modules is very welcome. Together with the acknowledgment, as nicely laid out by Burkart et al., that evolution is a tinkerer, not an engineer (Jacob 1977), we think these efforts will lead to progress in the understanding of the evolution and genetics of general intelligence.

We agree that integration between subdisciplines currently focused either on universals or individual differences (e.g., evolutionary psychology and behavior genetics) is necessary (Arslan & Penke 2015; Penke et al. 2007) and hope warnings about the lack of generalizability in nonhuman animal cognition research will be heeded (Arden et al. 2016; Thornton & Lukas 2012). On the other hand, we are unsure whether the effort to connect the appearance of *psychometric g* to the presence of *general intelligence* in a species succeeds. This leads us to examine what could cause *g* in the absence of a core intelligence trait.

We agree with the authors that psychometric *g* and domain-general intelligence should not be thoughtlessly equated (Penke et al. 2011). Although a species whose individuals vary in a core domain-general intelligence ability should exhibit a psychometric *g*, finding a psychometric *g* does not imply that variation in a core ability causes it. If *g* were caused by a core ability, then training this ability should show transfer effects to distal cognitive abilities. The authors cite such training studies, but acknowledge controversy about bias and methods (see also Colom et al. 2013; Redick 2015). Noack et al. (2014) concluded that the existing literature cannot establish such latent transfer effects. Claims of bilingual advantage have been similarly contested (Paap et al. 2015). If training of purported core abilities such as executive functions does not increase latent *g*, the case for core abilities causing the positive manifold weakens considerably. Moreover, positive correlations have not only been found among cognitive abilities but also between cognitive abilities and other fitness-related traits such as health, psychopathology, and height (Arden et al. 2016). Hagenaaers et al. (2016a) showed molecular evidence that a shared genetic aetiology underlies the phenotypic associations between health and intelligence.

Reasonable, less cognition-specific explanations have been put forward to explain such positive manifolds. First among them is probably genetic load (Hill et al. 2016a; Penke et al. 2007). Individuals vary in the number of deleterious genetic mutations they carry. Depending on where they occur, such wrong turns on the genotype-phenotype map could affect the integrity and condition of the whole organism, its brain, or more specific abilities. If many of the variants affecting cognitive abilities are pleiotropic (be that because they affect early development steps or because they disrupt frequently re-used genetic patterns), then we would also expect positive correlations between cognitive abilities and other fitness-related individual differences (Deary 2012; Houle 2000). Although causal inference from genetic correlations is hard (Johnson et al. 2011; Solovieff et al. 2013), we ought to consider the possibility that biological pleiotropy, not just health behavior, explains associations between intelligence and health (Hagenaaers et al. 2016b). For example, evolutionarily conserved genomic regions are strongly enriched for genetic variants affecting intelligence (Hill et al. 2016a). We think this can explain part of the *g* phenomenon. An explanation based on genetic load can even explain correlations between abilities resulting from primary modules. Other sources of individual differences such as stochastic events in early development can take an explanatory role similar to genetic load, by affecting early developmental steps and pervasive building blocks of the organism (Deary 2012).

Hence, our null hypothesis should not be complete independence of cognitive abilities, even if we knew they were primary modules. Some intercorrelation should be expected. The expected *degree* of intercorrelation depends on many unknowns, among them the degree of pleiotropy, the mutational target size, metabolic costs, and ontogeny of cognitive abilities.

With the nonhuman data available so far, we see a gap in the authors’ case: the absence of clear negative results in the search for *g/G*. The authors report no taxon where the search for the *g* factor was conducted with sufficient power and appropriate methods but still failed. We suggest that only after also gathering data from less social species can we ask whether, for example, social learning increases correlations between cognitive abilities. And only when correlations with non-cognitive abilities are compared can we ask what explains the increased correlation between cognitive abilities. As the authors point out, nonhuman research can help test explanations for *g* with designs infeasible in humans, such as cross-fostering experiments. This extends to genetic load. Using genetically uniform strains and mutation accumulation lines (although these are already extremely time-consuming in micro-organisms) could help clarify the involvement of genetic load.

We lack the space to fully address alternative explanations for interspecies G , but hope to also see joint phylogenetic tree analyses of sociality and variance explained by g . To be able to test this, recommendations for increased sample sizes in such studies should be followed (Thornton & Lukas 2012). Differential measurement error across subtests and species has to be modelled and corrected for, not just used to explain negative findings.

In conclusion, we would add the following to the authors' call for research: We need individual differences of data along the whole gradient of sociality including maybe even octopuses, and studies should also examine more distal traits such as health and size. Then, the specific added value of the proposed model can be tested. We want to echo this and previous calls (Arden et al. 2016; Thornton & Lukas 2012) for more individual differences research on nonhuman animal cognition. We hope for more stimulating evolutionary theorizing on individual differences, as in this target article.

G but not g: In search of the evolutionary continuity of intelligence

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Moran Bar-Hen-Schweiger,^a Avraham Schweiger,^b and Avishai Henik^c

^aDepartment of Psychology, Ben-Gurion University of the Negev, Beer-Sheva, Israel 84105; ^bDepartment of Behavioral Sciences, Academic College of Tel Aviv, Israel 61083; ^cNew York City Medical & Neurological Offices, New York, NY 11373

henik@bgu.ac.il <http://www.bgu.ac.il/~henik>
moranbar@post.bgu.ac.il schweige@mta.ac.il

Corresponding author: Avishai Henik

Abstract: Conceptualizing intelligence in its biological context, as the expression of manifold adaptations, compels a rethinking of measuring this characteristic in humans, relying also on animal studies of analogous skills. *Mental manipulation*, as an extension of object manipulation, provides a continuous, biologically based concept for studying G as it pertains to individual differences in humans and other species.

Burkart et al.'s review of studies involving g and G in animals is illuminating. However, the authors seem to assume that a century of studies settled the question of g in humans. In this commentary, we challenge this assumption. We suggest that the definition of intelligence (Gottfredson 1997) cited by the authors seems to be overly anthropocentric: It emphasizes skills characteristic of *Homo sapiens*. This very definition appears to constrain g in humans and, in our opinion, limits its generalizability in a biological context. Furthermore, the old debate about the cultural fairness of intelligence testing is testimony to the vicissitudes of defining and measuring g in humans.

As an alternative, we propose a description of intelligence in a biological context, inspired by the work of Piaget, who suggested that "Intelligence is an adaptation ... The organism adapts itself by materially constructing new forms to fit them into those of the universe, whereas intelligence extends this creation by constructing mental structures which can be applied to those of the environment" (Piaget 1952, pp. 3–4). Thus, intelligence is the ability of a species to adapt flexibly to many environmental challenges in the service of survival. Note that this definition is species relative: It follows naturally that the larger the range of environmental conditions to which an organism can potentially adapt, the more intelligent it might be relative to other organisms with more limited repertoire of adaptations (Piaget 1971).

Furthermore, we propose that intelligence is not a trait. Rather, it is the inference by the human observer in the face of increasing the potential and scope of domain-specific skills developed by species in adapting to a variety of environmental pressures. These domain-specific skills allow for increasing the range of

environments to which the organism is able to respond efficiently. Of course, the converse is also the case: Environmental changes will result in adaptation by the emergence of new domain-specific skills. Such increase is the consequence of evolving ever-larger brains, especially frontal lobes, which enables the development of an ever-greater repertoire of skills (Parker & Gibson 1977). Moreover, a procedure or skill developed specifically within a specific domain might become accessible to systems or brain structures that serve other domains (Anderson 2010). Such change in accessibility creates domain-general skills or procedures, thus improving intelligence (or adaptability) (Rozin 1976). The result appears to be g to the human observer. Lest we revert again to an overly anthropocentric view, we emphasize that increasing brain size is just one means of increasing survivability.

Instead of the mysterious g factor, we propose that G is reflected in a capacity: object manipulation in various species, with its evolution into a mental manipulation (MM) in humans – the hallmark of human activity. MM can be investigated by various tests using verbal, mathematical, or spatial manipulation of contents. These tests tend to correlate positively not because they reflect g , but because they reflect MM. We suggest that MM is the ability to perform transformations on concrete and abstract objects (e.g., mental rotation) and imagine the results, without needing the actual objects. This ability clearly improves adaptability to a wide range of environments. One example of MM is when a child learns to consider a situation from the perspective of another person. We claim that linguistic construction, as well as other cognitive processes, involves MM, so that it may be considered as an overarching principle of human operations and as the basis of human culture.

To illustrate the biological continuity and the development of domain-specific skill, we consider the ontogeny of mathematical skills in humans (described originally by Piaget 1971). Initially, babies develop the concept of *one*, *few*, and *many*, requiring direct perception of objects. Animals exhibit number concept at this level (Pahl et al. 2013). Later, children learn that abstract symbols represent quantities, and they learn how to manipulate them. Next, algebra supplants numbers at ever higher levels of abstraction, with ever more abstract manipulations (i.e., operations). An analogous analysis was offered by Greenfield (1991) regarding the development of linguistic structures from motor schemata in children. The essence of these developmental achievements is that they reflect the ability to perform transformations, translations, recombinations, projection, predictions, and so on, in infinite ways. What is crucial for adaptation is the ability to entertain the results of these MMs, and then select only the best one for action.

One challenge to which MM could offer a positive contribution is in measuring the nebulous g . Many, if not all, IQ testing instruments may be viewed as assessing domain-specific abilities. To what extent do they reveal an underlying, domain-general or universal ability? For example, the Raven Progressive Matrices is commonly used as a measure of the g factor (Deary et al. 2010). However, in a wider cultural context, this test may measure no more than a domain-specific, culturally acquired skill (Owen 1992). We suggest that MM is such an overarching set of operations. It is possible that MM started as an ability to manipulate or view actual objects designed for the visual-spatial domain. These visual-spatial specific abilities evolved to serve other domains (e.g., language) and have become accessible to other systems that serve other commitments.

In sum, we propose that the alternative conception of intelligence as offered here, compels rethinking g in humans. It is suggested that animal behavior, specifically, object manipulations, and perspective taking (a variant of MM) with increasing cortex, provide specific precursors to human abilities, as reviewed by Burkart et al. A good example of a transitional stage to MM demonstrating biological continuity is deception in apes (Byrne & Corp 2004). We further submit that MM may better serve as a biologically based concept for studying individual differences in humans, while providing for continuity across species.

Domains of generality

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Andrew Buskell^a and Marta Halina^b

^aLondon School of Economics, Department of Philosophy, Logic and Scientific Method, London School of Economics, London, United Kingdom, WC2A 2AE;

^bUniversity of Cambridge, Department of History and Philosophy of Science, University of Cambridge, Cambridge, CB2 3RH, United Kingdom.

a.buskell@lse.ac.uk mh801@cam.ac.uk

<http://people.ds.cam.ac.uk/mh801/>

Abstract: We argue that general intelligence, as presented in the target article, generates multiple distinct and non-equivalent characterisations. Clarifying this central concept is necessary for assessing Burkart et al.'s proposal that the cultural intelligence hypothesis is the best explanation for the evolution of general intelligence. We assess this claim by considering two characterisations of general intelligence presented in the article.

Recent studies suggest that general intelligence is not limited to humans, but can be identified in a number of nonhuman species. Such studies provoke the question: How does general intelligence evolve? Burkart et al. argue that the cultural intelligence hypothesis is the best explanation for the evolution of human and animal general intelligence. According to this hypothesis, the access to socially maintained knowledge generates selection pressures for increased reliance upon domain-general capacities. In order to assess the cultural intelligence hypothesis, one must have a good grasp of what is meant by general intelligence. The authors are quick to note that this is a tricky concept to pin down. Defining general intelligence in terms of specific measures of intelligence like problem solving and learning is problematic insofar as these skills can result from adaptive domain-specific modules. The authors thus characterise general intelligence as a domain-general ability best understood in contrast to the properties of domain-specific modules (sect. 1.2.1, para. 5, 6). There are many ways to make this contrast, however. As a result, the authors characterise domain-generality in a variety of ways: as phenotypic plasticity, as being non-modular in structure, as requiring learning or other processes of “ontogenetic construction” or canalisation, as involving reasoning, or as involving belief or belief-like states. The fact that domain-generality can be understood in many distinct and non-equivalent ways is worrisome insofar as different conceptualisations of domain-generality are likely to require distinct evolutionary narratives.

To take one example, domain-generality can be purchased quite cheaply if it is understood as mere phenotypic plasticity. Peter Godfrey-Smith (1996), for instance, makes a convincing case that phenotypic plasticity is selected for in heterogeneous environments—a scenario one expects to be common. To the extent that this is the case, phenotypic plasticity will be a widespread adaptive solution, seen quite deep in evolutionary history (Godfrey-Smith's central example of *Bryozoa*, sometimes known as “sea-moss,” behaviour makes this point clear). One does not need to invoke the cultural intelligence hypothesis in order to purchase such flexibility.

Elsewhere, the authors characterise domain-generality as involving reasoning and belief or belief-like states. The idea here is that domain-generality can be conceptualised as the ability to use a variety of distal cues to generate mental representations, which in turn can be used to produce adaptive behaviour (sect. 1.1.2, para. 4). Of course, mental representations can be understood more or less restrictively. In some extenuated way, simple neuronal systems like those of *Caenorhabditis elegans* “represent” or register their local environment. However, it seems clear that the authors are interested in representations in a richer sense, in line with what Kim Sterehny (2003) called “de-coupled representations.” These are representational states with the function of tracking features of the environment, but which

are not tightly coupled to specific types of response. Such representations identify what Sterehny called “action targets” which can be acted on in a variety of different ways to satisfy goals.

De-coupled representations are an interesting evolutionary phenomenon, and one that the cultural intelligence hypothesis may get some explanatory purchase upon. De-coupled representations are the kind of psychological structure one would expect of creatures who need to rationalise and predict the thoughts of conspecifics, as well as weigh the complex tradeoffs involved in acquiring knowledge from multiple sources. However, even here we urge caution. The coleoid cephalopods (cuttlefish, squid, and octopuses) seem to display de-coupled intelligent behaviour, particularly those of the order *Octopoda*. Octopuses display sophisticated cognitive capacities including problem solving, individual recognition, and perhaps imitation (Godfrey-Smith 2013; Mather & Kuba 2013; Roth 2013). Nonetheless, octopuses are not social, often interacting with conspecifics only during mating (Roth 2013). The existence of cephalopod intelligence may thus pose a counterexample to the cultural intelligence hypothesis even when general intelligence is understood in the restricted sense of involving de-coupled representations.

The authors might respond by arguing that the evolutionary phenomenon they are attempting to describe is not merely the existence and amplification of one of the aforementioned features of domain-general cognition, but how a conglomerate of such properties came about and increased in sophistication. This conglomerate might include flexible reasoning and learning generated by de-coupled representations, in turn underpinned by the contents of an increasingly large brain. If this conglomerate really is what the authors mean by domain-generality, however, then they need to do more in order to motivate it. Recent work on grackles and New Caledonian crows, for example, shows that behavioural flexibility occurs independently of innovativeness, problem-solving ability, problem-solving speed, and brain size (Logan et al. 2014; Logan 2016a; 2016b). Given that purported features of domain-general intelligence do not always co-occur, further justification is required to ground claims that “general intelligence” is a unitary explanandum.

We suggest that the consequences of this analysis are twofold. First, we urge the authors to be clearer about the terms they use, and to operationalise them when possible. Second, the arguments presented here suggest that the cultural intelligence hypothesis may be insufficient for explaining the evolution of general intelligence, understood as involving the evolution of de-coupled representational states. Although this hypothesis may capture some directional effects in some clades, more needs to be done in order to show that it is the best explanation for the evolution of general intelligence in all clades.

Theory of mind: A foundational component of human general intelligence

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David Estes and Karen Bartsch

Department of Psychology, University of Wyoming, Laramie, WY 82071

estes@uwyo.edu bartsch@uwyo.edu

Abstract: To understand the evolution of general intelligence, Burkart et al. endorse a “cultural intelligence approach,” which emphasizes the critical importance of social interaction. We argue that *theory of mind* provides an essential foundation and shared perspective for the efficient ontogenetic transmission of crucial knowledge and skills during human development and, together with language, can account for superior human general intelligence.

We commend Burkart et al. for their impressive review of current theory and research on the evolution of general intelligence.

Although their analysis yields a persuasive account of the empirical data regarding general intelligence across species, it also motivates increased attention to key components of human cognition that, in our view, will prove to be essential for a complete understanding of the evolution of cognition.

A comprehensive theory of general intelligence and its evolution must somehow account not only for the commonalities evident across species, as targeted by Burkart et al., but also for the obvious wide divide between humans and nonhuman primates. Although we agree that the “cultural intelligence approach” endorsed by the authors will be at the heart of a successful theory, we believe their analysis also suggests directions for further elucidation that would specifically address what is special about human cognition.

Specifically, and consistent with the cultural intelligence approach, we propose that language and theory of mind (ToM) together can go far toward explaining superior human general intelligence. Language and ToM arguably have the markings of primary modules, at least as characterized by Burkart et al. (sect. 1.2.3, Table 2): Both appear rapidly and dependably early in development across all cultures without explicit instruction and even in the most disadvantaged and deficient environments (e.g., Wellman et al. 2001).

Others can better address the role of language in human intelligence (see Dunbar 1998; Smith 1996), so we focus here on the contribution of ToM, defined as the universal propensity of humans to understand and explain their own and others’ behavior in terms of internal mental states and processes such as beliefs, desires, goals, and intentions (e.g., Wellman 1990). We note here that language and ToM are so ontogenetically and symbiotically intertwined that they are difficult to discuss separately. Indeed, some have made a strong case for their co-evolution: “The evidence at hand suggests that language and theory of mind evolved ... in constant interaction, serving one primary adaptive goal: to improve social coordination” (Malle 2002, p. 280).

Nevertheless, a conceptual case can be made for ToM alone being especially foundational for human general intelligence. As a developing domain-specific causal framework that supports advanced meta- and social cognition, such as recognition of the possibility of false beliefs and variation in knowledge states between individuals, ToM contributes essentially to social learning as characterized by the cultural intelligence approach. We offer here a few examples of phenomena illustrating the crucial role of ToM in social learning and, by extension, the evolution of human general intelligence. For a recent collection of relevant research and commentary on these issues, see Legare and Harris (2016), and especially Tomasello (2016).

Even children under age 2 engage in observational imitative learning that depends on attention to the actor’s intended action or goal. For instance, Meltzoff (1995) demonstrated that when shown an actor who tried and failed to achieve a goal, such as hanging a string of beads on a peg, 18-month-old children imitated what the actor *tried* to do rather than what the actor actually did (dropping the string of beads). Carpenter et al. (1998) found that young children shown adult demonstrations of action sequences containing both accidental and intentional actions more often reproduced the intentional actions, suggesting that even early observational learning is contingent on an appreciation of another’s intentional state.

Similarly, research on children’s early attunement to potential knowledge in others reveals the advantages for a social learner afforded by an emerging ToM. Even 2-year-olds attempting to locate a desired object efficiently seek help from informed rather than ignorant adults (O’Neill 1996), demonstrating an incipient appreciation of mental states that will eventually help them when they seek to obtain information rather than objects. Recent studies of children’s reaction to testimony suggest that, although children generally assume what they are told is truthful (e.g., Harris 2012), they are more willing to believe an expert or experienced source. Moreover, as children advance from early to

middle childhood, their evaluation of others’ testimony increasingly recognizes the possibility of deception or distortion (Mills 2013). On the positive side, children’s growing sophistication eventually includes recognizing the specifically pedagogical motives of adult teachers, as described in Gergely and Csibra’s (2006; Csibra & Gergely 2009) proposed *theory of natural pedagogy*. Children’s particular “readiness” to learn through social instruction (and also to teach others; see Flynn & Whiten 2008) hinges on a recognition of the internal content of others’ minds. From our own research, we can add that young children’s reflections on their own learning, as assessed in transcripts of at-home conversations, are in fact particularly focused on their teachers and what their teachers know as opposed to other aspects of learning events, such as how or when learning occurred (Bartsch et al. 2003).

Early childhood is replete with phenomena suggestive of the central role of ToM in social learning. In addition to these examples, the acquisition of belief understanding, widely recognized as a hallmark of developing ToM and first evident around 4 years of age in children’s explicit predictions and explanations of action (e.g., Wellman et al. 2001), can also be viewed as foundational to the most advanced human achievements, such as those that occur in the collaborative activity of scientific research and the uniquely human creation of formal methods to facilitate learning (e.g., Meltzoff et al. 2009). At a fundamental level, our greatest accomplishments must rest on our basic capacity to imagine and recognize the variations and vulnerabilities of human cognitive states. With this in mind, future researchers guided by Burkart et al.’s final recommendation to explore further the relationship between intelligence and socio-cognitive abilities would do well to direct those efforts toward theory of mind.

Understanding the relationship between general intelligence and socio-cognitive abilities in humans

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Pablo Fernández-Berrocal,^a Rosario Cabello,^b and María José Gutiérrez-Cobo^a

^aDepartment of Basic Psychology, Faculty of Psychology, University of Málaga, 29071, Spain; ^bDepartment of Developmental and Educational Psychology, University of Granada, Granada, 18071, Spain.

berrocal@uma.es

https://www.researchgate.net/profile/Pablo_Fernandez-Berrocal
rcabello@ugr.es

https://www.researchgate.net/profile/Rosario_Cabello
mjgc@uma.es

https://www.researchgate.net/profile/Maria_Jose_Gutierrez-Cobo

Abstract: Burkart et al. consider that the relationship between general intelligence and socio-cognitive abilities is poorly understood in animals and humans. We examine this conclusion in the perspective of an already substantial evidence base on the relationship among general intelligence, theory of mind, and emotional intelligence. We propose a link between general intelligence and socio-cognitive abilities within humans.

Burkart et al. assess what studies on general intelligence in nonhuman animals mean for current theories about the evolution of general intelligence. Although we agree with their conclusions in favor of the cultural intelligence approach, we do not entirely agree with their assessment that the relationship between general intelligence and socio-cognitive abilities is poorly understood in animals and humans (sect. 4.2, para. 4).

In this commentary, we aim to place their conclusion in the perspective of an already substantial evidence base demonstrating a relationship between general intelligence and socio-cognitive abilities in humans. We review recent meta-analyses on this relationship, focusing on connections among general intelligence, theory

of mind (ToM; Baron-Cohen et al. 1997; Baron-Cohen et al. 2001) and ability-based emotional intelligence (EI; Mayer & Salovey 1997).

