

[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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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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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,