ToM is the ability to attribute mental states (e.g., emotions, intentions, or beliefs) that differ from our own (Baron-Cohen et al. 1985; Baron-Cohen et al. 2001). ToM is widely assessed using the Reading the Mind in the Eyes Test (RMET; Baron-Cohen et al. 1997; 2001), which can reveal intersubject differences in social cognition and emotion recognition across different groups and cultures (Fernández-Abascal et al. 2013). A recent meta-analysis involving 3,583 participants revealed a small positive correlation between general intelligence and RMET score ($r = .24$), with both verbal and performance IQ showing similar correlations with RMET score (Baker et al. 2014). The authors of that meta-analysis concluded that intelligence contributes significantly to ToM, with verbal and performance IQ contributing equally.

EI is a construct central to conceptualizing and evaluating socio-cognitive abilities. EI refers to the ability to reason validly with emotions and with emotion-related information and to use emotions to enhance thought (Mayer & Salovey 1997; Mayer et al. 2008). The most common measure of ability-based EI is the Mayer-Salovey-Caruso Emotional Intelligence Test (MSCEIT; Mayer et al. 2002). This test assesses the four primary abilities (branches) of the Mayer and Salovey model of EI: perceiving emotions in oneself and others, using emotions to facilitate thought, understanding emotional information, and regulating emotions in oneself and others (Mayer & Salovey 1997). MSCEIT assesses these emotional abilities by asking the subject to solve a series of emotion-based problems, thereby avoiding the high risk of bias associated with self-report EI measures. MSCEIT-based studies have demonstrated a relationship between general intelligence and EI. For instance, Webb et al. (2013) found significant correlations of MSCEIT score with general IQ, verbal IQ, and performance IQ. A meta-analysis of 53 studies involving 3,846 participants found positive correlations of scores on the MSCEIT or its forerunner MEIS with general intelligence ($r = .30$), verbal intelligence ($r = .26$), and nonverbal intelligence ($r = .23$) (Kong 2014).

Factor-analytic exploration of how mental abilities correlate with one another suggests an even broader range of intelligences linked to ability-based EI, including fluid intelligence, crystallized intelligence, and quantitative reasoning (Legree et al. 2014; MacCann et al. 2014). These intelligences lie within the second stratum of the Cattell-Horn-Carroll model (McGrew 2009). Further evidence for the relationship of ability-based EI with a range of broad intelligences comes from a study involving more than 12,000 people ranging in age from 17 to 76 years (Cabello et al. 2016). In this study, MSCEIT scores varied with age according to an inverted-U curve: Younger and older adults scored lower than middle-aged adults, just as reported for several other intelligences.

In this way, the extensive literature on ability EI provides substantial evidence linking various types of intelligence to socio-cognitive abilities. Nevertheless, one thing that remains unclear is how the EI assessed on the MSCEIT relates to executive functions, some of which—such as inhibitory control and working memory—strongly correlate with general intelligence, as Burkart et al. point out (sect. 1.1.2, para. 2). Gutiérrez-Cobo et al. (2016) systematically reviewed 26 studies on the relationship between EI and cognitive processes reflected in tasks such as the Stroop task or Iowa gambling task. The authors found that performance-based ability EI (such as measured on the MSCEIT)—but not self-report EI—positively correlated with efficiency on emotionally laden tasks. In contrast, no correlations were observed between EI measured in various ways and non-emotionally laden tasks. These findings suggest that the greater intelligence reflected in higher ability-based EI can mean superior performance on emotionally laden socio-cognitive tasks, but not necessarily on other kinds of tasks.

In summary, the body of studies examining ToM and ability-based EI build a strong case that general intelligence, particularly

intelligence in the second stratum of the Cattell-Horn-Carroll model, is associated with socio-cognitive abilities in humans. Studies of ability-based EI and cognitive processes nuance that this relationship is likely to be complex: For example, higher ability EI may lead to more efficient cognitive processes in emotionally laden tasks but not other tasks. A link between general intelligence and socio-cognitive abilities coincides nicely with studies from affective and social neuroscience showing that emotion processing and cognition in the brain are highly intertwined and mutually determined (Phelps et al. 2014).

Future work should (1) examine to what extent different socio-cognitive abilities are related (e.g., how are ToM and EI related?), (2) analyze to what extent different socio-cognitive abilities relate to general intelligence, (3) test whether and how specific social inputs play a role during ontogenetic construction of socio-cognitive abilities, and (4) identify brain regions involved in different socio-cognitive abilities and examine their relationship and overlap with regions implicated in general intelligence.

Taking a multiple intelligences (MI) perspective

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Howard Gardner

Harvard Graduate School of Education, Harvard University, Longfellow Hall 235, Cambridge, MA 02138.

hgast@gse.harvard.edu <http://multipleintelligencesoasis.org/>

Abstract: The theory of multiple intelligences (MI) seeks to describe and encompass the range of human cognitive capacities. In challenging the concept of general intelligence, we can apply an MI perspective that may provide a more useful approach to cognitive differences within and across species.

In line with the view of most psychologists and psychometricians, Burkart et al. assume that there is a single general intelligence (g); controversy centers around the identity and nature of domain-specific computational capacities and the extent to which nonhuman animals can be said to have a g -like capacity.

Over the past several decades, researchers have challenged this consensus and developed alternative ways of conceptualizing human intellect (Guilford 1967; Sternberg 1984). In my case, I deliberately disregarded paper-and-pencil instruments of the sort favored in scholastic settings, and which almost always yield a “positive manifold.” Instead, culling evidence from a range of disciplines—from anthropology and education to neuropsychology and evolutionary biology—I put forth the claim that human beings are better described as having a set of relatively independent computational capacities, which I termed the “multiple intelligences” (Gardner 1983/2011).

According to my analysis, the kind of intelligence typically measured in IQ tests is scholastic intelligence—the bundle of skills needed to succeed in modern secular schools. In my terms, success on such instruments depends on a combination of linguistic and logical-mathematical intelligences, with spatial intelligence sometimes tapped as well. It is worth noting that, at the extremes, strength (or weakness) with one of these intelligences does not predict comparative strength (or weakness) with the other (Detterman 1993). Largely ignored in standard measures of intellect are several other intelligences that I identified: interpersonal and intrapersonal intelligences (often described as social or emotional intelligence), musical intelligence, bodily kinesthetic intelligence, and naturalist intelligence. Because we do not have comparable instruments to assess nonscholastic intelligences (but see Gardner et al. 1998), we do not know to what extent ability in, say, musical intelligence correlates with strength (or deficits) in, say, social or intrapersonal intelligence. Yet ample evidence confirms that these intelligences can be dissociated from one another, as happens with prodigies (Winner 1997) or

individuals on the autistic spectrum (Silberman 2016). Put differently, ability to succeed in school settings is decreasingly important, as one ventures to contexts that differ significantly from the canonical Western school.

Even as MI theory differs from a *g*-centric view of the world, it also differs from Fodorian modules. Intelligences may contain specific modules (e.g., linguistic intelligence may contain a parsing or phoneme discrimination module), but their exercise in the world is far less reflexive, far more adaptive. An individual skilled in linguistic intelligence is able to speak, write, communicate, and learn new languages and the like. Skill in spatial intelligence involves making sense of local two-dimensional arrays, as well as navigating around a neighborhood or, indeed, around the globe.

It may seem that the intelligences are a grab-bag of primary Fodorian modules as well as more-general secondary information-processing or problem-solving capacities processing certain kinds of content. And, indeed, as we attempt to make sense of human cognition, that characterization proves serviceable. MI theory stands out less in terms of the precision of its claims with respect to the execution of tasks in the world than in its challenge to the notion that there exists any sensible and defensible notion of general intelligence – even within *Homo sapiens*.

For those sympathetic to an MI view, formidable questions remain. What are the basic building blocks of intellect? To what extent is each heritable? How do strictly modular capacities interact with ones that are more permeable? Do we need to posit a separate “executive function,” a so-called “central intelligence agency,” or does such a capacity emerge naturally out of intrapersonal intelligence (the ability to know oneself accurately) and logical intelligence (the ability to reason about one’s actions)?

An MI perspective yields far more specific pictures of how human beings carry out the raft of tasks for which the species has specifically evolved as well as those tasks that have emerged over the centuries by virtue of newly emerging cultural artifacts and technologies, and, perhaps, acts of nature (e.g., diseases, volcanic eruptions). Furthermore, such a perspective suggests an alternative approach to the issue addressed in the target article.

Instead of invoking *g*, plus specific modules, one can instead break down any task in terms of its demands on specific intelligences (e.g., playing chess involves logical and spatial intelligence but little bodily or musical intelligence) as well as the various ways in which one can become proficient at the task (e.g., some chess players weigh interpersonal intelligence – knowing the opponent – much more than do others). We avoid the conundrum that human intelligence is most naturally assessed through language-based instruments, and yet such instruments cannot be employed with other animals – leaving us with a situation where we can do species comparisons only by eliminating what is widely regarded as the essence of human intellect. By the same argument, we cannot use “musical intelligence” of birds, or the “echoing intelligence” of bats, again ignoring a dominant intellectual capacity. More generally, we may be better able to trace the similarities and differences between human beings and particular species (be they birds, bats, or dolphins) if we think of them in terms of each species’ own dominant and less salient intelligences, rather than their having more or less of *g*.

Of mice and men, nature and nurture, and a few red herrings

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Marc D. Hauser

Risk-Eraser, West Falmouth, MA 02574.

marc@risk-eraser.com www.risk-eraser.com

Abstract: Burkart et al.’s proposal is based on three false premises: (1) theories of the mind are either domain-specific/modular (DSM) or

domain-general (DG); (2) DSM systems are considered inflexible, built by nature; and (3) animal minds are deemed as purely DSM. Clearing up these conceptual confusions is a necessary first step in understanding how general intelligence evolved.

“The best-laid schemes o’ mice an’ men,” penned Robert Burns in his ode to mice. It is an astute observation of how our intelligence has outwitted theirs. Though I appreciate Burkart et al.’s attempt to synthesize a wild and woolly comparative literature on general intelligence in mice, men, and many other species, they have introduced a few red herrings and false premises that muddy the waters and undermine suggestions for future research.

The problem starts with the authors’ initial premise: Scholars tend to view the mind as *either* domain-specific/modular (DSM) *or* domain-general (DG), and those who lean to DSM see the mind as predetermined and inflexible, and thus largely the work of nature. These views conflict with a theory of general intelligence. Burkart et al. claim that their framework shows “that human cognition involves elements of domain-specific and domain-general processes” (sect. 1.2.3, para. 4), and in contrast to prior views, “animal minds need not be bundles of specialized cognitive adaptations” (sect. 1.2.3, para. 4). But their premise is false as is their characterization of animal research. This commentary addresses these misconceptions and introduces some additional distinctions in order to productively explore how general intelligence evolved.

Those who have synthesized DSM perspectives (e.g., Pinker 1997) do not deny the existence or significance of DG capacities: evolutionarily ancient mechanisms that typically interface with and often constrain the outputs of each domain. Research on theory of mind (ToM), number, and language – domains often considered as modules – has long explored how executive functions interact with the computations and representations of each domain (Bradford et al. 2015; Soltész et al. 2011). For example, delays in the expression of ToM and number competence are intimately related to the development of working memory, whereas performance on ToM tasks can be improved by lifting constraints that arise from inhibitory control or perseverative responses. Thus, although it is inaccurate to pigeonhole scholars as either DSM or DG, it is true that those who have explored the nature of DSM systems are more interested in them and in how they can be characterized on the basis of evolutionary theory. Similarly, although the generative computations that subservise language competence (but also other domains such as music, number, and ToM) have no limit, our capacity to produce or comprehend sentences is limited by working memory. Thus, although DSM-focused researchers tend to emphasize the nature of the representations and computations within a domain or module, they don’t deny the existence or potentially constraining impact of DG processes.

Of relevance to the evolution of general intelligence is the underlying architecture of DSM systems. Here, too, Burkart et al. mischaracterize these as innate and inflexible. Research on faces reveals this error. Neurobiological studies in macaques and humans reveals dedicated circuitry that is consistent with a DSM perspective. However, this system matures slowly over time and depends on experience with faces as elegantly demonstrated by studies of individuals with early-appearing cataracts that were later removed (Rhodes et al. 2017). A similar characterization applies to language, wherein there are core underlying computations and representations, some specific to language and others shared (Hauser & Watumull 2016), but with experience selecting among the options to generate specific languages (e.g., French, English).

Lastly, it is simply not the case that nonhuman animals are perceived as mere bundles of modules, fixed and inflexible. Research on model systems such as *aplysia* and songbirds reveals both ancient, general mechanisms for learning and memory, as well as highly dedicated systems that nonetheless show plasticity. For example, although passerines acquire their song on the basis of

specialized circuitry that enables vocal imitation, this same system requires specific input (e.g., species-specific song), is not engaged for other vocalizations (e.g., alarm calls), and in some species, shows plasticity throughout life as individuals create new songs each season. In addition, many researchers have recognized and detailed other DG processes that go beyond what Burkart et al. discuss. For example, there is considerable comparative work exploring the concept of “sameness,” analogical reasoning, and algebraic computations (Martinho & Kacelnik 2016; Smirnova et al. 2015; ten Cate 2016). These are not part of the executive system, have not typically been linked to general intelligence, and yet they cut across domains and appear evolutionarily ancient.

Putting these strands together suggests that any approach to exploring the evolution of intelligence must consider the interaction between DSM and DG, understand the specificity of the content of DSM, examine a diversity of DG systems (i.e., beyond executive functions), and document how maturational changes in DG can impact the ontogeny of DSM. The content of a domain is particularly relevant as tasks within the general intelligence battery are often assumed to be part of a given domain without rigorous testing. Take, for example, work on tool use. Many researchers have considered tool technology a domain, one based in part on the functional design features of its objects. Thus, when animals such as chimpanzees and New Caledonia crows – natural tool users – show sensitivity to an object’s design features, using those objects that are most likely to lead to successful outcomes, we consider this to be evidence of domain-specificity. And yet, cotton-top tamarins – a species that never uses tools in the wild and shows virtually no interest in object manipulation in captivity – show the same kind of sensitivity to an object’s design features as chimpanzees and crows; furthermore, this sensitivity appears early in ontogeny in the absence of experience (Hauser et al. 2002a). This suggests that we should be more cautious with our claims of DSM capacities, and thus, how we classify the tasks within a general intelligence battery.

In conclusion, although Burkart et al. introduce a tension between DSM and DG that doesn’t exist, incorrectly consider DSM perspectives as innate and inflexible, and falsely accuse other scholars of classifying nonhuman animals as rigidly DSM, they are correct in emphasizing the importance of looking more deeply at general intelligence in animals. Progress will depend on a clear articulation of the different skills tapped in the general intelligence battery, and standard methods that can be implemented across a diversity of species.

The evolution of general intelligence in all animals and machines

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Kay E. Holekamp^{a,b,d} and Risto Miikkulainen^{c,d}

^aDepartment of Integrative Biology, Michigan State University, East Lansing, MI 48824-1115; ^bEcology, Evolutionary Biology and Behavior, Michigan State University, East Lansing, MI 48824; ^cDepartments of Computer Science and Neuroscience, University of Texas, Austin, TX 78712; ^dBEACON Center for the Study of Evolution in Action, Michigan State University, East Lansing, MI 48824

holekamp@msu.edu <http://www.holekamplab.org/>
risto@cs.utexas.edu <https://www.cs.utexas.edu/~risto/>

Abstract: We strongly agree that general intelligence occurs in many animals but find the cultural intelligence hypothesis of limited usefulness. Any viable hypothesis explaining the evolution of general intelligence should be able to account for it in all species where it is known to occur, and should also predict the conditions under which we can develop machines with general intelligence as well.

In their rich and thought-provoking review, Burkart et al. use impeccable scholarship to produce a heroic synthesis of multiple

complex literatures. Their two main goals are to critically evaluate the question of whether general intelligence exists in nonhuman animals, and to evaluate the implications of general intelligence for current theories about the evolution of cognition. In our view, they accomplish the first goal extremely effectively, making a compelling argument that general intelligence is indeed widespread among animals. Regarding their second goal, they argue that existing data from vertebrates support the cultural intelligence hypothesis, which stresses the critical importance of social inputs during the ontogenetic construction of survival-relevant skills. However, the general intelligence explained by the cultural intelligence hypothesis is actually quite limited, so we must seek a more robust explanation for its evolution.

We believe that the cognitive buffer hypothesis (Allman et al. 1993; Deaner et al. 2003; Sol 2009a; 2009b; Lefebvre et al. 2013) offers a better alternative because it can account for phenomena the cultural intelligence hypothesis leaves unexplained. The cognitive buffer hypothesis posits that general intelligence is favored directly by natural selection to help animals cope with novel or unpredictable environments, where it enables individuals to exhibit flexible behavior, and thus find innovative solutions to problems threatening their survival and reproduction. In our view, Burkart et al. dismiss the cognitive buffer hypothesis prematurely. They argue that fundamental preconditions for the evolution of large brains include a slow life history and high survivorship, possible only in species not subject to unavoidable extrinsic mortality such as high predation pressure (van Schaik et al. 2012). However, much can be learned by considering apparent exceptions to “rules” like these, so we offer the octopus as one such exception.

Most octopuses are strictly solitary except when copulating, have very short lives, have countless predators, and produce thousands of offspring, most of which die. Nevertheless, they have some of the largest brains known among invertebrates (Hochner et al. 2006; Zullo & Hochner 2011); they exhibit a great deal of curiosity about their environments (Montgomery 2015); they recognize individual humans (Anderson et al. 2010); they exhibit pronounced individual differences (Simm et al. 2001; Mather et al. 2012); they use tools; and they play (Mather 1994; Mather & Anderson 1999). Octopuses thus appear to exhibit a considerable amount of general intelligence without any opportunity whatsoever for social learning. Clearly, the cultural intelligence hypothesis cannot account for the general intelligence apparent in creatures like these.

Similarly, the cultural intelligence hypothesis offers little promise with respect to evolving general intelligence in machines. Computer scientists and robotic engineers have understood for decades that the embodiment of intelligent machines affects their ability to adapt and learn via feedback obtained during their interactions with the environment, mediated by sensors and activators (Brooks 1990; 1991; Sharkey & Ziemke 1998; Goldman & de Vignemont 2009). Most hypotheses forwarded to explain the evolution of intelligence in animals, including the cultural intelligence hypothesis, fail to address the question of how morphological traits outside of the nervous system might have shaped intelligence. In creatures such as octopuses and primates, mutations affecting nervous system structure or function, which might generate less-stereotyped and more-flexible behavior, are visible to selective forces in the environment because they can be embodied in the limbs. Thus, greater intelligence is likely to evolve in these animals than in those whose interactions with their environments are more highly constrained.

Roboticians have also realized that logic alone cannot generate much intelligent behavior in their machines, and that to achieve better performance, their robots must also want things. The skills discovered by evolutionary algorithms are diverse, and many such skills may occur within a single population of digital organisms, but individual agents are rarely motivated to acquire a large array of skills. As a result, most current evolutionary algorithms produce domain-specific intelligence in machines that

rarely possess more than a small set of skills, and they are thus suited to performing only tasks that demand that particular skill set. Although an intrinsic motivation to explore the environment has been imitated in artificial agents via machine learning (Schmidhuber 1991; Oudeyer et al. 2007), the production of generalist learners within an evolutionary context remains highly problematic (Stanton & Clune 2016).

Any selection pressure that promotes behavioral diversity or flexibility within the organism's lifetime, including the ability to learn from experience, should theoretically result in enhanced general intelligence. Novel or changing environments should select for individuals who can learn as much as possible in their lifetimes, as suggested by the cognitive buffer hypothesis. Indeed, Stanton and Clune (2016) recently developed an evolutionary algorithm that produces agents who explore their environments and acquire as many skills as possible within their lifetimes while also retaining their existing skills. This algorithm encourages evolution to select for curious agents motivated to interact with things in the environment that they do not yet understand, and engage in behaviors they have not yet mastered. This algorithm has two main components: a fitness function that rewards individuals for expressing as many unique behaviors as possible, and an intra-life novelty score that quantifies the types of behaviors rewarded by the algorithm. Agents are also provided with an intra-life novelty compass that indicates which behaviors are considered novel within the environment. The intra-life novelty compass may simply identify and direct agents toward areas of high expected learning because new knowledge often promotes the ability to perform new skills. Aligned with these results, we suggest that the primary value of the cultural intelligence hypothesis is to offer social learning as an intra-life novelty compass, but that this hypothesis provides neither the requisite fitness function nor anything analogous to an intra-life novelty score.

A viable hypothesis explaining the evolution of large brains and general intelligence should be able to account for general intelligence in any species where it is known to occur, and it should be able to predict the conditions under which we can develop machines with general intelligence as well. The cultural intelligence hypothesis simply cannot do these things.

Where is the evidence for general intelligence in nonhuman animals?

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Ludwig Huber

Messerli Research Institute, University of Veterinary Medicine Vienna, Medical University of Vienna, University of Vienna, 1210 Vienna, Austria.

ludwig.huber@vetmeduni.ac.at www.vetmeduni.ac.at/messerli

Abstract: This commentary contrasts evolutionary plausibility with empirical evidence and cognitive continuity with radiation and convergent evolution. So far, neither within-species nor between-species comparisons on the basis of rigorous experimental and species-appropriate tests substantiate the claims made in the target article. Caution is advisable on meta-analytical comparisons that primarily rely on publication frequencies and overgeneralizations (from murids and primates to other nonhuman animals).

In this thought-provoking, highly inspiring article, Burkart et al. explore the possibility of the existence of general intelligence in nonhuman animals. Given the evidence for g in humans, it is a reasonable and worthwhile endeavor to look for its existence in other taxa. However, to pursue a psychometric approach to nonhuman intelligence, it is necessary to obtain relevant and reliable data. As the authors themselves admit, evolutionary plausibility does not amount to empirical evidence.

Within-species comparisons. For more than a century, psychometricians have devised IQ tests to measure human intelligence. However, the breadth of test items is quite narrow. The tasks are, for the most part, administered in the same manner, with no or only modest variation of test-taking situation, motivation, or sensory domain (Locurto et al. 2006). For instance, the WAIS-IV (Wechsler et al. 2008) comprises four index scores, focusing on verbal comprehension, perceptual reasoning, working memory, and processing speed. This paper-and-pencil task may be enough to represent major components of human intelligence, but it does not tap the most interesting cognitive abilities in nonhuman animals, especially in the technical and social domains.

A crucial question in the search for the influence of an underlying general mental ability is the rationale behind which tests are included in the test batteries and the reliability of those tests for uncovering cognitive abilities. Tests measure performance, not cognitive abilities per se. A huge number of possible noncognitive factors may influence performance, from anatomical to perceptual and motivational. Therefore, it is important to know which cognitive tasks and which controls are included in the test battery. Human IQ tests are often constructed in the manner of a best-case scenario, in that tasks are included in the final battery only if they correlate positively with other tasks and loaded positively on the first component. That is, the presence of g is assumed and tasks chosen that verify its presence (Locurto et al. 2006). Furthermore, human IQ tests are standardized with several hundreds to thousands of people of all age classes. This is not feasible with (most) nonhuman animals.

Between-species comparisons. Large data sets for valid comparisons are only possible if we collect data from different labs. But can we rely on data sampled in different labs, using (slightly) different methods (different stimuli, apparatuses, procedures, etc.) and groups of subjects differing in important features like housing and rearing conditions, individual experiences, age, and sex composition? This is both a practical and a theoretical problem. It would demand an enormous amount of labor, money, space, and other resources to test a large sample of species in one lab. Even if one has access to a zoo or game park, testing the abilities that tap reasoning in nonhuman cognition is a difficult and time-consuming business. Furthermore, if the tasks were designed to tap different response systems, sensory modalities, and motivations, it would be a huge undertaking.

Therefore, the evidence for general intelligence on the inter-specific level so far rests on meta-analyses. This strategy is based on the assumption that the frequency of reported observations of complex traits associated with behavioral flexibility is a reflection of that species' intellectual capability. For instance, Reader and Laland (2002) used indices of innovation, tool use, and social learning for their correlations. But is innovation really a direct outcome of a cognitive trait of a species? The relation is vague and the behavioral definitions are rather slippery. Furthermore, most of these meta-analyses rely on observation frequency, which may deviate widely from the experimentally proven existence of a cognitive trait in a species. For instance, reports of true imitation in callithrichids are very rare, but rigorous laboratory tests have proven its existence (Voelkl & Huber 2000; Voelkl & Huber 2007). The same is true with invisible displacement in *Callithrix jacchus* (Mendes & Huber 2004). Tool use may be the best example of the problem with drawing conclusions about species differences in general intelligence based on publication counting. It is an important ability in chimpanzees, New Caledonian crows, and Galápagos woodpecker finches. However, these species have no clear, experimentally proven cognitive superiority over their non-tool-using relatives, bonobos, carrion crows, or tree finches, respectively (Gruber et al. 2010; Herrmann et al. 2010a; Teschke et al. 2011; 2013). This led to the conclusion that habitual tool use is not a clear predictor of general intelligence, not even physical intelligence (Emery & Clayton 2009). Although

it would be unfair to dismiss the meta-analytical studies completely, at least they require substantiation by experimental data collected with similar methods across large samples of species (Healy & Rowe 2007). So far, such experimental comparisons are rare, and if available, they don't support the meta-analytical studies. All four experimental comparisons listed in Table 5 of Burkart et al.'s target article lack clear-cut evidence for *G*.

Reasoning. Burkart et al. claim that “recent studies are consistent with the presence of general intelligence in mammals” (in the Abstract), which is defined as the ability to reason, plan, and think abstractly (Gottfredson 1997). However, the only cited reasoning study outside of rodents (Anderson 1993; Wass et al. 2012) has not found evidence for *g* (Herrmann & Call 2012). The author of this commentary has found evidence for reasoning by exclusion in several human animals (Aust et al. 2008; Huber 2009; O'Hara et al. 2015; 2016), but so far, evidence for *g* in these species is lacking.

Finally, concerning the search for *g* or *G* in nonhuman animals, caution toward overgeneralization is warranted. The few supportive studies in rodents and primates, two taxa that together represent about 20% of mammalian species and only 2% of vertebrates, cannot be generalized to “nonhuman animals.” Especially primatologists may be at risk of overemphasizing cognitive continuity between humans and nonhuman animals, instead of seeing radiation of traits outward in all directions (Hodos & Campbell 1969; Shettleworth 2010a). The search for (human-like) general intelligence (based on reasoning) should be compensated by an appreciation of convergent evolution (Emery & Clayton 2004; 2009; Fitch et al. 2010; Güntürkün & Bugnyar 2016).

The false dichotomy of domain-specific versus domain-general cognition

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Ivo Jacobs and Peter Gärdenfors

Cognitive Science, Department of Philosophy, Lund University, 221 00, Lund, Sweden.

ivo.jacobs@lucs.lu.se <http://www.fil.lu.se/person/IvoJacobs>
 peter.gardenfors@lucs.lu.se <http://www.fil.lu.se/person/PeterGardenfors>

Abstract: The qualitative division between domain-general and domain-specific cognition is unsubstantiated. The distinction is instead better viewed as opposites on a gradual scale, which has more explanatory power and fits current empirical evidence better. We also argue that causal cognition may be more general than social learning, which it often involves.

Burkart et al. view domain-specific and domain-general intelligence as qualitatively different categories and then attempt to find plausible evolutionary scenarios. However, viewing intelligence as a

scalar trait is more consistent with biological gradualism. Exclusive categories do not exist for the complex continuous interplay between genes and environment resulting in unique individual development and their evolutionary interactions (Laland et al. 2011; Osvath et al. 2014; Ploeger & Galis 2011; West-Eberhard 2003). The authors also do not explain how any cognitive adaptation can be fully independent of brain size and executive functions, as they posit in Figure 3 of the target article. Although it is true that small brains can house many cognitive adaptations with poor executive functions, they must clearly be at least somewhat related. For instance, primary modules can be inhibited or stored in working memory. The tendency of kittens to respond to small moving objects with behaviours from the hunting repertoire is considered an example of a primary module (Table 2 of target article), yet they can wait for the right time to pounce (inhibitory control) and recall where they have last seen objects (working memory).

The problems of the dichotomy can also be illustrated by considering precocial birds such as ducks and chickens, which are born relatively well-developed; they walk, have open eyes, and forage. Their cognitive abilities can therefore be tested soon after hatching. Precocial animals are perfect for distinguishing between primary and secondary modularization because they can be tested with minimal experience. Filial imprinting occurs when a newly hatched precocial chick limits its social behaviour to a particular object. Under normal circumstances, this means that the chick will attend to and follow its mother. It is one of the most extensively described phenomena in ethology (Bolhuis 1991) and is traditionally considered to be the archetype of instinct, so categorizing it as domain specific and modular should be straightforward. Imprinting indeed appears to be a species-wide adaptive specialisation to a predictable situation that is stable across generations, with relatively quick learning in a specific domain following a characteristic ontogeny.

The concepts of primary modules and instinct resemble each other greatly (see Table 1), so we can criticize them on similar grounds – mainly, that they are not truly qualitatively distinct from their supposed polar opposites (Bateson & Curley 2013; Bolhuis 1991). Many aspects of imprinting go beyond instinct or primary modules. It can be considered domain general and may involve secondary modules because it is phylogenetically and ontogenetically canalized; it is learned until automated; and it can have variable contents with individual differences. Moreover, ducklings understand the relational concept of “same or different” based on imprinting (Martinho & Kacelnik 2016), and chicks are born with advanced folk biology, psychology, and physics (Vallortigara 2012a; 2012b). This suggests massive modularity, which according to Burkart et al. is “entirely compatible with the co-existence of domain-general processes and general intelligence” (sect. 1.2.1., para. 4). It is possible that imprinting is more of the one than the other, but according to their view it has to be *either* general *or* specific, which is incompatible with current empirical evidence.

Table 1 (Jacobs & Gärdenfors). *The description of primary modules by Burkart et al. (Table 2 of target article) strongly resembles the nine different meanings of instinct by Bateson and Curley (2013) when rearranged.*

	Primary Modules	Instinct
Etiology	Evolutionary; reflect natural selection for domain-specific cognitive adaptation	Adapted during evolution; genetic – highly heritable; controlled by a specialised neural module
Development	Skill matures, motor practice (experience-expectant)	Present at birth or particular stage of development; develops before function is established
Content of skills	Pre-set, highly predictable	Developmentally robust – well-canalized; not learned; a functional behavioural system
Distribution	Uniformly present in a given species	Shared by all members of species/sex/age group

The theoretical and empirical evidence for an absolute divide between domain-specific and domain-general intelligence is thus poor. One might argue that certain individuals have general intelligence in the sense that they consistently perform well on various tests across domains, but this hardly seems surprising or controversial. A gradual notion of intelligence means its evolution is more plausible – even repeatedly in different clades (Osvath et al. 2014) – than the potential “hard step” of categorically unique general intelligence.

We are also sceptical of Burkart et al.’s focus on cultural intelligence. Social learning has undoubtedly played an important role in the cognitive evolution of many species, but perhaps it is not as central or exclusive as they claim. In fact, they are concerned that socio-cognitive abilities too often yield inconclusive results or are not even included in test batteries.

Causal cognition can arguably overcome the problems of Table 1 in the target article equally well or better than social learning, which in many cases can be considered to be causal. Woodward (2011) distinguished three levels of causal reasoning (see also Gärdenfors 2003); one can learn to shake a branch to cause fruit to fall because of one’s own experience shaking branches (egocentric causal learning), observing others shake branches (agent causal learning), or observing the wind shake branches (observation/action causal learning). It is reasonable that these three levels represent an evolutionary order of expansion of causal cognition. This would constitute another argument that the dichotomy between domain-specific and domain-general intelligence is not plausible.

Rather than learning many one-to-one relations, representing a causal network based on individual and social learning can be highly advantageous and at the base of novel causal interventions (Tomasello & Call 1997; Woodward 2011). This sort of causal cognition can be tested empirically in a variety of species (Blaisdell et al. 2006; Jacobs et al. 2015), and may be of the general nature that Burkart et al. are seeking.

The evolution of fluid intelligence meets formative *g*

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Kristof Kovacs^a and Andrew R. A. Conway^b

^aEszterházy Károly University, 3300, Eger, Hungary; ^bClaremont Graduate University, Claremont, CA 91768.

kristof340@gmail.com andrew.conway@cgu.edu

Abstract: The argument by Burkart et al. in the target article relates to fluid (not general) intelligence: a domain-general ability involved in complex, novel problem solving, and strongly related to working memory and executive functions. A formative framework, under which the general factor of intelligence is the common consequence, not the common cause of the covariance among tests is more in line with an evolutionary approach.

The authors present a wide-ranging theory of the evolution of intelligence. However, Burkart et al. seem to have confused the general intelligence factor (psychometric *g*) with fluid intelligence (Gf). Psychometric *g* is a statistical way of describing the positive manifold: the phenomenon that ability tests, each with different content, all correlate positively. As such, psychometric *g* is a necessary algebraic consequence of the positive manifold itself (Krijnen 2004). The concept of general intelligence interprets psychometric *g* as a within-individual, domain-general cognitive ability that permeates all human mental activity so that different tests are functionally equivalent in the sense that they all measure this general ability to a varying extent. This is a sufficient,

but not necessary, explanation of the positive manifold. Moreover, it is contradicted by evidence from cognitive neuroscience, neuropsychology, and the study of developmental disorders (e.g., Duncan et al. 1995; Vicari et al. 2007; Wang & Bellugi 1994).

Contrary to *g*, fluid intelligence can be meaningfully conceptualized as a domain-general ability involved in complex, novel problem solving – according to its definition, it is “an expression of the level of relationships which an individual can perceive and act upon when he does not have recourse to answers to such complex issues already stored in memory” (Cattell 1971, p. 115.) or “the use of deliberate and controlled mental operations to solve novel problems that cannot be performed automatically” (McGrew 2009, p. 5). In humans, fluid reasoning is usually measured with tests of nonverbal inductive reasoning. Gf shares nearly half of its variance with working memory (Kane et al. 2005; Oberauer et al. 2005), probably because they both tap executive/attentional processes to a large extent (Engle & Kane 2004).

There are reasons that can lead one to think that Gf and *g* are the same: Gf is central to variation in cognitive abilities to the extent that *g* and Gf are statistically near-indistinguishable (Gustafsson 1984; Matzke et al. 2010). Yet general intelligence and fluid reasoning are clearly different constructs (Blair 2006) – and so are the psychometric factors *g* and Gf (Kovacs et al. 2006). Additionally, whereas the neural substrate of fluid intelligence is in the prefrontal and partly in the parietal cortex (Kane & Engle 2002; Kane 2005), it is difficult to localize *g*, as results depend on the actual battery of tests used to extract *g* (Haier et al. 2009). Also, different components of *g* are differently affected by aging or the Flynn effect (the secular increase in IQ), both of which manifest themselves more strongly on nonverbal than verbal tests (Flynn 2007; Horn & Cattell 1967; Trahan et al. 2014).

Verbal cognition itself is crucial from the target article’s perspective when interpreting *g*. In humans, *g* is composed of crystallized intelligence (Gc), too: the ability to apply already acquired skills and knowledge, with an emphasis on language – vocabulary, reading comprehension, and verbal reasoning. This does not translate to nonhuman animals, making it very implausible that general factors reflect the same construct across species. The authors’ approach to general intelligence, emphasizing problem solving in novel contexts, also in fact reflects fluid intelligence – the central component of *g*, but not the same as *g*. Finally, executive functions are more strongly related to Gf than to other components of *g* (Conway & Kovacs 2013). In fact, given the authors’ emphasis on problem solving in novel situations as well as on the role of cognitive flexibility and executive functions, we often had the impression when reading the target article that Burkart et al. in fact discussed fluid intelligence under the term general intelligence.

If *g* does not reflect a unitary domain-general cognitive ability and is not identical to Gf, then how can the general factor of intelligence be conceptualized? Or, more importantly, if mental tests do not all measure the same general intelligence, then why do tests with different content correlate so strongly?

There are two recent explanations of the positive manifold (with corresponding mathematical formulations) that do not propose a psychological equivalent of psychometric *g*: the mutualism model (van der Maas et al. 2006) and process overlap theory (Kovacs & Conway 2016). Mutualism explains the positive manifold with mutually beneficial interactions between cognitive processes during development. Process overlap theory proposes a functional overlap of cognitive processes when people solve mental test items, such that executive/attentional processes are tapped by a large number of different items whereas domain-specific processes are tapped by specific types of tests only.

Both explanations conceptualize intelligence as a set of independent specific abilities and processes. According to the process overlap theory, *g* is an emergent rather than latent property of mental test scores. Technically, this means that *g* is conceptualized as a formative rather than reflective latent variable: the common consequence of the covariance among tests rather than

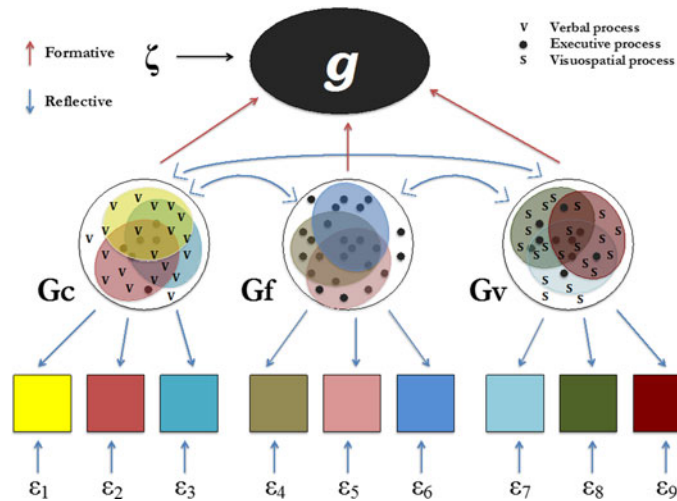


Figure 1 (Kovacs & Conway). The structural model corresponding to process overlap theory on a simplified model.

its common cause. Another common example is socioeconomic status (SES), which clearly is the outcome, and not the cause of a number of indicators like family income, parental education, and so on (Fig. 1).

Such a stance would contribute greatly to the authors' comparative approach, in which *g* would vary from species to species (depending on whether its exact composition includes social skills, language, etc.), whereas a reflective fluid intelligence could indeed be plausibly interpreted as an ability whose evolution was shaped by evolutionary pressures to solve novel problems. The evolution of fluid intelligence could probably be understood through disentangling the evolution of the prefrontal cortex and executive functions in a number of different species.

At the same time, applying a formative framework to *g* could contribute to a functionalist approach, because the primary role of formative constructs is predicting important real-life outcomes (Bagozzi 2007; Howell et al. 2007); in this case, evolutionary ones. Under such a formative/functionalist agenda, the focus would be on individually identifying the cognitive capabilities of each species, ranging from olfactory abilities to social cognition, and how they uniquely contribute to the given species chances of survival and reproduction.

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Genomic data can illuminate the architecture and evolution of cognitive abilities

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James J. Lee^a and Christopher F. Chabris^{b,c}

^aDepartment of Psychology, University of Minnesota Twin Cities, Minneapolis, MN 55455; ^bInstitute for Advanced Application, Geisinger Health System, Lewisburg, PA 17837; ^cDepartment of Psychology, Union College, Schenectady, NY 12308.

leex2293@umn.edu <https://umn.academia.edu/JamesLee>
 chabris@gmail.com <http://www.chabris.com>

Abstract: Does general intelligence exist across species, and has it been a target of natural selection? These questions can be addressed with genomic data, which can rule out artifacts by demonstrating that distinct

cognitive abilities are genetically correlated and thus share a biological substrate. This work has begun with data from humans and can be extended to other species; it should focus not only on general intelligence but also specific capacities like language and spatial ability.

In 1904, Charles Spearman discovered *g*, the factor measured in common by correlated tests of diverse human mental abilities. The existence of possible *g* homologues in other species and the extent to which the evolutionary trend in our own primate lineage can be characterized as an increase in *g* are among the most important issues facing researchers across the disparate fields interested in cognitive evolution. We applaud Burkart et al. for recognizing the centrality of *g* to any complete understanding of human and animal differences.

Burkart et al. are not alone in expressing concern over the possibility that the correlations between factors defining a statistical *G* (and its between-species analog *G*) might not reflect common information-processing mechanisms (general intelligence) but rather artifacts of various sorts (e.g., Hampshire et al. 2012). In humans, at least, data from twins and genome-wide association studies (GWAS) can rule out various conceivable artifacts by demonstrating that distinct abilities are genetically correlated. The existence of a genetic correlation means that there are polymorphic sites in the genome affecting both traits—either because one trait is on the causal path to the other, or because distinct causal paths emanate toward both traits from a common biological substrate (whose function is influenced by the genetic variants). Empirically estimated genetic correlations between ability tests of different kinds are as large as the simple phenotypic correlations (Kovas & Plomin 2006; Loehlin et al. 2016; Trzaskowski et al. 2013), thus pointing to common biological mechanisms. For instance, Trzaskowski et al. estimated the genetic correlation between *g* and a test of mathematics to be 0.74. A genetic correlation is a coarse-grained summary statistic, but in the near future we believe it will be possible to use DNA-level data to determine whether a given polymorphic site is associated with multiple abilities in a manner consistent with a common mediating mechanism (van der Sluis et al. 2010).

The methodology of GWAS is enabling this revolution because certain special properties of genomic data—such as the natural randomization of genotypes within the offspring of the same parents—enable a high degree of trust in the causal inferences that can be drawn from it (Lee 2012; Lee & Chow 2013; Lee et al. 2016). Unfortunately, genetic methods along these lines may be somewhat difficult to apply to nonhuman species because of the large sample sizes required for adequate statistical power (Chabris et al. 2015). Even in the face of this obstacle,

however, indirect progress may be possible. In recent work, we identified a large number of polymorphic sites in the human genome associated with educational attainment, a heritable trait (Heath et al. 1985) that is genetically correlated with both *g* and intracranial volume (Okbay et al. 2016). More specifically, we found that sites associated with education are much more likely to be found in regions of the genome annotated as likely to affect gene expression in the brain. Armed with such predictive functional annotations, we may be able to determine whether a substitution of one allele for another that has occurred at any point in mammalian evolution would be likely to affect educational attainment – even if the site of the substitution is not polymorphic in modern human populations.

There are some outstanding methodological issues with this approach, such as which parts of the genome should be used as a control for purposes of determining whether likely *g*-affecting sites have undergone an unusual number of base-pair substitutions that would be consistent with the action of natural selection (e.g., Dong et al. 2016). More work also needs to be done to ensure that the functional annotations truly predict causal effects on *g* or some cognitive trait rather than other intermediate phenotypes (e.g., personality traits like neuroticism) that are also genetically correlated with educational attainment in modern Western societies. If these issues can be addressed, however, then many powerful inferences will become possible. For instance, we may be able to find evidence of directional selection increasing *g* in the human lineage or a correlation between the number of substitutions from the time of the common ancestor to the present and the rank of a taxon in some measure of *G* (Johnson et al. 2002). Such findings would bolster many of the points tentatively advanced in the target article, including the identification of the statistical *g/G* factors in other species with general intelligence in *Homo sapiens*.

We also urge Burkart et al. and other researchers to consider important ability factors other than *g*. The correlations between distinct human abilities can be attributed to their common measurement of *g*, but the “error” or “residual” inherent in each ability when it is regarded in this way is also of substantive interest. The authors mention the Cattell-Horn-Carroll (CHC) model of these lower-order factors; setting aside various controversies over terminology and substance, we single out two of these factors because of their ecological validity in the prediction of human behavior (Kell et al. 2013; Lee & Kuncel 2015). The factor that we will call verbal comprehension is characterized by tasks requiring the translation of meanings into verbal units (words, sentences, discourses) and vice versa. Burkart et al. do not emphasize human language, but the search for its evolutionary antecedents has raised many issues – including whether language is independent of other cognitive capacities – that may be illuminated by an interdisciplinary approach (Hauser et al. 2002b; Hurford 2007; Pinker & Jackendoff 2005). We call the other non-*g* factor of interest *spatial visualization*, which is characterized by tasks requiring the mental transformation of representations of objects and scenes in a manner preserving spatial relationships. We suspect a relationship between spatial visualization and tool manufacture analogous to the one between verbal comprehension and language; confirming such a relationship may prove to be a worthwhile research program.

Given the prominence of both language and tool manufacture in human evolution, we are intrigued by the prospect of a mapping between these two capacities and the two arguably most important lower-order ability factors in the hierarchy of human individual differences. Of course, these are not the only abilities relevant to human evolution; various aspects of social cognition, such as face recognition and theory of mind, should also be explored. But in any case, it is now time for this line of research to incorporate and make maximal use of the abundance of genetic data that are becoming available.

Contemporary evolutionary psychology and the evolution of intelligence

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David M. G. Lewis,^a Laith Al-Shawaf,^b and Mike Anderson^a

^aSchool of Psychology and Exercise Science, Murdoch University, Murdoch, Western Australia 6150; ^bDepartment of Psychology, Bilkent University, 06800 Bilkent, Ankara, Turkey.

d.lewis@murdoch.edu.au <http://davidmglewis.com>

laith@bilkent.edu.tr <http://laithalshawaf.com>

mike.anderson@murdoch.edu.au

Abstract: Burkart et al.’s impressive synthesis will serve as a valuable resource for intelligence research. Despite its strengths, the target article falls short of offering compelling explanations for the evolution of intelligence. Here, we outline its shortcomings, illustrate how these can lead to misguided conclusions about the evolution of intelligence, and suggest ways to address the article’s key questions.

Burkart et al. offer an impressive integration of intelligence research across humans and nonhuman species. Their commendable synthesis will serve as a valuable, centralized resource. Despite these strengths, the target article falls short of offering compelling explanations for the evolution of intelligence.

We observe three major issues with the target article. First, it poses multiple questions about intelligence but does not consistently differentiate between them – despite their likely different answers. For example, the question of whether interspecific variation in psychometric intelligence (*G*) exists is fundamentally distinct from whether *G* taps the same construct as within-human variation in intelligence (*g*). Independent of these questions are *why G* exists and *why g* exists – two independent questions that may have different answers.

Conflating these questions can lead to misguided conclusions about the evolution of intelligence. The article establishes the existence of both *G* and *g*. However, it does not logically follow that they therefore (1) tap the same construct or (2) share the same evolutionary origins. First, the authors offer little defense of the implicit position that *g* and *G* tap the same construct. Second, it is plausible that some species exhibit superior performance on intelligence batteries as a consequence of cross-species differences in the information-processing demands of survival- and reproduction-related problems. Individual differences in intelligence among humans may have entirely different origins. Prokosch et al. (2005) proposed that *g* captures individual differences in “developmental stability at the level of brain development and cognitive functioning” (p. 203). For several reasons, this alternative evolutionary model deserves consideration alongside the target article. First, the term “evolved” refers not to the products of just selection, but also of genetic drift, gene flow, and mutation. The target article neglects these non-selective forces and how they could produce *g*. By contrast, Prokosch et al. considered a more comprehensive set of evolutionary forces and posited that *g* reflects the outcome of a balance between selection and genetic mutation. The target article offers no consideration of the mechanistic basis of variation in intelligence. Second, Prokosch and colleagues generated clear, novel predictions based on their model. It is not immediately clear what new predictions the target article’s “cultural intelligence” (CI) approach yields. The crucial idea is not that we favor Prokosch et al.’s model, but rather that their work exhibits hallmarks of sound evolutionary science that the CI approach, in its current form, lacks. These include a consideration of selective and non-selective forces, as well as the generation of specific, falsifiable predictions. At present, it is not clear what evidence *could* disconfirm the CI model. We suggest that the CI approach could benefit from more clearly articulating its empirical

predictions, with an emphasis on identifying where it and alternative models advance divergent predictions.

A second, related issue is that the target article attempts to use inappropriate criteria to discriminate between the CI and alternative evolutionary models. Here, we provide four examples of this. First, Figure 1b in the target article presents a pattern of cognitive performance expected from domain-general mechanisms in homogeneous developmental conditions. However, this pattern is identical to that expected when selective forces favor domain-specific mechanisms but non-selective forces (e.g., mutation) impair the performance of these mechanisms. Second, the target article acknowledges that intelligence tests are culture-biased. If we recognize this, then we – the creators of these tests – should certainly acknowledge that they could be *species*-biased. Intelligence batteries tap cognitive performance on different tasks. If the computational demands of these tasks align more closely with the computational demands of the adaptive problems faced by some species, then we should expect interspecific variation in performance on these tasks – *G*. As such, the existence of *G* is *not* “particularly difficult to reconcile” (sect. 2.5, para. 5) with domain-specific mechanisms. We agree with the authors that reconciliation between the massive modularity hypothesis and domain-general views of intelligence is needed, but the mere existence of *G* is insufficient for adjudicating between them.

Third, the target article interprets the absence of “empirical evidence ... of specialized adaptive behavioral functions to specific modular neural units” (sec. 1.2.1, para. 2) as evidence against domain-specific mechanisms. This reflects a deep misunderstanding of domain-specificity. A domain-specific mechanism is one that has specialized computational functions, not one that has a delimited neural area.

Fourth, the article ascribes an inability to learn to “primary modules” (sec. 1.2.3, para. 2), which it synonymizes with domain-specific mechanisms. Consequently, the authors use learning as an evidentiary criterion against domain-specific mechanisms. This misconception has been addressed in two recent publications in the flagship journal of the American Psychological Association (e.g., Confer et al. 2010; Lewis et al. [2017]).

These problems point toward our third major issue: the target article badly mischaracterizes contemporary evolutionary psychological thinking. The domain-specific mechanisms proposed by evolutionary psychologists process inputs from the environment, execute computational procedures on these inputs, and produce outputs – *including social learning* (see Henrich & Gil-White 2001; Lewis et al. [2017]). Accordingly, portraying social learning and domain-specific mechanisms as competing alternatives is highly misleading. Domain-specific adaptations can ontogenetically canalize social learning (e.g., see Henrich & Gil-White 2001; see also Karmiloff-Smith’s “domain relevant” approach [2015, p. 91]). Crucially, this view squares with the literature presented in the target article *without* forcing the unnecessary and outdated dichotomy between innate versus learned.

We have critiqued several aspects of this article, but we believe it has the potential to advance research on the evolution of intelligence. In particular, the article implicitly points toward cost-benefit analysis as a valuable tool. Applying this tool to cross-species differences in the computational complexity of survival- and reproduction-related problems could be fruitful for understanding *G*. For example, whether a species faces a heterogeneous or homogeneous environment and whether the adaptive problems it faces are characterized by social contingencies (e.g., the psychology of conspecifics) may influence the information-processing complexity of the species’ adaptive problems. Comparative analysis of the information-processing complexity of these problems, in conjunction with cost-benefit analyses of the cognitive architecture needed to solve them, has the potential to yield new and testable hypotheses about the evolution of *G*.

G and g: Two markers of a general cognitive ability, or none?

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Charles Locurto

College of the Holy Cross, Worcester, MA 01610.

clourto@holycross.edu

Abstract: The search for general processes that underlie intelligence in nonhumans has followed two strategies: one that concerns observing differences between nonhuman species (*G*), the second that concerns observing individual differences within a nonhuman species (*g*). This commentary takes issue with both attempts to mark a general factor: Differential responding to contextual variables compromises the search for *G*, and the lack of predictive validity compromises *g*.

The target article by Burkart et al. is a valuable study, bringing together lines of evidence that have heretofore seldom been considered together (Locurto 1997). I do have several concerns about the viability of marking a general factor in nonhumans using either species differences or individual difference. I also have a more minor quibble about the definition of general intelligence (*g*) itself. The authors, quoting Gottfredson (1997, p. 13) offer a rather complex definition of general intelligence that one might call unnecessarily impenetrable, as follows: “the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience” The authors add: “It is thus not merely book learning, a narrow academic skill, or test-taking smarts. Rather it reflects a broader and deeper capability for comprehending our surroundings – ‘catching on,’ ‘making sense’ of things, or ‘figuring out what to do’” (sect. 1.1, para. 1; from Gottfredson 1997, p. 13).

I offer a simpler definition, based on Charles Spearman’s original work in this area. It was Spearman (1904) who first developed the idea of a general faculty, based on his study of individual differences in the performance of school children across a variety of tasks, some sensory/perceptual, as in pitch discrimination, others more fully representative of cognitive functioning, such as school grades (see, in particular, Spearman 1904, p. 291). Spearman defined the general factor as tapping “the eduction of correlates” (or, more fully, “the eduction of relations and correlates,” Spearman 1927, pp. 165–66). I love the simplicity and sheer elegance of “the eduction of correlates” expression, and I think it suffices in the stead of more complex definitions. The implication of Spearman’s definition was that *g* was better conceptualized as a single process – mental energy and the like – instead of a series of strung-together mechanisms that functioned as a whole because of overlapping microprocesses (see Mackintosh 1998, for presentation of the overlapping mechanisms idea for *g*). Although the essence of the target article favors density in the definition of *g*, I think Spearman’s original simplicity remains defensible.

The marking of a general factor by looking for systematic differences between nonhuman species (*G*) is potentially compromised by Euan Macphail’s argument that species differences in cognitive performance may be the result of differences in what he called *contextual variables* (Macphail 1982; 1987) – that is, all of the sensory/motoric/motivational and so on factors that might differ between species, and consequently might masquerade as cognitive differences. The end point of this argument is that we may not be able to reject Macphail’s hypothesis that all nonhuman species are capable of all types of learning/cognition. This argument may appear easily rendered moot (after all, isn’t a chimpanzee capable of more complex cognition than a frog?), but it has proven more resilient than initially expected. To their credit, the authors cite Macphail’s argument, and they offer a reasonable rebuttal in the form that perhaps not all tasks are affected by this problem to the same extent. Reversal learning tasks, for instance, adapt each species to the task in the form of initial acquisition before measuring the rapidity of reversal. Therefore, tasks like this might be seen as mitigating what might be initial between-species differences in

reaction to contextual variables. But the problem posed by contextual variables is more insidious than the authors recognize. To fully account for the influence of these contextual confounds, one would have to expose different species to rather strenuous parametric work, where potential contextual confounds are systematically examined across a given dimension, such as studying species differences in reversal learning across a number of sensory dimensions: visual, olfactory, tactile, and so forth. That kind of work is unlikely to be done, and, as a consequence, Macphail's argument remains a thorn in our collective side.

The study of within-species individual differences is a more promising avenue for identifying markers of a general process. Systematic individual differences have been observed in nonhumans, particularly in mice, and these differences are not confounded by differences in noncognitive factors: for instance, overall activity levels (Locurto & Scanlon 1998; Locurto et al. 2006). However, an important, perhaps even critical limitation of such studies is that they lack something that is commonplace in studies of human g – namely, what is called *predictive or criterion-related validity* (Anastasi 1961). In psychometrics, validity refers to what a test measures. Predictive validity refers to the effectiveness of a test in forecasting behavior in domains outside of the test content per se. To assess it, there need to be independent measures of what the test is designed to predict. Independence in this sense can be taken to mean measures outside of the province of the test items themselves. In the human literature, predictive validity of an intelligence test is not at issue: g is a reasonably good predictor of various measures of life outcome, including school achievement, the probability of occupational success, social mobility, and even health and survival. g is better at predicting such variables than are specific cognitive abilities on their own (Locurto 1991). The many criteria external to the test itself that correlate with human g represent a powerful measure of real-life success.

There is nothing similar in the nonhuman literature on g , although there have been important findings that stretch the initial g battery to include a number of additional processes that seem reasonably related to what g should measure, such as selective attention, working memory, and tests of reasoning (Matzel et al. 2011b; Sauce et al. 2014). These extensions are valuable, but they do not constitute extra-domain assays. They are simply additional cognitive tasks that load on the initial g . This form of adding tasks is itself a type of validity called *content validity*, but it is not predictive validity. The authors recognize this issue, and in their Table 7 they offer a series of additional categories of evidence, some of which are forms of predictive validity, that would be useful going forward. The authors end by raising the critical question: does (nonhuman) g predict success in real life? Only if that question can be successfully addressed can we conclude that g is not uniquely human.

Hierarchy, multidomain modules, and the evolution of intelligence

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Mauricio de Jesus Dias Martins^{a,b} and Laura Desirée Di Paolo^{c,d}

^aMax Planck Institute for Human Cognitive and Brain Sciences, 04103 Leipzig, Germany; ^bHumboldt Universität zu Berlin, Berlin School of Mind and Brain, 10117 Berlin, Germany; ^cLichtenberg-Kolleg Institute, University of Göttingen, 37075 Göttingen Germany; ^dLeibniz ScienceCampus and Research Group Primate Social Evolution DPZ-German Primate Centre, 37077 Göttingen, Germany

mmartins@cbs.mpg.de

https://www.researchgate.net/profile/Mauricio_Martins4

lauradesiree.dipaolo@gmail.com

<https://sites.google.com/site/lauradesireedipaolo>

Abstract: In this commentary, we support a complex, mosaic, and multimodal approach to the evolution of intelligence. Using the arcuate

fasciculus as an example of discontinuity in the evolution of neurobiological architectures, we argue that the strict dichotomy of modules versus G , adopted by Burkart et al. in the target article, is insufficient to interpret the available statistical and experimental evidence.

Burkart et al.'s premise is that cognitive abilities can be supported either by the evolution of "primary modules" (sect. 1.2.3, para. 2; domain-specific adaptations to specific environmental challenges), or by the expansion of domain-general intelligence (G). If this premise were true, then the current empirical research, based largely on principal component analyses (PCAs), would be more consistent with the idea that a large portion of cognition in several species is explained by G rather than by collections of primary modules. Reviewing this empirical literature, the authors admit the results are somewhat ambiguous. Nevertheless, they predict we will find stronger evidence for the evolution of G in the future, because the data seem largely inconsistent with the primary modular perspective.

Here, we argue that the strict dichotomy of primary module versus G is misleading: There are occasional evolutionary *discontinuities* in neurobiological architectures that support a range of cognitive abilities, which are neither domain general nor *modular adaptations* for specific environmental challenges.

Our target example is the arcuate fasciculus (AF), which is a neural fiber tract enabling a direct connection between temporal cortex (including auditory cortex) and inferior frontal gyrus (involved in cognitive control) (Catani et al. 2005). This tract, exceptionally well developed in humans in comparison with other primates (Rilling et al. 2008), is a neurobiological evolutionary discontinuity. By neurally binding the regions responsible for auditory processing and cognitive control, this new architectural feature greatly enhanced (1) the working memory for verbal information (vWM) – quite poor in nonhuman primates (Plakke et al. 2015; Scott et al. 2012); and (2) the capacity to process sequences (Dehaene et al. 2015).

This peculiar connectivity pattern seems to be a crucial prerequisite for the evolution of multiple abilities relying on hierarchical *sequential* structure (e.g., language, music, and complex action) (Fadiga et al. 2009; Fitch & Martins 2014). However, improvements in vWM and sequence processing do not necessarily permeate other (nonsequential) cognitive domains, thus not allowing any interpretation in terms of modules or G . For instance: (1) Some nonhuman primates (e.g., chimpanzees) seem to show spatial WM superior to that of humans (Inoue & Matsuzawa 2007), and (2) although the capacity to represent social hierarchies seems to be within the range of nonhuman primate cognition (Seyfarth & Cheney 2014), and the ability to process spatial hierarchies is conserved among nonhuman mammals (Geva-Sagiv et al. 2015), the capacity to process sequential structures nonetheless remains limited in these clades.

Another source of evidence for this specialization comes from neuroimaging. Although the processing of sequential hierarchies activates the inferior frontal gyrus (a region strongly connected with the AF) (Fadiga et al. 2009; Fitch & Martins 2014), the same is not true for nonsequential hierarchies in the visual, spatial, and social domains (Aminoff et al. 2007; Kumaran et al. 2012; Martins et al. 2014). Instead, the latter group of hierarchies seems to be represented by a domain-general episodic memory system.

This cognitive mosaic argues against a simple gradual expansion of G . When performing a PCA, including individuals of different primate species, the emergence of the human AF (and enhanced vWM) would be more easily classified as multidomain or multipurpose cognitive ability, but neither as domain-specific (because it increases the capacity within a range of domains) nor as domain general (because these improvements are specific to sequential but not to nonsequential domains).

In sum, we suspect that the research program advanced by Burkart et al. is designed to distinguish only between modules and G , leaving aside other possible interpretations that would fit better with the available data (e.g., Anderson 2016; Karmiloff-

Smith 2015). In our opinion, a third way between modules and G will give a more suitable account for clade-specific discontinuities (grounded on neurobiological architectural changes), which would fit better the statistical models. These discontinuities offer a great opportunity to capture capacities that are neither gradual expansions of G nor specific modular adaptations to specific environmental problems. Therefore, they are required to overcome intrinsic limitations of current models, theoretically improving them and achieving a more realistic account of the evolution of cognition across different species.

Evolution, brain size, and variations in intelligence

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Louis D. Matzel and Bruno Sauce

Department of Psychology, Program in Behavioral and Systems Neuroscience, Rutgers University, Piscataway, NJ 08854.

matzel@rci.rutgers.edu

https://www.researchgate.net/profile/Louis_Matzel

sauce.bruno@rutgers.edu

https://www.researchgate.net/profile/Bruno_Sauce

Abstract: Across taxonomic subfamilies, variations in intelligence (*G*) are sometimes related to brain size. However, within species, brain size plays a smaller role in explaining variations in general intelligence (*g*), and the cause-and-effect relationship may be opposite to what appears intuitive. Instead, individual differences in intelligence may reflect variations in domain-general processes that are only superficially related to brain size.

The “evolution” of interest in individual differences in the intelligence of nonhuman animals has followed a circuitous route. Individual differences in intelligence were a central focus of early psychologists (note the inclusion of chapters in our first textbooks; e.g., Seashore 1923), as well as, some decades later, of the first animal learning theorists (e.g., Thorndike’s studies in the 1930s). However, with the increasing fixation on the “experimental approach” and reductionism, interest in individual differences waned overall, and systematic studies of variations in intelligence *within* animal species were virtually abandoned between 1940 and 2000. This trend has shifted dramatically in recent times, with increasing interest in between-species comparisons of intelligence (*G*), and more dramatically, in within-species variations in intelligence (*g*). In this spirit, Burkart et al. have done commendable work summarizing the advances, insights, and limitations of animal research on individual differences in intelligence, and have placed this work in the important context of contemporary evolution theory.

Although we agree with many of Burkart et al.’s conclusions, we are skeptical of their inference that the evolution of intelligence, as well as individual differences in intelligence, is inextricably tied to brain size. Brain size does appear to explain differences in the cognitive capacities of closely related species, although the relationship begins to break down across families and higher taxonomic groups. It is similarly problematic that while Neanderthal brain size ranged from 1,300–1,600 grams, their human counterparts had brain sizes of 1,200–1,500 grams. Current theory suggests that competition between the cognitively superior humans and cognitively inferior Neanderthal accounted for the latter’s rapid extinction (Banks et al. 2008; Gilpin et al. 2016). Relatedly, the size of the human brain has *decreased* during the last 100,000 years (Aiello & Dean 1990), a time during which we underwent unusually rapid cognitive gains.

Although brain size does have *some* value in explaining the cognitive capacities of closely related species (i.e., *G*), it is less successful when applied to individual differences *within* a species.

Early estimates suggested a weak relationship between brain size and intelligence ($r^2 = 0.02–0.07$; reviewed in Van Valen 1974), and meta-analyses based on modern imaging techniques find only a marginal increase in this estimate ($r^2 = 0.08$; reviewed in McDaniel 2005). Furthermore, the strength of correlations between brain size and intelligence vary across specialized abilities, and in the case of some abilities, *no* correlation is observed (van Leeuwen et al. 2009; Wickett et al. 2000), suggesting that variations in brain size may instantiate differences in specific abilities, but not variations in *general* intelligence. So why might any correlation exist between brain size and intelligence? A possibility that is widely ignored is that more intelligent individuals interact more extensively with their environments (e.g., they explore more, they learn more; Light et al. 2011; Matzel et al. 2006), and this “environmental enrichment” promotes brain growth (Rosenzweig & Bennett 1996). Simply stated, brain size might be *influenced* by intelligence, but might not itself *cause* differences in intelligence. This possibility has received wide support outside of the field of intelligence (Clayton 2001; Maguire et al. 2000; van Praag et al. 2000; Will et al. 2004), and can explain the paradoxical observation that the correlation between IQ and brain size only emerges after age 7 (by which time differential experiences will have begun to accumulate; McDaniel 2005).

The role of brain size in intelligence may matter less than we intuit. It is important to be reminded that brain size is only a very indirect measure of how general intelligence is instantiated. Higher cognition is highly complex, and the circuitry, neurochemistry, and intracellular components of the brain all contribute to its computational capacity. For example, as noted by Burkart et al., we have reported that general intelligence in mice is correlated with the expression in the prefrontal cortex (PFC) of a dopaminergic gene cluster (Kolata et al. 2010), and smarter mice express higher dopamine-induced activity in the prefrontal cortex (Wass et al. 2013). In humans, the dopaminergic system in the PFC seems also to be closely linked with executive functions and intelligence (McNab et al. 2009; Miller & Cohen 2001). And whereas the brain of birds differs strikingly from the mammalian brain (e.g., it lacks the 6 layers of lamination in the neocortex), the avian nidopallium caudolaterale (NCL) is remarkably similar to the mammalian PFC. Like the PFC, the NCL is a hub of multimodal integration connecting the higher-order sensory input to limbic and motor structures (Gunturkun & Kroner 1999), and dopamine in the avian NCL seems to play a similar functional role in higher cognition as it does in the mammalian PFC (Karakuyu et al. 2007; Veit et al. 2014). This confluence of evidence across taxonomic groups (humans, mice, and birds) is compelling, and at least as parsimonious as the descriptions of intelligence based on variations in brain size.

Burkart et al. imply in their current article and state explicitly elsewhere (van Schaik et al. 2012) that “general intelligence is not a uniquely derived human trait but instead a phylogenetically old phenomenon, found among primates, rodents and birds” (p. 280). However, the PFC and NCL are on opposite ends of the cerebrum and possess distinct genetic expression patterns, leading some to claim that these regions are not homologous but, rather, represent a case of evolutionary convergence (Gunturkun 2012). Thus, non-homologous fields converged over the course of 300 million years into mammalian and avian prefrontal areas that generate the same cognitive functions (e.g., working memory capacity; Diekamp et al. 2002; Matzel et al. 2013) that contribute to the establishment of general intelligence. In other words, general intelligence could have evolved multiple times in different taxonomic groups. Of course this is a matter of considerable controversy (Karten 2015), and the question is far from resolved. Nonetheless, this type of solution is more parsimonious than one based solely on brain size, and mitigates the extant problem of the “cost” of bigger brains. We hope that the “evolution” of interest in the variation in general intelligence follows this route for the next decade.

Habit formation generates secondary modules that emulate the efficiency of evolved behavior

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Samuel A. Nordli and Peter M. Todd

Department of Psychological and Brain Sciences and the Cognitive Science Program, Indiana University, Bloomington, IN 47405-7007.

snordli@indiana.edu pmtodd@indiana.edu

<http://www.indiana.edu/~abcwest/>

Abstract: We discuss the evolutionary implications of connections drawn between the authors' learned "secondary modules" and the habit-formation system that appears to be ubiquitous among vertebrates. Prior to any subsequent coevolution with social learning, we suggest that aspects of general intelligence likely arose in tandem with mechanisms of adaptive motor control that rely on basal ganglia circuitry.

Burkart et al. conclude that many or all vertebrate minds consist of two sets of modular skills: one hardwired and the other ontogenetically constructed—primary and secondary skills respectively. They seem to define general intelligence operationally in terms of its facilitatory role in the process by which an organism obtains secondary skills. If this is correct, the next step should be to identify and understand the neurobiological mechanisms that underlie this process. Studying the evolution of general intelligence in terms of the evolutionary history of its constituent neural structures should provide valuable direction to the comparative research recommended by Burkart et al. Here, we offer a mechanistic explanation for these two skill types and why they could be indistinguishable from one another; this centers around the basal ganglia, a set of subcortical nuclei that are good candidate structures for the foundations of general intelligence. In particular, learning and automatizing secondary skills appears to be what cognitive neuroscientists describe as habit formation, a process reliant on basal ganglia circuitry (Smith & Graybiel 2016).

Certain aspects of almost any ecological context cannot be directly addressed by natural selection simply because those aspects are too transitory to support intergenerational selection, which is required for specific adaptive solutions to evolve. Although inaccessible to evolved primary skills, some transitory ecological factors nevertheless remain stable for significant portions of an individual organism's life span—the specific geographical features surrounding a given animal's den, for example, or the physical layout of the controls in a personal automobile (and the associated actions required to operate those controls). Transitory stability is itself an ecological factor that is susceptible to adaptive exploitation via natural selection. Species that evolved the general capacity to identify, learn, and exploit instances of transitory ecological stability will have obtained organismal objectives more successfully and more efficiently than species lacking this capacity. Secondary skills as described by Burkart et al. are the exploitative products of such a capacity; that is, although evolved primary skills exploit the stability of specific perennial factors, the capacity to form secondary skills exploits transitory stability as a perennially general characteristic of temporary factors (Nordli 2012). From this perspective, as primary and secondary skills have each arisen to exploit ecological stability (whether long-term or transitory), it is unsurprising that their shared properties—speed, efficiency, automaticity—render them effectively indistinguishable (absent knowledge of their ontogeny), as Burkart et al. point out.

Supporting this perspective, research suggests that primary and secondary skills are each encoded within basal ganglia-based circuits (Graybiel 1995), such as the fixed sequence of grooming behaviors that is ubiquitously exhibited in rats (Aldridge et al. 2004) and learned paths rats take in a maze (Barnes et al. 2005). These nuclei also appear to be integral to goal-directed action selection, stringing behaviors together in service of achieving contextualized reinforcement (Graybiel 2008). As a sequence of reinforced behaviors (e.g., a maze path) is repeated within a

specific context (e.g., a chocolate reward at the end), the entire string is encoded within the basal ganglia as a single behavioral "chunk" that then exhibits quick and efficient cue-based automaticity (Jin et al. 2014). The basal ganglia contribute centrally to cognition as well, through working memory, attention, decision making, and other processes (Stocco et al. 2010). In this context, it is intriguing that mice with a humanized version of their *Foxp2* gene—the so-called "language gene"—develop neurons in the basal ganglia with increased plasticity and significantly lengthened dendrites (Enard et al. 2009), and also exhibit accelerated habit learning relative to normal mice (Schreiweis et al. 2014).

If general intelligence is the set of processes that allow organisms to discover, learn, and automatize secondary skills, the basal ganglia may be largely responsible for much of what qualifies as intelligence: (1) modulating rewards to direct or "canalize" attention and motivate goals (e.g., inclining to attend toward and imitate conspecifics); (2) exploring a potential action space and achieving targeted objectives by selecting goal-directed behaviors (e.g., practicing/refining an approximation of what conspecifics do); and (3) automatizing contextualized behavioral sequences that have been repeatedly reinforced (e.g., reproducing efficient skill behavior that may now be imitated by others). This is consistent with the cultural intelligence perspective advocated by Burkart et al., but the coevolutionary enhancement of social learning and general intelligence does not itself explain the evolutionary origins of general intelligence. Instead, we should look to basal ganglia circuitry, which is functionally conserved across all vertebrate species, and which likely evolved over 560 million years ago (Reiner 2010; Stephenson-Jones et al. 2011).

The most basic function of basal ganglia circuitry is adaptive motor control, directing goal-oriented motor sequences (Grillner et al. 2013). Energy demands and reproductive success are the main fitness pressures, and most organisms adapt to that pressure by moving about through space—foraging for food and mates—as efficiently and effectively as possible (see Stephens & Krebs 1986); competition over limited resources in these domains likely resulted in an evolutionary arms race. The capacity to automatize stereotyped patterns of learned motor behaviors into secondary skills is a powerful weapon in that war, enabling the execution of learned motor patterns with the same speed, efficiency, and specificity of evolved motor patterns. We suspect that general intelligence initially coevolved with mechanisms of adaptive motor control to facilitate the search for and learning of new adaptive motor skills. This intelligent search capacity may subsequently have been generalized through exaptation to facilitate the search for new adaptive cognitive skills: spatial foraging and searching through memory space appear to be expressions of the same general exploratory capacity, the goal-directed nature of which is modulated by basal ganglia circuitry via the dopaminergic reward system (Hills et al. 2008; Hills et al. 2015). Comparative investigations of interspecies differences in basal ganglia-based circuitry may provide further clues regarding the evolution of general intelligence; future studies should pay attention to these structures and the mechanisms of habit formation to which they contribute.

The evolution of analytic thought?

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Gordon Pennycook and David G. Rand

Department of Psychology, Yale University, New Haven, CT 06520-8205.

gordon.pennycook@yale.edu <https://gordonpennycook.net>

david.rand@yale.edu davidrand-cooperation.com

Abstract: We argue that the truly unique aspect of human intelligence is not the variety of cognitive skills that are ontogenetically constructed, but

rather the capacity to *decide* when to develop and apply said skills. Even if there is good evidence for *g* in nonhuman animals, we are left with major questions about how the disposition to think analytically can evolve.

In their admirably broad discussion, Burkart et al. review many important distinctions in the study of human cognition, including fluid versus crystallized intelligence and domain-general versus domain-specific mechanisms. Nonetheless, by focusing on *g*, the authors did not acknowledge that individual aspects of human intelligence – some of which presumably evolved separately – may have been particularly important for the evolution of human intelligence. In our view, the capacity to *decide* when to develop and use intellectual skills is not only a crucial aspect of human intelligence, but also it may in fact be unique to *human* intelligence. Human metacognition of this sort was not discussed by Burkart et al.

Consider the following problem (Frederick 2005):

A bat and ball cost \$1.10 in total. The bat costs \$1.00 more than the ball. How much does the ball cost?

Most educated adult humans are capable of generating a response to this question intuitively and automatically (namely: 10 cents). This likely occurs through a domain-general canalization process (see “The urgency problem” in the target article, Table 1). However, the automatic response is not the correct answer (if the ball cost 10 cents, the bat would have to cost \$1.10 and together they would cost \$1.20 – the correct answer is 5 cents). Although the majority of people simply give the incorrect intuitive response to this question (e.g., 64.9% of University of Waterloo undergraduates; Pennycook et al. 2016a), some are capable of answering it correctly. This exercise of intelligence requires not just the capacity to solve the problem, but also the willingness to apply effortful cognitive processing to a problem despite the presence of what initially appears to be a suitable response (Stanovich & West 1998; 2000). There is now a great deal of evidence that human rationality (however imperfect, see Kahneman 2011; Kahneman & Frederick 2005) involves not simply computational cognitive operations (i.e., *g*), but also algorithmic-level operations that determine the course of reasoning and decision making (see Stanovich 2009a; 2009b; 2011).

Moreover, recent research indicates that the propensity to think analytically as a means to override automatic responses has consequences for our everyday lives (Pennycook et al. 2015b). For example, more analytic individuals have less-traditional moral values (Pennycook et al. 2014; Royzman et al. 2014) and are less likely to hold beliefs that are religious (Gervais & Norenzayan 2012; Pennycook et al. 2012; 2016b; Shenhav et al. 2012), paranormal (Pennycook et al. 2012), and/or conspiratorial (Swami et al. 2014). Analytic thinking disposition has also been linked with increased acceptance of science (Gervais 2015; Shtulman & McCallum 2014) and lowered acceptance of complementary and alternative medicine (Browne et al. 2015) and pseudo-profound bullshit (Pennycook et al. 2015a). Analytic thinking can also undermine cooperation and prosociality (Rand 2016; Rand et al. 2016; Rand et al. 2014; Rand et al. 2012), as well as punishment (Grimm & Mengel 2011; Halali et al. 2014; Sutter et al. 2003).

Consideration of the evolutionary dynamics of metacognition is, therefore, of key importance for understanding the evolution of human intelligence (Bear & Rand 2016b). Recent work using formal evolutionary game theory models has begun to shed light on this issue from a theoretical perspective, both in the domains of intertemporal choice (Tomlin et al. 2015; Toupo et al. 2015) and cooperation (Bear & Rand 2016a; Bear et al. 2016). These models illustrate how the willingness to override intuitive responses can be favored by natural selection in settings where flexibility and planning are particularly useful, and also how complex cyclical dynamics of automatic versus controlled cognition can emerge. This growing body of theoretical work calls for empirical examination of cognitive control in nonhuman animals (e.g., MacLean et al. 2014; Rosati & Santos 2016).

Burkart et al. discuss executive functions like inhibitory control, working memory, and cognitive flexibility (sect. 1.1) and highlight the importance of “reasoning ability and behavioral flexibility” for human and nonhuman intelligence (sect. 1.1, para. 1). Thus, the human capacity for overriding intuitive outputs (such as 10 cents in the bat-and-ball problem) is clearly acknowledged. Nonetheless, treating these aspects of human cognition as other types of cognitive processes suppresses a distinction we think should be emphasized. Can humans alone *decide* when (or if) to initiate cognitive processes, as well as when (or if) to reflect upon their outputs? The findings highlighted previously suggest that the capacity to *decide to think* is a core intellectual skill that distinguishes humans from each other. We assert that this skill is also crucial to distinguishing humans from nonhuman animals.

Although we agree that the pursuit of *g* (and *G*) in nonhuman animals is worthwhile, it is not simply that the current body of work is preliminary (as the authors state). Rather, understanding the evolution of human intelligence requires a broader view of human rationality. Thus, unfortunately, we are even further from definitive conclusions than is intimated by the target article. Even if there is good evidence for *g* in nonhuman animals and this ultimately informs us about the evolution of cognitive skills in humans, we will still be left with major questions about how the human capacity to decide when to think (i.e., the disposition to think analytically, over and above *g*) can evolve.

“Birdbrains” should not be ignored in studying the evolution of *g*

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Irene M. Pepperberg

Department of Psychology, Harvard University, Cambridge, MA 02138.

impepper@media.mit.edu impepper@wjh.harvard.edu

Abstract: The authors evaluate evidence for general intelligence (*g*) in nonhumans but lean heavily toward mammalian data. They mention, but do not discuss in detail, evidence for *g* in nonmammalian species, for which substantive material exists. I refer to a number of avian studies, particularly in corvids and parrots, which would add breadth to the material presented in the target article.

I agree with the authors’ basic thesis, depicted in the target article’s Figure 3, which argues for combinations of heritable and learned abilities that result in general intellectual achievements, whether in humans or nonhumans. However, in their discussion of nonhuman subjects, the emphasis on nonhuman primate, and to a lesser extent mammalian, species is discouraging. The few references to avian cognition do not do justice to the wide variety of abilities and studies – sometimes in a single individual or species – that provide evidence for generalized intelligence. Thus, the point of my commentary is to advocate strongly for avian *g*.

I do, of course, understand that formal *g* analyses (i.e., batteries of different tests on numerous individuals within and across species) are lacking for avian cognitive capacities, as compared to the several existent analyses on nonhuman primates and rodents. Nevertheless, I hoped that Burkart et al. would have discussed the large number of studies on a wide variety of topics performed on avian species, particularly on corvids and psittacids ... and maybe would have attempted some kind of review, if not analysis, of their own. For example, early in the article the authors suggest that *transfer* of knowledge from one domain to another novel context provides evidence for *g*, yet little discussion exists of instances of such behavior in avian subjects (for example, transfer of the trained use of the label “none” from describing the absence of similarity and difference of specific attributes between objects [Pepperberg 1988] to the spontaneous use of the label for describing the absence of a size differential

[Pepperberg & Brezinsky 1991] to the additional spontaneous use for describing the absence of a specific numerical set in a collection [a zero-like concept; Pepperberg & Gordon 2005]).

The authors note that g has “robust correlates to brain structure and function” (sect. 1.1, para. 3), yet do not mention significant research on avian brains. Recent studies, although not always performing the correlations themselves, have shown that avian brain anatomy would correlate with many g -related abilities; see, for example, in addition to those references cited, Iwaniuk et al. (2009) or Jarvis et al. (2005). Specifically, Olkowitz et al. (2016) have found that parrots and corvids have forebrain neuron counts equal to or greater than primates with much larger sized brains, and argue that this finding likely explains the advanced cognitive abilities found in these avian species.

In general, the authors only partially consider parallel/convergent evolution of g with respect to avian species, again particularly concerning corvids and parrots. For example, K-selected traits (e.g., long lives, few offspring that are relatively slow to mature, etc.), are discussed at various points in the target article as being associated with the evolution of g ; these traits are found in most corvid and parrot species. The authors highlight the importance of sociality in driving intelligent behavior (sensu Jolly [1966] and Humphrey [1976]): Notably, the majority of parrot and corvid species live in complex social groups, and evidence exists for several types of learning that are enhanced via conspecific or allospecific social influences (e.g., corvids: Miller et al. 2014; New Zealand kea parrots: Heyse 2012). Myriad papers on corvid social cognition have been published by Bugnyar and his colleagues (e.g., Bugnyar & Heinrich 2006). Acquisition of referential use of human speech by Grey parrots occurs through social learning (e.g., Pepperberg 1981; 1999); similarly, “bilingual” songbirds learn the form and likely use of heterospecific vocalizations via intense social interaction (e.g., Baptista 1981).

Furthermore, as with nonhuman primates, the dominance hierarchies that are prevalent in social groups of corvids (e.g., Chiarati et al. 2010) require an understanding of advanced cognitive processes such as individual recognition (e.g., Izawa & Watanabe 2008) and transitive inference (e.g., Paz-y-Miño et al. 2004). Granted, the references I cite involve different corvid species; nevertheless, the cognitive requirements across species would likely be quite similar given their similar ecology/ethology. And, although dominance hierarchies in parrot flocks have not been studied in the wild, hierarchies have been observed in captivity (Szabo et al. 2016; parrots in my lab also exhibit a hierarchy), and understanding linear ordering can also be related to cognitive capacities such as the spontaneous comprehension of ordinality (Pepperberg 2006).

Tests used as evidence of general intelligence, even by the authors’ admission, are mostly basic, but other tests, even if performed on only a limited number of subjects, strongly demonstrate advanced avian capacities. For example, evidence for executive function (planning, delayed gratification) is evident in corvids (Hillemann et al. 2014; Raby et al. 2007). One cannot argue that such behavior is modularly related to caching, as success on the same tasks can be seen in parrots that do not cache (Auersperg et al. 2013; Koepke et al. 2015). Grey parrots understand not only categories (e.g., what is or is not green), but also concepts such as “color,” “shape,” and “matter” (i.e., the existence of these hierarchical concepts, under which categories such as green and wood are sorted; Pepperberg 1983) and that two objects can be related based on just a subset of these concepts; that is, for second-order concepts of same-different (Pepperberg 1987). The authors mention reasoning by exclusion: for such abilities in parrots and corvids, see Pepperberg et al. (2013), Schloegl (2011), and Schloegl et al. (2009). Likewise, for advanced avian understanding of number concepts, see Smirnova (2013) and Ujfalussy et al. (2014); these abilities are often at a level more advanced than those shown to date for nonhuman primates (e.g., Pepperberg 2006; Pepperberg & Carey 2012). Research

papers on tool use by corvids that do not use tools in nature are too numerous to mention; for aspects of physical cognition in parrots, note van Horik and Emery (2016).

The authors have, essentially, performed a meta-analysis on a number of meta-analyses, and I have no arguments about their basic thesis – my criticism is merely that readers interested in this thesis, particularly readers with little knowledge of nonhuman capacities, would unfortunately be left unaware of a large number of striking *avian* abilities that provide considerable evidence for g .

General intelligence is an emerging property, not an evolutionary puzzle

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Franck Ramus

CNRS, Ecole Normale Supérieure, EHESS, PSL Research University, 75005 Paris, France.

franck.ramus@ens.fr <http://www.lscp.net/persons/ramus/en/>

Abstract: Burkart et al. contend that general intelligence poses a major evolutionary puzzle. This assertion presupposes a reification of general intelligence – that is, assuming that it is one “thing” that must have been selected as such. However, viewing general intelligence as an emerging property of multiple cognitive abilities (each with their own selective advantage) requires no additional evolutionary explanation.

As the authors acknowledge, the concept of general intelligence is empirically grounded solely in the observation of positive correlations between all test scores, as reflected by a general factor termed g explaining a large share of variance in all tests (Spearman 1904). All other accounts are simply debatable interpretations or hypotheses attempting to relate g to some other cognitive or biological constructs. They run the risk of reifying what is primarily a statistical construct, and also of seriously confusing the search for an evolutionary explanation. For instance, Gottfredson’s (1997) definition of intelligence is little more than a scholarly formulation of the folk concept of intelligence, but offers no guarantee of matching psychometric g . Burkart et al. initially conflate g with executive functions, but this changes the nature of the problem. If general intelligence reduced to executive functions, then to the extent that each executive function offers a selective advantage, the evolution of general intelligence would not be a major puzzle. Similarly, general intelligence is also identified with domain-general cognitive processes, which is a different, and unnecessary, hypothesis as we will show. Furthermore, many putative domain-general cognitive functions turn out to be less general than they seem. For instance, there are separate working memory systems for verbal, visuospatial, and other modalities. Similarly, words such as *inhibition* and *attention* wrongly suggest unitary phenomena, whereas they are used to describe a host of distinct processes, none of which can be said to be truly domain-general, and none of which is an evolutionary puzzle. Finally, certain cognitive functions can serve domain-general purposes while having been selected for more specific adaptive value. This may be the case of language, which serves as a mediator across many cognitive functions, yet may have evolved for purely communicative purposes (Jackendoff 1999; Pinker & Bloom 1990).

More generally, every attempt to reduce general intelligence to a single cognitive (processing speed, working memory, etc.) or biological (brain volume, nerve conduction velocity, etc.) construct has failed, each construct showing moderate correlation with g and being best described as simply one contributor to the g factor (e.g., Mackintosh 2011). Thus, trying to tackle the evolution of general intelligence by addressing the evolution of any of these constructs is a form of attribute substitution (Kahneman & Frederick 2002).

Understanding the evolution of psychometric *g* requires understanding how it comes about. As early as 1916, Thomson (1916) showed that it is sufficient to postulate underlying group factors that influence several tests to obtain a positive manifold without a general factor (see also Bartholomew et al. 2009). Reframed in modern psychological terms, an elementary analysis of tests shows that no test is a pure measure of a cognitive function (or construct). The relationship between cognitive functions and test scores is many-to-many: Each test score is influenced by several cognitive functions, and each cognitive function influences several test scores (in the same direction). The latter observation suffices to explain that test scores are positively correlated. We submit that the logic of Thomson's bonds model is much more general, as it also applies to factors underlying cognitive functions. Indeed, each brain function or property (e.g., frontal gray matter volume, nerve conductance velocity, dopamine synthesis, etc.) influences several cognitive functions, thereby inducing intrinsic positive correlations between cognitive functions. One step further back, each gene expressed in the brain (e.g., genes that code for neurotrophic factors, transcription factors, and any molecule involved in neurotransmission) typically influences several brain functions and properties, thereby inducing positive correlations between them. In parallel, many environmental factors (e.g., nutrition, socioeconomic status, education, diseases, and so on) influence more than one brain or cognitive function, thereby inducing further correlations. Finally, van der Maas et al. (2006) have shown that positive correlations between cognitive functions may emerge through mutual interactions in the course of cognitive development, even in the absence of intrinsic correlations. Thus, all of the factors underlying test performance are pleiotropic and conspire to produce positive correlations at all levels of description, hence the emergence of the positive manifold.

Note that, according to the explanation given previously, the positive manifold can arise in an entirely modular mind (because modules selected for different purposes nevertheless have to share underlying factors), and therefore there is no antagonism between modularity and general intelligence. Furthermore, the very same pleiotropic mechanisms are at work in other species and, therefore, readily explain that a *g* factor can be measured in nonhuman primates, rodents, and probably all organisms with a nervous system. Finally, in the speciation process, genes that progressively diverge between two populations influence more than one brain and cognitive function; therefore, the two populations are bound to eventually differ in more than one brain and cognitive function. This directly predicts that performance in different tests should covary across species, or what the authors term *G*. Thus, all of the evidence that the authors gather in support of a reified notion of general intelligence is more parsimoniously explained by the pleiotropy of the underlying factors, within and across species. The "independent evolution of large numbers of modules instead of general intelligence" is not "particularly difficult to reconcile with interspecific findings of *G*" (sect. 2.5, para. 5); it directly follows from an understanding of what modules are made of: the same building blocks, shared between species.

There is, therefore, no need to postulate that the positive manifold reflects one particular cognitive function or one brain function, whose evolution would require a special explanation. The positive manifold emerges spontaneously from the pleiotropy of all of the underlying factors. Only these underlying factors require an evolutionary explanation. It is indeed very interesting to inquire about the evolution of genes involved in brain development and function, the evolution of brain functions and properties, and the evolution of cognitive functions. If there is any brain or cognitive function whose evolution is a major puzzle, then it should be identified and studied as such. However, this is not the case for general intelligence, which does not reduce to a single brain or cognitive function, and whose evolution follows directly from that of the underlying biological, cognitive, and environmental factors.

General intelligence does not help us understand cognitive evolution

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David M. Shuker,^a Louise Barrett,^b Thomas E. Dickins,^c Thom C. Scott-Phillips,^d and Robert A. Barton^d

^aSchool of Biology, University of St Andrews, St Andrews KY16 9TH, United Kingdom; ^bDepartment of Psychology, University of Lethbridge, Lethbridge, Alberta T1K 3M4, Canada; ^cSchool of Science & Technology, University of Middlesex, London NW4 4BT, United Kingdom; ^dEvolutionary Anthropology Research Group, Durham University, Durham DH1 3LE, United Kingdom.

dms14@st-andrews.ac.uk <https://insects.st-andrews.ac.uk/>
 louise.barrett@uleth.ca <http://directory.uleth.ca/users/louise.barrett>
 T.Dickins@mdx.ac.uk <https://www.mdx.ac.uk/about-us/our-people/staff-directory/profile/dickins-tom>
 t.c.scott-phillips@durham.ac.uk <https://thomscottphillips.wordpress.com>
 r.a.barton@durham.ac.uk <https://www.dur.ac.uk/anthropology/staff/academic/?id=122>

Abstract: Burkart et al. conflate the domain-specificity of cognitive processes with the statistical pattern of variance in behavioural measures that partly reflect those processes. General intelligence is a statistical abstraction, not a cognitive trait, and we argue that the former does not warrant inferences about the nature or evolution of the latter.

Is "the presence of general intelligence" the "major evolutionary puzzle" that Burkart et al. claim? Like much of the literature on general intelligence in animals, the target article draws inferences about the nature and evolution of cognitive traits from the correlations among measures of performance, both within and between species. The "positive manifold" (sect. 1.1, para. 1) is thus taken to be a nontrivial finding, and *g* is treated as being – or reflecting – a trait with causal effects (a mechanism). *g*, however, is of course a statistical construct: When the authors refer to "the structure of cognition" (sect. 1.1.1, para. 1), what they actually describe is the statistical structure of variance in performance on behavioural tests. What can this statistical structure tell us about cognitive traits? We suggest that it tells us very little, or possibly nothing, because of the multiple plausible ways in which it might arise. Moreover, the analysis of *g* fails to provide a clear framework for empirical research, because the putative underlying mechanism, general intelligence, cannot be meaningfully defined in the absence of the correlations that are used as evidence for its existence.

More specifically, the reification of *g* involves a conflation of the proposed domain-generality of cognitive processes with the statistical pattern of variance in the behavioural output of those processes. Thus, "Massive modularity would appear to be irreconcilable with general intelligence" (sect. 1.2.1, para. 4) – well, only in the sense that apples are irreconcilable with oranges. Burkart et al. follow many in assuming that the positive manifold can be explained "by positing a dominant latent variable, the *g* factor, associated with a single cognitive or biological process or capacity" (van der Maas et al. 2006, p. 842). As pointed out by the latter authors, other explanations, which account for not only the presence of *g* but also its heritability and neuro-anatomical correlates, are not only possible, but also plausible. In citing van der Maas et al. (2006), Burkart et al. explicitly "equate general intelligence with the positive manifold" (sect. 1.1.1, para. 3), implying that their position and that of van der Maas et al. are in harmony. The point emphasised by van der Maas et al., however, and the point we also emphasise, is that the positive manifold provides little or no constraint on the possible architectures of cognition.

To labour the point, correlated variance does not imply any particular kind of cognitive process. That said, we might still want an explanation for why performance or behaviours are correlated across domains. Here, in brief, are some possibilities.

(1) They are not really different domains. For example, Reader et al. (2011) and Fernandes et al. (2014) found positive correlations among the rates of social deception, social learning, innovation,

extractive foraging, dietary breadth, percentage of fruit in the diet, and tool use across primate species, leading both sets of authors to conclusions about the domain-generalness of cognitive processes. Neither these authors nor Burkart et al. explain how a domain is to be identified, and therefore how these behavioural measures can, in principle, be used to test for domain-generalness. We can envisage plausible arguments to the effect that at least some of these behaviours draw on the same domain-specific processes. It is a question of natural ontologies: How do we carve nature at her joints? The only way that makes sense to us is in an evolutionary context where we identify a domain with a selection pressure. Deciding that “social” and “non-social” are distinct domains is, therefore, a hypothesis about what selection pressures have operated, not necessarily a fact about the world. Burkart et al. recognise this problem (“The issue of task selection is thus closely linked to the identification of domains in animal cognition” [sect. 2.4.2, para. 5]) but do not offer a convincing solution.

(2) Related to (1), it may well be that the behaviours measured are influenced by cognitive processes they share in common, but this does not mean it is helpful to describe those processes as “general processes,” or that together they comprise “general intelligence.” For example, primate species vary in their sensory-motor adaptations – in particular, in their stereo visual acuity and manual manipulative abilities – and these differences correlate with the evolution of binocular convergence supporting stereo vision, the size of visuomotor structures in the brain, and consequently overall brain size (Barton 2012; Heldstab et al. 2016). Clearly, such sensory-motor specializations may influence performance of a range of behaviours and/or experimental test procedures. Yet, describing them as “domain general” tells us nothing about how they work or how they evolved. We also do not share the optimism of Burkart et al. that reversal learning is free of such problems.

(3) Niche dimensions tend to be correlated (Clutton-Brock & Harvey 1977). For example, folivorous primates generally live in smaller social groups, have smaller home ranges, and engage less in extractive foraging and tool use than more omnivorous primates. Cognitive adaptations for specific niche dimensions could therefore theoretically be completely informationally encapsulated and yet performance across domains would still be correlated.

(4) The rates of naturally occurring behaviours in the wild (Reader et al. 2011; Fernandes et al. 2014, cited by Burkart et al.), may be systematically biased, leading to spurious correlations. Although these studies attempt to control for observation effort, they don't control for the number of individuals under observation. Rates of all behaviours will, other things being equal, correlate positively with group size and therefore with each other, because more individuals are under observation per unit time in larger groups. Variation in observability due to habitat will only exacerbate the problem. The implications are obvious.

For a theory to be useful, it has to be well defined in such a way as to generate testable predictions that differentiate it from other theories. Burkart et al., along with the wider literature on general intelligence and *g*, fail to achieve this. If we are to make progress in our efforts to understand the evolution and structure of cognition, we need to stop confusing the map for the territory.

It's time to move beyond the “Great Chain of Being”

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Robert J. Sternberg

Department of Human Development, Cornell University, Ithaca, NY 14853.

robert.sternberg@gmail.com www.robertjsternberg.com

robert.sternberg@cornell.edu

Abstract: The target article provides an anthropocentric model of understanding intelligence in nonhuman animals. Such an idea dates

back to Plato and, more recently, Lovejoy: On Earth, humans are at the top and other animals at successively lower levels. We then evaluate these other animals by our anthropocentric folk theories of their intelligence rather than by their own adaptive requirements.

Burkart et al. have written a very interesting, erudite, and anthropocentric account in the target article of how principles discovered for human intelligence might be generalized to animals other than humans. The presuppositions behind this article are captured well by Lovejoy (1936) in his book, *The Great Chain of Being*. The general idea, which goes back to Plato and Aristotle, is that there is a Great Chain of Being containing, among other entities, God at the top, then humankind, and then successively lower animals. At the top of the Earthly beings are humans. So if we want to understand other organisms, according to this view, we can do so by comparing them to humans and seeing in what ways they are similar and in what ways they are different and lacking. Much of early comparative psychology was based on this idea (e.g., Bitterman 1960).

Other areas of psychology and other behavioral sciences have not been immune from the logic of the Great Chain of Being, except that, in some cases, they viewed different cultures or races of people as occupying differentially elevated positions on the Great Chain (Sternberg 2004; Sternberg et al. 2005). Many eminent behavioral scientists, such as Sir Francis Galton and Raymond Cattell, believed in some version of the Great Chain (see <https://www.splcenter.org/fighting-hate/extremist-files/individual/raymond-cattell>). Moreover, traditional cross-cultural psychological studies of intelligence involved (and still involve) translating Euro-centric intelligence tests, such as the Wechsler, and then administering them to people in other cultures (e.g., Georgas et al. 2003).

But in the field of cultural studies of intelligence, progress has been made, largely due to the pioneering work of Luria (1976). Luria, in testing individuals in non-European cultures, found that the problems that were alleged to measure intelligence in European populations did not do so in other cultures because the individuals did not accept the presuppositions of the problems they were given. For example, when Uzbekistan peasants were given a syllogisms problem, such as, “There are no camels in Germany. The city of B. is in Germany. Are there camels there or not?”, subjects could repeat the problem precisely and then answer “I don't know. I've never seen German villages ...” The subjects did not accept the problems in the abstract modality for which they were intended. Of course, one could argue that they could not do so. But then, Cole et al. (1971) found that Kpelle tribesmen seemed not to be able to sort items categorically but rather sorted only functionally, until they were told to sort the way a stupid person would, at which point they had no trouble sorting categorically. In our own research (see Sternberg 2004), we found that rural Kenyan children and rural Alaskan Yup'ik Eskimo children could do tasks that were extremely important for adaptation and even survival in their own cultures (e.g., treating malaria with natural herbal medicines, finding their way across the frozen tundra from one village to another with no obvious landmarks) that their White teachers never could do, but were considered stupid by their teachers because they underperformed in school and on standard Euro-centric cognitive tests. Who was lacking intelligence: the children or the psychologists who gave them tests inappropriate to the demands of their everyday adaptation?

The tests we used for the Kenyan and Alaskan children cut to the heart of what intelligence is – ability to adapt to the environment. That is the core of intelligence, according to surveys of experts in the field of intelligence (“Intelligence and Its Measurement” 1921; Sternberg & Detterman 1986). But the tests that Burkart and her colleagues have devised are not tests highly relevant to animal adaptation; at best, and even then questionably, they are tests of folk conceptions of what animal intelligence should be from a human viewpoint.

An appropriate way to look broadly at the intelligence of any organism is to look at how well it adapts to the range of

environments it confronts. Gibson's (1979) concept of an affordance—an action possibility latent in the environment—is perhaps key here. The humans and other animals that are intelligent, in this view, are those that adapt well to the challenges of the range of environments they can encounter over the course of their lives. To understand animal intelligence, we should be looking at skills that are relevant to the animals' everyday adaptation, such as how well they can forage for food, create adequate shelter, and most important, avoid predators, including humans and the traps humans set for them.

Perhaps, furthermore, we humans should test human intelligence not with the often trivial tests we use (Sternberg 1990), but rather with tests of how well we humans can avoid the traps—for example, global warming, violence, pollution, poverty, inequality—that we set for ourselves.

Humans, with the serious problems they have created for themselves—pollution, global warming, weapons of mass destruction, terrorism, inequality, among others—may not be well positioned to be the judges of what intelligence looks like in other organisms, or of how intelligent they are. To hold other various animals to the standards of human folk conceptions of intelligence is perhaps an act of intellectual hubris. In the end, how intelligent, really, is a species that may be the only species ever to live on Earth actually to create and sow the seeds for its own destruction (Sternberg 2002)? If nonhuman animals were to create tests of intelligence for humans, perhaps they would create tests that would measure which humans were not intent on destroying both the animals' habitats and their own.

Disentangling learning from knowing: Does associative learning ability underlie performances on cognitive test batteries?

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Jayden O. van Horik and Stephen E. G. Lea

Centre for Research in Animal Behaviour, Washington Singer Laboratories, Department of Psychology, College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4QG, United Kingdom.

jayden.van.horik@gmail.com www.jayden-van-horik.blogspot.co.uk
s.e.g.lea@exeter.ac.uk <http://people.exeter.ac.uk/SEGLea/>

Abstract: Are the mechanisms underlying variations in the performance of animals on cognitive test batteries analogous to those of humans? Differences might result from procedural inconsistencies in test battery design, but also from differences in how animals and humans solve cognitive problems. We suggest differentiating associative-based (*learning*) from rule-based (*knowing*) tasks to further our understanding of cognitive evolution across species.

In the target article, Burkart et al. highlight the importance of identifying variations in domain-general intelligence across species. However, with the exception of mice and possibly primates, there remains little evidence suggesting that variations in domain-general intelligence (*g*) underlie intraspecific variations in cognitive performance in nonhuman animals. Moreover, such an attribution remains debatable as procedural differences in test battery design may confound interpretations of the underlying mechanism. Our concern is exacerbated where support for a *g* factor is sparse and limited to studies that predominantly test subjects in the wild. For example, the mechanisms underlying success on test batteries designed to assess performances of birds in the wild (Isden et al. 2013; Keagy et al. 2011; Shaw et al. 2015) bear little resemblance to those effective in tasks presented to non-avian species tested in captivity (Herrmann et al. 2010b).

To accurately address whether it is meaningful to talk about domain-general intelligence in animals, it is important that the inherent design of the items within a cognitive test battery

accurately capture domain-specific cognitive abilities, independent of procedural factors, and that relevant testing paradigms are used to assess the cognitive performances of subjects in the wild as well as in captivity. Direct comparisons between species are unavoidably difficult as different animals possess different adaptive specialisations; for example, a human cognitive test battery may assess verbal skills whereas nonhuman test batteries cannot. Test batteries, therefore, also need to consider the inherent differences in cognitive processes between species.

Performances on nonhuman cognitive test batteries, particularly those presented to subjects in the wild, require individuals to first interact with a novel apparatus before experiencing its affordances. Accordingly, such test batteries often use tasks that involve trial-and-error learning to quantify subjects' performances and assess their ability to learn to attend to cues based on reward contingencies. For example, subjects may be presented with tasks that assess how quickly they can learn to differentiate rewarded from unrewarded colours, or learn about the spatial location of concealed rewards. Although performances on such tasks are considered to capture domain-specific abilities, success will inevitably also be mediated by fundamental processes of learning that are common to the inherent design of these problems. As a result, an individual may perform well when learning both colour and spatial discrimination problems, not because this individual excels in anything we would want to call intelligence but because it is a relatively rapid learner of all kinds of association, including those involved in the two novel problems. Hence, what seems to be evidence for domain-general intelligence may reflect individual consistency in speed of associative learning, rather than individual consistency in cognition across different domains.

Between-species comparisons may be further confounded because associative learning ability plays a greater role in task performance in animals than it does in humans, and may play a greater role in some nonhuman species than others. Such differences may be particularly pronounced between evolutionarily disparate species such as primates and birds. Pigeons consistently show purely associative solutions to problems that humans, and to some extent nonhuman primates, tend to solve by the use of rules (e.g., Lea & Wills 2008; Lea et al. 2009; Maes et al. 2015; Meier et al. 2016; Smith et al. 2011; 2012; Wills et al. 2009). In humans, preferential attention to rules may expedite performances on rule-based tasks (Danforth et al. 1990), but may also impair responses to experienced contingencies (Fingerman & Levine 1974; Hayes et al. 1986). Consequently, as different cognitive processes govern the performances of different species on psychometric test batteries, analogous performances between human and nonhuman animals may be difficult to capture.

To overcome these issues, we highlight the importance of differentiating between performances on tasks that require subjects to “learn” to solve a problem, from performances on tasks that assess whether subjects “know” the solution to a problem. We therefore advocate the use not only of associative tasks such as discrimination learning of colour cues that require trial-and-error experience to solve, but also of tasks that require subjects to be trained beforehand to a particular learning criterion, so that their performance on a subsequent novel test or “generalization” condition can be assessed. Such conditions provide a controlled version of the tests of “insightful” or “spontaneous” problem solving that, from the time of Köhler (1925) on, have often been considered critical in assessing animal intelligence.

Learning tasks are particularly relevant when assessing individual differences in associative performances and may be more relevant when investigating the cognitive performances of nonhuman animals. Binary discriminations involving spatial or colour cues can be presented to subjects and their rates of learning quantified across these different cognitive domains. Although rates of associative learning may differ across domains (Seligman 1970), individual differences in such tasks may still be correlated, leading to a general factor reflecting associative learning ability

(hereafter “*a*”). However, for reliable comparisons, it also remains important to show that subjects’ performances are consistent within domains.

Knowing tasks, by contrast, can be designed to assess the more flexible cognitive processes associated with rule-based learning or generalisation and may be more relevant when assessing cognition in humans. Such tasks require training subjects to a predetermined criterion of success to standardise their understanding of the problem, and then presenting subjects with a single test trial using novel cues. Importantly, performances on *knowing tasks* may highlight whether the mechanism underlying *g* in humans resembles that which may be found in nonhuman animals.

By incorporating both *learning* and *knowing* tasks into cognitive test batteries, we can address whether a general factor of cognitive performance in human and nonhuman animals is better represented by *g* or *a*. Distinguishing *learning* and *knowing* problems, therefore, provides a measure of individual variation in both domain-specific and domain-general abilities that do not just reflect speed of associative learning, and so can be used to assess whether variation in nonhuman cognitive performance reflects a dimension of general intelligence of the same kind as is thought to underlie human variation.

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A pointer’s hypothesis of general intelligence evolved from domain-specific demands

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X. T. (Xiao-Tian) Wang

Psychology Department, University of South Dakota, Vermillion, SD 57069.
xtwang@usd.edu <http://usd-apps.usd.edu/xtwanglab/>

Abstract: A higher-order function may evolve phylogenetically if it is demanded by multiple domain-specific modules. Task-specificity to solve a unique adaptive problem (e.g., foraging or mating) should be distinguished from function-specificity to deal with a common computational demand (e.g., numeracy, verbal communication) required by many tasks. A localized brain function is likely a result of such common computational demand.

The authors of the target article provide an excellent discussion on the evolution of human intelligence, particularly on the formation of secondary modules that are more variable and domain-general. As discussed in section 1 of the target article, general intelligence seems evolutionarily implausible because the mind is populated by a large number of adaptive specializations that are functionally organized to solve evolutionarily typical and recurrent problems of survival and reproduction (see also Cosmides et al. 2010; Wang 1996). To resolve this paradox, the authors propose a model that construes the mind as a mix of truly modular skills (primary modules) and more variable and flexible skills (secondary modules) that are ontogenetically acquired via the guidance of general intelligence (see sect. 1.2.3). In the following, I propose a novel hypothesis to extend this discussion by showing that secondary or higher-order modules can be formed not only ontogenetically, but also phylogenetically as adaptations, evolved from domain-specific modules.

If general intelligence consists of a set of secondary modules, each secondary module may be an evolved programming solution for a function that could be shared by multiple primary modules. These secondary modules of general intelligence can be either ontogenetically constructed or phylogenetically evolved. Imagine that a computer architect was creating a system called *Unix* using the programming language C. At the

beginning, the operating system was written in assembly, where nearly every line would contain memory addresses. Would it be possible to program the system for its input/output devices without repetitively stating these tedious memory addresses? This problem has been solved by creating a pointer variable, whose value specifies the address of a memory location. If a memory address is called upon repeatedly, creating a pointer to store the address would be an effective programming solution. Similarly, if a random number generator is used repeatedly by many local modules, it would be more efficient to make it globally accessible by each of the modules.

Now imagine you are using a computer and have created many folders for different papers. At the beginning, you included a copy of a word processor in each folder. You then realized that all of these papers require a word processor. It would be more efficient if you place a single copy of a generic word processor in a visible place that is accessible by all of the papers. This word processor has then become a general tool for a common requirement of different tasks. Similarly, numeracy, as a component of general intelligence, may be evolved as a result of a common demand by multiple specific adaptations (e.g., counting foraging outcomes; gauging social exchanges, assessing mate values, tracking reciprocal activities, etc.). A general-purpose device would be cognitively economical if it is utilized for multiple tasks. From a design viewpoint, general intelligence comes as a solution for overlapping components of primary modules or for coordinating secondary modules via executive functions (see sect. 1.2.2). From this perspective, task-specificity to solve a unique adaptive problem (e.g., foraging, hunting, or mating) should be distinguished from function-specificity to deal with a common computational demand (e.g., numeracy, verbal communication, etc.)

By the same token, if a particular emotion is a common component of many specific adaptations, this basic emotion would become a general mechanism shared by these adaptations. For instance, anger is the expression of a neurocomputational system that evolved to adaptively regulate behavior in the context of resolving conflicts of interest in favor of the angry individual (Cosmides & Tooby 2013). Anger can be triggered by multiple task-specific adaptations, such as territory defense, mating competition, sibling rivalry, and cheater detection. Once triggered, the anger system would produce one of two outputs: threatening to inflict costs (aggression) or threatening to withdraw expected benefits (Cosmides & Tooby 2013). Similarly, fear is a basic emotion that plays a role in multiple adaptations and has its brain center mainly located in the amygdala. This localized brain function allows the organism to react not only to specific and typical fear-inducing stimuli, but also to learn to react to non-specific stimuli with fear via fear conditioning (e.g., Phelps & LeDoux 2005).

General intelligence and basic emotions may both be solutions for multiple primary modules that demand some common functions. This pointer’s hypothesis of general intelligence challenges a couple assumptions in the research literature of cognitive evolution. As indicated by the authors, many previous accounts of evolution of human intelligence assume that domain-specific modules ought to be cheaper and simpler than domain-general cognitive mechanisms (see sect. 1 for relevant discussion). However, being specific does not necessarily mean that the mechanism is simple or cognitively economical. Because a domain-specific mechanism is designed for solving a specific problem, its design purpose is to do whatever it takes to solve the problem instead of achieving structural simplicity, computational economy, or functional efficiency. Such designs can be either as exquisite as the human visual system or as patchy and lousy as a male’s reproductive system, revised and modified from the Wolffian duct. Thus, these adaptive specializations can either be cheap and simple or costly and complex. Unlike engineering designs, evolutionary designs cannot afford to erase existing blueprints and start from scratch. Evolutionary efficiency is inevitably an efficiency under phylogenetic constraints.

The pointer's hypothesis also challenges the notion that domain-specific mechanisms are more localized in the brain than domain-general mechanisms (see also sect. 1.1 for relevant discussion). However, this notion is at odds with the following two observations. First, a specific adaptation can be implemented by a distributed neural network. Second, a localized brain function is likely a result of a common demand of multiple primary modules. Thus, a more general-purpose mechanism may be implemented by allocating a particular brain region to perform a function shared by multiple primary modules. For instance, a localized motor cortex (e.g., the precentral gyrus) can be used for motor controls in foraging, hunting, gathering, mating competition, and so on. For the same reason, localized brain regions for language processing serve as a general-purpose system for all of the tasks that require information exchange and verbal communication.

When does cultural transmission favour or instead substitute for general intelligence?

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Andrew Whiten

University of St Andrews, Centre for Social Learning and Cognitive Evolution, School of Psychology and Neuroscience, University of St Andrews, St Andrews KY16 9JP, United Kingdom.

aw2@st-andrews.ac.uk www.st-andrews.ac.uk/profile/aw2

Abstract: The cultural intelligence hypothesis is an exciting new development. The hypothesis that it encourages general intelligence is intriguing, but it presents a paradox insofar as social learning is often suggested to instead reduce reliance on individual cognition and exploration. There is thus a need to specify more clearly the contexts in which cultural transmission may select for general intelligence.

Burkart et al. provide a comprehensive and erudite review offering new perspectives on the burgeoning developments in human and nonhuman animal research on intelligence. I particularly welcome the eventual focus on the relatively recently formulated cultural intelligence hypotheses, which I have collaborated in developing (Whiten & van Schaik 2007; and see Whiten [in press] for relationships with the broader, earlier research on social intelligence). However, I have a few comments and puzzlements to share.

The first concerns the authors' conclusion in section 1.2.2 that "natural selection for social learning seems to automatically trigger selection on individual learning and general cognitive ability, suggesting that ontogenetic canalization through social learning may have contributed to enabling the evolution of domain-general cognition" (para. 8). This principle is elaborated further in section 3.3, hypothesising that selection for cultural intelligence offers an explanation for the evolution of greater general intelligence in some species, largely because the rewards consequent on the efficiency of learning from experienced others minimise energetic constraints on encephalization required for greater general intelligence. However, this is an "enabling" explanation rather than one positing positive selection on general intelligence through an emphasis on cultural transmission, and I suggest there is something of a paradox here, or at least a conundrum.

The conundrum is that Burkart et al. propose that cultural learning encourages general intelligence, whereas it is common in the social learning literature to assert, to the contrary, that a core adaptive advantage of this form of learning is that it reduces the costly needs of individual learning. Thus, for example, it appears from the restriction of chimpanzees' nut-cracking to only far West Africa that most chimpanzees have insufficient general intelligence to invent the practice, despite availability of the requisite raw materials (excepting at least one rare innovator, at some stage); however, a suite of experiments has shown that naïve chimpanzees (some from East Africa) can learn the skill following observation of a

nut-cracker (Whiten 2015). This suggests that most wild chimpanzees in the West achieve the skill via observational learning, removing selection pressure on the general intelligence necessary to invent the skill.

If this is the case, it suggests that Burkart et al. have more work to do to specify just exactly what aspects of general intelligence they propose may be selected for in such scenarios. They mention practice in this context, which is certainly protracted in the example of nut-cracking (Whiten 2015). But the practice involved in perfecting nut-cracking learned from others seems rather far from the definition that "general intelligence, as defined in either humans or nonhuman animals, stresses reasoning ability and behavioural flexibility" (sect. 1.1, para. 1). In the human case, the phenomenon of "over-imitation," in which children (apparently unlike other apes) copy others' visibly causally irrelevant actions suggests a marked relinquishing of reasoning and flexibility, commonly interpreted as a correlate of our species' extreme reliance on cultural transmission (Whiten et al. 2009).

Does the authors' emphasis on the potential knock-on effects of cultural intelligence on general intelligence perhaps neglect the direct effects of selection for cultural transmission encouraging other, socio-cognitive enhancements with implications for encephalization? The cultural intelligence hypothesis was originally developed to explain the encephalization and intelligence of the great apes (Whiten & van Schaik 2007), which was not accounted for by broader social intelligence theories that work well for primates in general (Dunbar & Shultz 2007a). Consistent with this, a recent study reported multiple-tradition cultures for gorillas (Robbins et al. 2016) that are consistent with those earlier described for chimpanzees (Whiten et al. 1999) and orangutans (van Schaik et al. 2003) and appear rich compared to the putative cultures of other animals, although a parallel analysis for spider monkeys, in some ways a New World chimpanzee-like niche, reported a quite similar complexity (Santorelli et al. 2011), and studies of capuchin monkeys suggest something similar may await systematic assessment (e.g., Coehlo et al. 2015). Both the latter species are relatively encephalized, and of course the same is true for cetaceans for which a strong evidential case has been made for multiple-tradition cultures including foraging techniques, migration routes, and song (Whitehead & Rendell 2015). The social learning capacities of such animals with heavy dependence on extended cultural repertoires may themselves need to be cognitively sophisticated, including imitative and emulative processes, with neural demands (Whiten 2017; in press). In addition, encephalization may be extended simply to facilitate the storage of a greater cultural repertoire. In the human case, this may be very significant when one contemplates the vast scope of the cultural information we assimilate, from language to all aspects of social and material culture.

The latter leads to a related but different comment. The authors tend to run together two threads in the literature when referring to "the cultural intelligence hypothesis" (sect. 3.3, para. 3), and I think it would reduce potential confusion to separate these. The first thread is exemplified by the writings of Tomasello et al. that are cited, such as Moll and Tomasello (2007). The second thread is exemplified by the writings of van Schaik et al. (e.g., Whiten & van Schaik 2007; van Schaik & Burkart 2011). It is this second thread that sets out a cultural intelligence hypothesis addressed originally to the problem of great ape intelligence and encephalization, but in principle relevant to any relevant animal species. By contrast, the first thread was specifically concerned with what makes humans different from all other animals, and was originally and appropriately dubbed "the Vygotskian intelligence hypothesis" (Moll & Tomasello 2007, p. 639). This made sense to me, until Herrmann et al. (2007) then referred to these ideas as "the cultural intelligence hypothesis" (p. 1360). This was potentially quite confusing insofar as the argument was that it did not apply to nonhuman species. I feel it is important to recognise these differences, whether that is achieved by reverting to the "Vygotskian" tag to distinguish the "human" focused

version. This is not, of course, to deny that there is a potentially important linkage between the sets of ideas embedded in these two theories.

General intelligence is a source of individual differences between species: Solving an anomaly

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Michael A. Woodley of Menie,^{a,b,1} Heitor B. F. Fernandes,^{c,1} Jan te Nijenhuis,^d Mateo Peñaherrera-Aguirre,^e and Aurelio José Figueredo^c

^aScientist in Residence, Technische Universität Chemnitz, 09111 Chemnitz, Germany; ^bCenter Leo Apostel for Interdisciplinary Studies, Vrije Universiteit Brussel, Brussels 1050, Belgium; ^cDepartment of Psychology, University of Arizona, Tucson, AZ 85721; ^dDepartment of Work and Organizational Psychology, University of Amsterdam, 1000 GG Amsterdam, The Netherlands; ^eDepartment of Psychology, University of New Brunswick, Fredericton, NB E3B 5A3, Canada.

Michael.Woodley@vub.ac.be hbf Fernandes@gmail.com
 nijen631@planet.nl Mateo.PA@unb.ca ajf@u.arizona.edu

Abstract: Burkart et al. present a paradox – general factors of intelligence exist among individual differences (*g*) in performance in several species, and also at the aggregate level (*G*); however, there is ambiguous evidence for the existence of *g* when analyzing data using a mixed approach, that is, when comparing individuals of different species using the same cognitive ability battery. Here, we present an empirical solution to this paradox.

As Burkart et al. note in the target article, it is possible that the *g* factors that exist within species at the level of individual differences have somewhat different factorial characteristics for each species. For instance, certain cognitive elements that combine to give rise to *g* in chimpanzees may fall outside of the positive manifold in other species (e.g., humans). In other words, performance in certain abilities may be driven by *g* in some species but not in others. Lack of *measurement invariance* (i.e., discordance between species in terms of which cognitive abilities give rise to *g*) renders single batteries unable to identify a *g* factor

common to individuals of different species (i.e., the mixed approach). One cause of these compositional differences may be the different ways in which ancestral selection pressures shaped the *g* factors across different species. Some species may have highly integrated abilities, dominated by a strong *g* factor, whereas others might have highly specialized and largely independent abilities, where the positive manifold of correlations underlying *g* is weaker.

Another potentially significant cause of the failure of measurement invariance across individuals of different species may be *floor* or *ceiling* effects upon performance. For example, a cognitive task that may be hard for one species may be trivially easy for another, more intelligent species. The latter condition is characterized by all or most individuals performing maximally well, revealing a ceiling effect. Hence, the *g* loading of the success rate at solving this task may be high for the less intelligent species, but will be low for the more intelligent one – this species having hit the test ceiling.

Operationally, both (1) species-specific specialization or modularization of cognitive abilities and (2) floor/ceiling effects can be identified empirically based on within-species statistical distributions in performance. The two conditions are likely to share a common observable feature: that is, low within-species variability in certain tasks. Highly specialized abilities are proposed to be species-typical and monomorphic, with little to no interindividual variation (Tooby & Cosmides 1990). Consistent with this, human and nonhuman primate data indicate that cognitive functions that are more specialized (and thus less *g*-loaded) exhibit lower phenotypic and genetic variability (Spitz 1988; Woodley of Menie et al. 2015). The presence of ceiling or floor effects in measurement when testing abilities in a given species also, by definition, limits variation. These alternative scenarios are therefore connected, as any apparent floor or ceiling effect in the performance of modularized abilities may not be due to a poor measurement approach but, rather, due to adaptive species-typical modularization.

We propose that the mixed design would support the presence of a *g* factor inclusive of individuals of different species if species differences in cognitive ability are larger on tasks that share more variance with others (larger part-whole correlations, representing *g*-loadings) but not if species differences are uniform across tasks. Here, we use combined data from two sources (Herrmann et al.

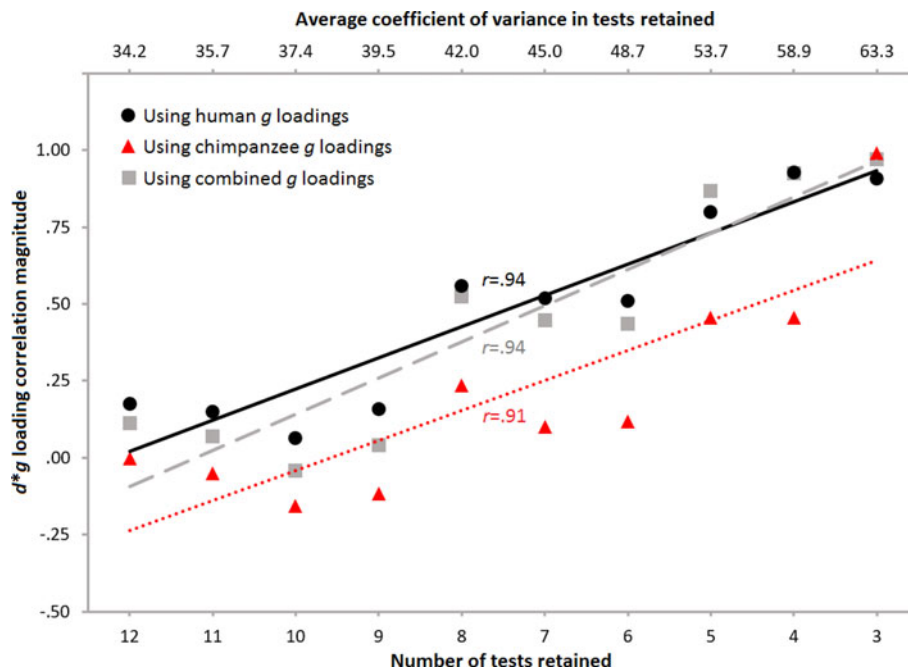


Figure 1 (Woodley of Menie et al.). Increasing magnitude of the vector correlations between task *g* loadings and the difference scores (*d*) between human children and chimpanzee performance, as a function of the average coefficient of variance of the tests kept in analyses.

2010b; Woodley of Menie et al. 2015) on the Primate Cognitive Test Battery (PCTB; Herrmann et al. 2007) performance in human children and chimpanzees to test this hypothesis and examine the importance of the confounding role of tasks on which individuals of at least one of the two species exhibit limited variability in scores.

Human children outperform chimpanzees to a greater degree on more *g*-loaded PCTB tasks – this can be demonstrated by correlating the vector of task *g* loadings with the vector of the between-species differences in performance (*d*) on those same tasks. To examine whether the true strength of this relationship was masked by the inclusion of tasks that yielded little within-species variation, we eliminated tasks from the analyses sequentially, starting with those that yielded the smallest coefficients of variance (CV) in human performance. The relationship between *g* loadings and the size of human-chimpanzee differences was thus examined in multiple stages, with each successive step having a more stringent cutoff for CV. Recall that the ceiling effects are a feature of the ease with which humans can execute certain basic cognitive tasks, suggesting that these abilities are modularized in human populations. CV was in fact smaller among humans on all tasks, suggesting that they solved all tasks more easily than chimpanzees.

Figure 1 shows that the g^*d vector correlation magnitude increased inversely to the number of tasks retained, with smaller numbers of tasks exhibiting larger variation among the human participants yielding bigger vector correlations. The vector correlation magnitude approached unity when only the three tests with the highest human CV values were used. The association was indifferent to the use of different *g* loadings (human, chimpanzee, and averaged) as the basis for computing the g^*d vector correlations (the correlations between the vector correlation magnitudes and average CV across tasks ranged from .91 to .94, $p < .05$).

Furthermore, as expected, tasks yielding smaller CV values were also less *g*-loaded in humans ($r = .52$; one-tailed $p < .05$), which replicates prior findings involving chimpanzees (Woodley of Menie et al. 2015).

This approach is currently being applied by our group to comparisons involving a larger number of species. The implication of our finding is that differences between individuals of different species may be consistently concentrated on *g* – this being especially apparent when focusing on experimental tasks whose design permits sufficient within-species variation. This finding furthermore indicates that the patterning of species differences in the *g* and *G* factors are concordant, meaning that they are likely one and the same, reinforcing the arguments put forward by Burkart et al.

NOTE

1. The two first authors contributed equally to this commentary.

Authors' Response

Future directions for studying the evolution of general intelligence

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Judith M. Burkart, Michèle N. Schubiger, and
Carel P. van Schaik

Department of Anthropology, University of Zurich, CH-8125 Zurich, Switzerland
Judith.Burkart@aim.uzh.ch

<http://www.aim.uzh.ch/de/Members/seniorlecturers/judithburkart.html>

michele.schubiger@aim.uzh.ch

<http://www.aim.uzh.ch/de/Members/phdstudents/micheleschubiger.html>

vschaik@aim.uzh.ch

<http://www.aim.uzh.ch/de/Members/profofinstitute/vanschaik.html>

Abstract: The goal of our target article was to lay out current evidence relevant to the question of whether general intelligence can be found in nonhuman animals in order to better understand its evolution in humans. The topic is a controversial one, as evident from the broad range of partly incompatible comments it has elicited. The main goal of our response is to translate these issues into testable empirical predictions, which together can provide the basis for a broad research agenda.

R1. Introduction

We are grateful to the commentators for raising a wide variety of issues. Because these generally fall into a number of distinct categories, we organized our response around them, as follows:

Section R2: Domains of cognition

Section R3: Tasks for test batteries

Section R4: Domain-specificity versus domain-generality

Section R5: What is *g/G*? (More) on the necessity of validation

Section R6: *g/G* and brain size

Section R7: *g* and biological fitness

Section R8: Cultural intelligence

Whenever commentators provided input in more than one of these categories, we discuss them in more than one of the sections. Some of the commentaries show that we did not always present our points with sufficient clarity, so we also take the opportunity to make these clarifications as well as to highlight what we did *not* claim.

The complicated nature of the issues is illustrated by the fact that different commentators made confident claims that are mutually incompatible. For instance, **Ramus** and **Arden & Zietsch** argue that the evolution of *g* is no puzzle at all, and that it is most likely present in all organisms with a nervous system, **Jacobs & Gärdenfors** similarly argue that it is hardly surprising or controversial that some individuals consistently perform well, and **Pepperberg** recites the impressive examples from bird cognition that to her necessarily imply the presence of general intelligence in at least some birds. On the other hand, other commentators question whether there is evidence for *g* or *G* in any nonhuman species at all (**Huber**) or feel the importance of *g* is overestimated (**Amici, Call, & Aureli [Amici et al.]**).

The goal of our target article was to make progress on understanding animal intelligence without getting bogged down in terminological debates on what exactly *g* represents. We suggested complementing the psychometric approaches, which are a necessary first step to establish the possibility of general intelligence, with a variety of validation measures and more demanding tests that look for domain-generality of cognitive processes. This is even more important because animal studies are unlikely to ever reach the sophistication in terms of tests and the sample sizes needed to attain the practical level of utility achieved by human intelligence testing (pace **Arden & Zietsch**). We will focus, therefore, especially on these forward-looking points.

R2. Domains of cognition

One of the unresolved issues in nonhuman psychometrics is what an ideal test battery should look like. The criteria are

obvious: (1) A test battery should be composed of tasks from a broad range of domains rather than tasks that re-sample performance in the same domain, and (2) the tasks should reliably assess the cognitive abilities they are supposed to assess, both within and across species.

To fulfill criterion (1), it is crucial to know what a domain is. In the classical psychometric tradition, a domain of mental ability refers to a statistically derived group factor on which a set of tasks show strong loadings. For instance, Deary et al. (2010) referred for humans to the group factors processing speed, memory, spatial ability, reasoning, and vocabulary. Thus, the straightforward approach to identify domains in nonhuman animals is to likewise use large batteries of tasks and identify the factor structure statistically. This bottom-up, data-driven approach in animals is ambitious because it requires very large sample sizes. However, this does not mean that, in the meantime, we are unable to correctly identify g in animals. Empirical tests with human subjects have revealed that as long as there is sufficient variety in the tasks of test batteries, g factors derived from different test batteries are almost perfectly correlated (Johnson et al. 2008).

Evolutionary approaches often consider domains to be functional contexts (see also Wang). These can be very specific such as finding food, finding mates, deterring predators, outwitting conspecifics, or cooperating with others (Figure R1), or rather broad, such as in the classic trichotomy in physical, spatial, and social cognition, as followed by Tomasello & Call (1997). Obviously, the individual may fail to show a particular ability that it is shown to possess in one context, when tested in a functional context different from the one for which it evolved. Thus, it remains challenging to identify domains.

Importantly, it is not useful to decide a priori that one notion of domain would be more correct than the other one. Rather, acknowledging that a domain can refer to both a mental ability (as in the psychometric tradition) and a functional context (as in evolutionary approaches; see also the proposal by Shuker, Barrett, Dickins, Scott-Phillips, & Barton [Shuker et al.] or Hauser's

examples of abilities that “cut across domains”) allows us to ask the questions that are at the core for understanding the evolution of general intelligence: Under what circumstances can a species that evolves a cognitive ability for a specific context generalize this ability to other contexts as well (cf. Stevens et al. 2016)? Can this be true for some abilities, but not others? And are these the same species that also show correlated performance across mental abilities and thus show psychometric g ?

Thus, rather than committing to one specific notion of a domain, it is better to identify ways to combine these perspectives to ultimately better understand the evolution of intelligence. Furthermore, this combined perspective will also clarify many of the issues surrounding domain-specificity and domain-generality, and modularity (sect. R4).

Due to the sample size problems in identifying domains using the psychometric approach, some have defined domains a priori (e.g., Herrmann et al. 2007). However, as we point out in the target article, empirical data do not necessarily confirm that tasks supposed to tap into one such domain actually also cluster around it (see sect. 2.4.1 in target article). Although we agree in principle with the proposal of Amici et al. that it is important to take multifactorial approaches into account (see also Lee & Chabris), we think more empirical work is needed to identify which tasks indeed measure particular cognitive operations (such as inference) or mental capacities (such as working memory). In fact, most tasks probably tap into more than one operation and/or capacity, and it therefore is highly unlikely that one specific test measures one specific cognitive ability, as also pointed out by Huber and Ramus. Even for humans there is often a lack of agreement on how to quantify specific cognitive constructs such as, for instance, working memory (Oberauer et al. 2005).

Finally, Figure R1 also helps us to answer how ecologically valid a test should be. An often-made claim is that in order to fully appreciate a given species' cognitive potential, one should look only at problems of high ecological relevance to this species (e.g., Sternberg). However, when

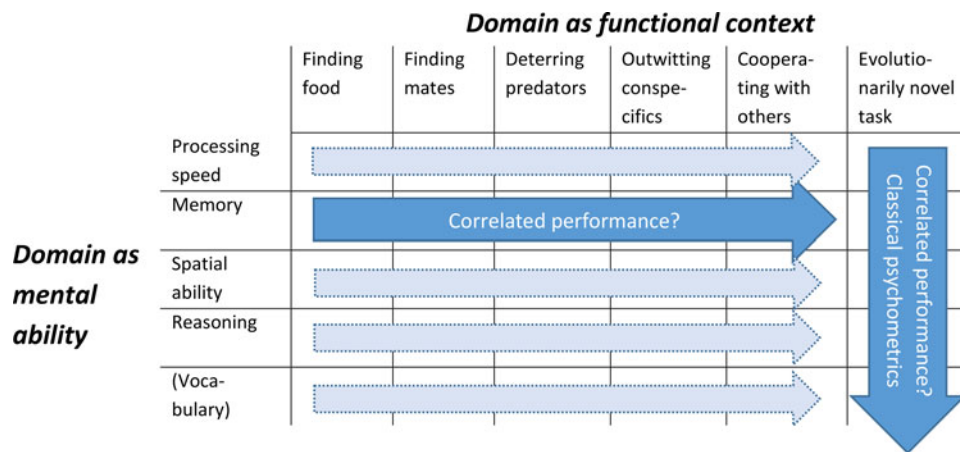


Figure R1. Domains can refer to statistically derived group factors such as processing speed, memory, spatial ability, reasoning, or vocabulary in humans (Deary et al., 2010) or to evolutionarily functional contexts. Classical psychometric studies (vertical arrow), in humans and nonhuman animals, typically refer to domain as mental ability. From an evolutionary perspective, however, it is equally informative to ask to what extent a given cognitive ability is correlated across functional contexts (horizontal arrows). Because performance across functional contexts is likely to vary, evolutionarily novel tasks are most suitable for classical psychometric studies that aim at testing individuals across mental ability domains.

we look only at ecologically relevant problems we will never be able to disentangle whether we are dealing with a primary module or with the result of true and flexible problem-solving ability. As indicated in [Figure R1](#), there are at least two ways to demonstrate this kind of flexibility. A psychometric approach would compare different abilities in evolutionarily novel tasks, precisely in order to avoid tapping into predominantly hard-wired solutions to recurring adaptive problems. This approach is particularly powerful in combination with validation studies (sect. R5). The other one is to compare the same ability across functional domains (e.g., asking whether the excellent memory abilities in the ecologically relevant context of caching in food-caching birds also generalize to other functional contexts). Although this second possibility has received surprisingly little attention (but see [Stevens et al. 2016](#)), it presents an excellent opportunity to externally validate a psychometrically derived g factor (see also [Locurto](#), sect. 2.5 in target article, and sect. R4).

R3. Tasks for test batteries

Many commentators have proposed specific tasks, and we think these are excellent proposals that will help construct broad and diverse test batteries. [Van Horik & Lea](#) stress the necessity to also include what they call *knowing tasks*, which can assess rule-based learning or generalization. Such knowing tasks, as for instance reversal learning, also have an additional advantage, linked to criterion 2 of a good test battery: that the tasks should reliably assess the cognitive abilities they are supposed to assess, both within and across species (sect. R2). The advantage is that knowing tasks are less vulnerable to producing variation in performance due to differences in sensory-motor specializations between species (see [Shuker et al.](#), and sect. 2.4.2 in the target article for a detailed discussion of Macphail's critique of species comparisons). We are confident that many of these issues can be resolved, particularly in closely related species, but also agree that it remains problematic for comparisons of very diverse species, such as cephalopods, with completely different sensory-motor traits and even body plans ([Holekamp & Miikkulainen](#)).

Commentators [Jacobs & Gärdenfors](#) highlight causal cognition tasks; [Huber](#), reasoning by exclusion; and [Buskell & Halina](#), tasks suggestive of de-coupled representations. Tasks in which birds excel may also be useful additions to existing test batteries. As stressed by [Pepperberg](#), corvids and parrots are particularly prime candidates for exhibiting high levels of general intelligence, and we look forward to future empirical studies that explicitly address this question with psychometric test batteries combined with predictive validation studies ([Locurto](#); see also sect. R5). [Pennycook & Rand](#) add the possibility to include studies of cognitive control and metacognition.

Commentators [Pennycook & Rand](#) also argue that variation in performance between individuals may not only reflect cognitive capacity per se, but also the willingness to engage in effortful cognitive processing when a simpler, more routine solution seems available. They thus refer to the concept of *need for cognition*, which is an individual predisposition rather than a cognitive ability, even though in humans it is correlated with general intelligence ([Hill et al. 2016b](#)). This link is entirely consistent with our

view that cognitive skills emanating from general cognitive capacity (i.e., the downward pathway in [Figure 3](#) of the target article) are ontogenetically constructed. Therefore, individuals with higher levels of need for cognition will more systematically expose themselves to situations that require effortful processing and are, therefore, more likely to establish a larger and more powerful set of cognitive skills. To what extent substantial variation in willingness to engage in effortful processing is also available in nonhuman animals remains to be established, but an increasing body of research suggests that this may account for the systematic differences in cognitive performance between captive and wild primates such as orangutans ([van Schaik et al. 2016](#)).

R4. Domain-specificity versus domain-generality

Several commentators ([Arden & Zietsch](#); [Hauser](#); [Jacobs & Gärdenfors](#); [Martins & Di Paolo](#)) think we advocate a strict dichotomy between a mind made up of modules and one that has general intelligence. This is surprising, because in the target article, we devote an entire section (1.2.2 including [Table 1](#)) to exactly why such a dichotomy is not helpful for the debate, and in [Figure 3](#) we present what we believe is the most promising working model given the current state of evidence on g/G in human and nonhuman animals. This working model suggests that the actual skill set of an individual can be construed as a mix of primary or secondary modules. Whereas both can be sensitive to experience (as detailed in [Table 2](#) in the target article and unlike the claim by [Lewis, Al-Shawaf, & Anderson \[Lewis et al.\]](#)), this sensitivity differs: Primary modules are experience-expectant; secondary modules, experience-dependent.

The extent of domain-specificity and domain-generality obviously critically depends on the notion of domain one adopts (see sect. R2). This distinction between domain as mental ability or as functional context, as detailed in [Figure R1](#), is also reflected in the many different notions of modularity that have been the focus in the modularity debate ever since Fodor. Proposals range from defining modules as adaptive behavioral functions localized in delimited neural areas to seeing them as being nothing else than components and processes into which a phenotype can be decomposed ([Barrett 2015](#)). When referring to domain specificity, we focus on functional specialization in the biological, ultimate sense (as used, for instance, in the commentary by [Amici et al.](#)), rather than referring to any other specific notion of domain-specificity ([Lewis et al.](#)). This allows us to ask under which conditions a cognitive adaptation to a specific problem, – for instance, the impressive memory of food-caching birds – can also be used in a different context. From comparative studies, we know that cognitive abilities in nonhuman animals sometimes do generalize to other domains, sometimes do so partially, and sometimes do not at all ([Cauchoix & Chaîne 2016](#); [Stevens et al. 2016](#)). When cognitive abilities do generalize, domain-general cognition emerges, and the fundamental question we are interested in is under what conditions this can happen.

If it is not straightforward to define domain-specificity or modularity, this is even truer for domain-generality in cognition or general intelligence. Not unexpectedly, several

authors have commented on this. **Sternberg** suggests that “an appropriate way to look at the intelligence of any organism is to look at how well it adapts to the range of environments it confronts” (see also **Bar-Hen-Schweiger, Schweiger, & Henik** [Bar-Hen-Schweiger et al.]). This is problematic because intelligence is only one way among many to adapt to the environment. Under this conception, the thickening of the fur in autumn clearly is an adaptation to the environment but most would agree it has nothing to do with intelligence. For the same reason, it is problematic to refer to domain-general ability as phenotypic plasticity (**Buskell & Halina**) because it is merely one aspect of that. Equally unhelpful is the proposal by **Sternberg** to look at skills that are relevant to an animal’s everyday adaptation. If we go back to our food-caching birds and assess only their memory capacities in the context of food caching, we are simply not able to exclude the possibility that we are dealing with a highly domain-specific capacity.

It is this latter issue that makes psychometric *g* studies so appealing to comparative psychologists. As highlighted in the target article (sect. 2.4 and sect. 2.5) and by several commentators, this approach comes with a whole suite of issues, addressed here in sections R5, R6, and R7. However, at least in humans, *g* is well established, known to reflect general intelligence as broadly defined in the target article (following **Gottfredson 1997** and **Nisbett et al. 2012**), has a variety of genetic correlates, including those linked to neurobiological features, and is a good predictor for various measures of life outcome and thus shows high levels of predictive validity. In nonhumans, more validation is critically required, as also emphasized by **Locurto**.

R5. What is *g*/*G*? (More) on the necessity of validation

A common concern not only to many commentators, but also to ourselves (see sect. 2.5 in the target article), is that once one has statistically established a reliable *g* factor in a given species, based on adequate tasks from a broad range of domains, it does not necessarily follow that this corresponds to general intelligence as broadly defined and predictive for a variety of life outcome measures, as is the case in humans. Furthermore, even for humans, despite the predictive validity of *g*, it does not necessarily follow that the predominant hierarchical CHC model (see para. 1.1.1 in the target article) is the only compelling interpretation. Some suggest that a statistical *g* simply results from variation in non-cognitive factors, such as developmental stability, and thus reflects general health (**Lewis et al.**), or genetic load or heterozygosity (**Arslan, von Borell, Ostner, & Penke** [Arslan et al.]). Several commentators discuss plausible alternative models to the hierarchical CHC model. Thus, the process overlap theory of **Kovacs & Conway** (see also **Kovacs & Conway 2016**) and the responses in the same issue of *Psychological Inquiry* argue that performance in a specific task is determined by several cognitive abilities, and different tasks resample the same abilities to different extents. The mutualism model of **van der Maas et al. (2006)** (see **Ramus; Shuker et al.**) argues that *g* arises because of mutual interactions during cognitive development. These alternatives thus see *g* as a composite of independent but overlapping

or interacting processes, rather than as a single top-down ability (which **Bar-Hen-Schweiger et al.** see as the ability to engage in mental manipulation). Hence, they regard *g* more as a developmental consequence or emergent property, rather than as an underlying latent variable, and are fully compatible with the constructive nature of domain-general cognition.

Nonetheless, these varying interpretations still argue for the presence of some domain-general ability, even if it is entirely emergent, and remain compatible with the various neurobiological and genetic correlates of *g*. For instance, if *g* arises as a result of process overlap because cognitive tests from different domains tap the same domain-general executive processes such as working memory, this would exactly correspond to domain-general ability as identified by the horizontal arrow in **Figure R1**.

The exact nature of *g* continues to be a major puzzle (**Deary et al. 2016**). But we would argue that this puzzle doesn’t have to be fully solved for studies of domain-general processes to be useful, provided *g* in nonhuman animals survives future tests of external validation, as we discuss next. Some argue that emergent properties or statistical constructs cannot be meaningful individual-level variables subject to natural selection (**Arden & Zietsch; Ramus**). We do not think this is correct, because even if *g* is an emergent property of several cognitive and even non-cognitive processes, natural selection should evaluate the degree to which these processes are compatible or even how they synergize to produce organized and appropriate behavior. Indeed, each of the models for *g* discussed previously is compatible with natural selection having honed *g*. Hence, considering *g* a measurable property of an organism is not reification.

These ambiguities in the interpretation of *g* necessarily spill over into interpretations of animal studies, especially in light of the weaknesses of intraspecific studies, as highlighted by **Arden & Zietsch, Lee & Chabris**, and **Lewis et al.** Nonetheless, as we have argued in section 2.4 of the target article, the fact that all purely interspecific studies produce clear evidence for *G* is incompatible with the notion of *g* as an artifact of testing the same basic ability or of inadequate test batteries. One can, of course, criticize the use of the rate of naturally occurring behaviors as applied in some *G* studies (e.g., **Huber; Shuker et al.** See also **Reader et al. [2011]** for a discussion of the advantages and disadvantages of this procedure). However, if this method would only produce noise, one would not find strong correlations with brain size or aspects of executive functions, or that *G* is the principal locus of selection in the macroevolution of primate intelligence (**Fernandes et al. 2014**). Moreover, the anomaly of the lack of success of the mixed intraspecific and interspecific studies to generate a common main factor has been solved by **Woodley of Menie, Fernandes, te Nijenhuis, Aguirre, & Figueredo**. They suggested that variables with floor or ceiling effects may obscure differences in general intelligence across species because they cannot load on *g*. Their analysis supports this idea because species differences are especially striking for tests that load highly on *g*. Overall, then, the increasing plausibility of the idea that *g* and *G* can be equated automatically supports the argument that animals have something that closely resembles human *g*, and may even be homologous to it. This position would also be consistent with the increasing knowledge of the nature of

cortical development and especially plastic responses to external inputs during brain development (Anderson & Finlay 2014). It also should serve to refute the alternative interpretations of G as totally unrelated to g , offered by **Arden & Zietsch** and **Lewis et al.**

In order to resolve current debates, we believe empirical work is needed that confirms the presence of domain-general processes. First, if g were all about health, myelination, or developmental stability – that is, non-cognitive features – we would expect a correlation between all cognitive abilities, regardless of whether they derive from primary or secondary modules. But if we were dealing with general intelligence, the pairwise correlations between abilities deriving from primary modules should be weaker (largely because they should all be at ceiling or floor values).

Second, more specific tests can be done to provide external validation for the interpretation of domain-general intelligence, along the lines outlined in the target article (sect. 2.5, Table 7) and as also stressed by **Locurto**. We can derive additional ones from the commentators' comments. **Arslan et al.** propose to use genetically uniform strains and mutation accumulation lines to help clarify the role of genetic load, and **Lee & Chabris** propose to use genome-wide association studies to test if distinct cognitive abilities are genetically correlated and thus potentially the target of natural selection. More specifically, **Pennycook & Rand** suggest to focus on meta-cognitive abilities; **van Horik & Lea** stress the usefulness of reversal learning paradigms; and **Jacobs & Gärdenfors**, causal reasoning. **Pepperberg** summarizes additional fruitful paradigms in which several bird species excel. **Bar-Hen-Schweiger et al.** propose to also include object manipulation. This is intriguing because recent results show that object manipulation complexity is indeed correlated with brain size (Heldstab et al. 2016), but to what extent mental manipulation can be seen as a direct extension of object manipulation requires additional research, in particular in nonhuman animals. For interspecific studies, species differences in basal ganglia-based circuitry may provide further insight into the evolution of G , as highlighted by **Nordli & Todd**.

In sum, we acknowledge and agree that the mere presence of a first PCA factor (g) in intraspecific psychometric studies is not sufficient evidence for general intelligence, but that such an interpretation critically requires evidence for predictive or criterion-related validity as stressed by **Locurto** and outlined in section 2.5 in the target article. However, we also argue that if a g factor becomes manifest in psychometric studies, and if this g is not an artifact and shows predictive and criterion-related validity, how exactly the positive intercorrelations arise no longer matters for the claim that g was the target of selection. In other words, it may well be that g is an emergent property of the central neural system, and we in fact think it is unlikely that it can be reduced to any specific psychological or biological trait or construct, and thus agree on this with **Ramus** or **Arden & Zietsch**. But this does not imply that g as potentially emergent property cannot be the target of selection. This view is supported by the majority of results from interspecific G studies.

R6. g/G and brain size

Brain size is reliably associated with G in interspecific primate studies, and less strongly with g in intraspecific

studies. **Matzel & Sauce** argue that brain size cannot be important in intelligence. First, they argue that Neanderthals had larger brains than humans, but were “cognitively inferior” to modern humans. However, cultural intelligence can explain this difference because modern humans had much larger groups (Mellars & French 2011), and social inputs play a crucial role in affecting the size of a population's skill repertoires (see also Henrich 2016). Thus, differences in brain size (provided they also extended to differences in relative brain size) can be compensated for by differences in the quality and quantity of inputs during development. This observation also deals with their second objection, namely that brain size predicts only a modest proportion of variation in human g .

The second argument by **Matzel & Sauce** as to why brain size should not matter for intelligence was that intelligence can look quite similar in lineages with very different absolute or relative brain sizes, particularly in birds versus mammals. This can partly be explained by major between-lineage differences in neuron densities, between cetaceans and other mammals, and between mammals and birds (Olkowicz et al. 2016). Accordingly, comparative studies on relative brain size within birds are consistent with the presence of general intelligence in this lineage (Lefebvre et al. 2004). Nonetheless, it would be useful to examine the degree to which more extensive tests of general intelligence in birds (e.g., Isden et al. 2013; Shaw et al. 2015) show the same structure of cognition as in humans and presumably other mammals. If multiple independent origins can indeed be demonstrated, as suggested by **Matzel & Sauce**, this would support the contention that beyond a certain level of complexity, domain-general processes evolve to take over the control of procedures that serve a useful function in many different domains (**Wang**).

R7. g and biological fitness

If general intelligence is an adaptation, then we expect some link to fitness. Thus, one intuitive way of assessing predictive validity of g is to ask if individuals scoring higher on g have better survival and higher reproductive success. This basic idea is compelling, but both empirical and conceptual caveats need to be carefully considered.

In humans, reproductive success is often no longer maximized in modern societies due to the demographic transition (Coale 1989). Survival, however, continues to be a high individual priority and, therefore, is a better measure for this link in humans. There is in fact extensive evidence that g scores predict survival or longevity (Deary 2008).

If general intelligence is an adaptation in nonhuman species, too, then the estimates of this ability should also correlate with fitness measures. This correlation has in fact been proposed as a test of the predictive validity of the concept (**Locurto**). Tests in the wild presuppose that we can actually estimate general intelligence in wild animals. This may be feasible in birds (Isden et al. 2013; Shaw et al. 2015), but will be extremely difficult in many other species that show strong neophobia in the wild (Forss et al. 2015). Moreover, as stressed by **van Horik & Lea**, it is more difficult to control for confounds or selective participation, or to retest the same individuals (see also Rowe & Healy 2014).

Yet, we must also be careful for conceptual reasons. General intelligence is developmentally constructed, and investment in increased intelligence may trade off against other vital activities. It is, therefore, quite conceivable that estimates of general intelligence need not show a positive relationship with fitness but, rather, an inverted U-shaped relationship. Thus, if investment in general intelligence and the brain requires resources that also positively affect other vital processes such as growth and reproduction, this can have a negative impact on an individual's fitness. The positive relationship in modern humans may thus be something of an anomaly, perhaps linked to the absence of such tradeoffs (although it could well be that it existed for reproduction). Indeed, the emerging work examining the link between cognitive abilities and fitness (Morand-Ferron & Quinn 2015) produces mixed results. One reason for this may be that a direct positive relationship with fitness is expected for primary modules, but not for secondary modules. This topic is worth exploring in greater depth if practical obstacles can be overcome (see also Morand-Ferron et al. 2015; Rowe & Healy 2014).

R8. Cultural intelligence

The presence of high general intelligence in animals poses something of a conundrum. Individual problem solving based purely on general cognitive ability will only rarely produce useful behavioral innovations, but will often also carry risks of injury or poisoning. Moreover, rarely invented innovations are not transmitted to the next generation; only the ability to make such inventions is. The cultural intelligence hypothesis, therefore, suggests that general intelligence is most likely to evolve where the process of problem solving is socially canalized—that is, in species that strongly rely on social learning, because social canalization increases the odds of actually finding a solution. It stresses that social information can efficiently guide exploration during development. It is, therefore, as **Whiten** correctly points out, an enabling hypothesis, which concerns the acquisition process of cognitive skills (and the conditions selecting for them), but is silent on the actual nature of the cognitive benefits. The latter could often be cognitive flexibility serving as a cognitive buffer, allowing animals to survive in seasonal habitats, as suggested by **Holekamp & Miikkulainen** (cf. van Woerden et al. 2012). However, this functional benefit should have been favored in many species, and the cultural intelligence hypothesis argues that selection is more likely to produce this adaptive benefit for behavioral flexibility where costs remain low due to many opportunities to acquire social information.

Cognition requires brains, and brains are energetically expensive. Thus, the significant increase in energy need accompanying increased brain size must be met, directly or indirectly. As shown in **Figure R2**, natural selection would, therefore, favor those mechanisms that either provide a direct energy boost (for instance, ecological effects of cognition leading to reduced fluctuations in food intake: arrow 1) or allow for reduced allocation to growth and reproduction due to improved survival (arrow 2). The far greater efficiency provided by skill acquisition through social learning rather than inefficient and risky innovation (arrow 3) is another selective benefit highlighted

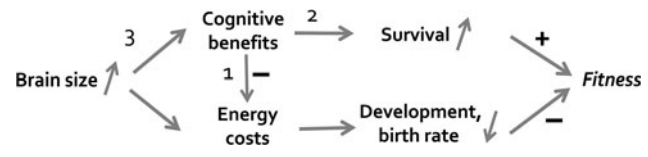


Figure R2. Processes that could be affected by selection for increased brain size: (1) an immediate effect of improved cognition on reduction in energy costs; (2) an unusually large fitness benefit from possessing cognitive skills; or (3) an unusually efficient translation of brain tissue into cognitive skills, as argued by the cultural intelligence hypothesis. The argument may hold especially for domain-general processes, because the latter appear to require exceptional amounts of brain tissue.

by the cultural intelligence hypothesis. This argument clearly implies, although we did not point this out explicitly, that the cultural intelligence hypothesis is, like almost all evolutionary hypotheses, a *ceteris paribus* hypothesis: Holding all other conditions constant, the availability of social information should make it easier to evolve the supporting infrastructure for increased behavioral flexibility in a particular lineage.

There may also be other conditions favoring the evolution of intelligence. Cephalopods, especially octopus, have no contact between generations, and mustelids disperse at a very young age and then remain solitary, yet show signs of strong cognitive performance (**Holekamp & Miikkulainen**; cf. Holekamp et al. 2015). In the expensive brain framework, this would suggest unusual payoffs from exploration and innovation (arrow 2 in **Figure R2**), or unusually low risks of exploration—which are testable predictions. These seemingly intelligent solitary species, therefore, would appear to be exceptions to the cultural intelligence hypothesis that should be acknowledged, although the impressive imitation ability of solitary octopus (Fiorito & Scotto 1992) is puzzling. The possibility of alternative evolutionary pathways to intelligence makes it even more important to explicitly deploy extensive test batteries to examine if these species truly show evidence of general intelligence, or whether we find specialized (albeit quite impressive) domain-specific cognitive adaptations.

R9. Conclusions

Our goal is to understand the evolutionary origin of general intelligence. The case is still open, even though the body of evidence suggests we also find it in other species and that the cultural intelligence approach can help us understand why it arose in some species but not in others. But identifying the evolutionary origin of *g* or *G* in nonhumans is not the full answer to how the human mind evolved. Humans are more than *g* (**Amici et al.**; **Gardner**; **Pennycook & Rand**) and other components are important too, first and foremost language, but also components summarized as multiple intelligences by **Gardner**. In principle, the same approach as taken here can be applied to each of these components, by asking what the interspecific distribution of this trait is, and what factors may best explain this distribution. For general intelligence, the most likely factor is brain size, whereas for prosocial attitude, allomaternal care seems to explain interspecific distribution (Burkart et al. 2014).

Cultural intelligence effects are particularly pronounced in humans. Among others, this is evident in the Flynn effect, and the strong influence of environment on general intelligence, particularly early in ontogeny when individuals still cannot seek out an environment that matches their abilities (Flynn 2016). Human cultural intelligence is supported by additional adaptations such as language and pedagogy, which involves strong theory-of-mind abilities and intentional teaching as pointed out by **Estes & Bartsch** (see also Burkart et al. 2009). For humans in particular, one would expect, therefore, that socio-cognitive abilities predict general intelligence, and **Fernández-Berrocal, Cabello, & Gutiérrez-Cobo** present evidence for humans supporting this prediction (for interspecific tests of this link, **Arslan et al.** suggest joint phylogenetic tree analyses of sociality and variance explained by g , but this will not work because the amount of variance explained is not a good measure for how much “ g ” a given species “has,” as detailed in the target article (sect. 2.4.1)).

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[The letters “a” and “r” before author’s initials stand for target article and response references, respectively]

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