



## Discussion

Possible evidence for the *Law of General Intelligence* in honeybees (*Apis mellifera*)Mateo Peñaherrera-Aguirre<sup>a,\*</sup>, Matthew A. Sarraf<sup>b</sup>, Michael A. Woodley of Menie<sup>c</sup>, Aurelio Jose Figueredo<sup>d</sup><sup>a</sup> University of Arizona, School of Animal and Comparative Biomedical Sciences, Tucson, AZ, USA<sup>b</sup> Independent Researcher, Boston, MA, USA<sup>c</sup> Independent Researcher, London, UK<sup>d</sup> University of Arizona, Department of Psychology, Tucson, AZ, USA

## ARTICLE INFO

## Keywords

General cognitive ability  
 Measurement models  
 Honeybees  
 Comparative cognition

## ABSTRACT

Finke, Scheiner, Giurfa, and Avarguès-Weber (2023) published correlational data on the performance of honeybees (*Apis mellifera*) in three learning tasks (associative, reversal, and negative patterning, capturing the domains of *operant conditioning*, *executive-functioning-like ability*, and *inhibition plus configural processing*, respectively) evaluated under both visual and olfactory stimulus conditions. They speculate that general cognitive ability (GCA) may be weakly causing all-positive correlations between performance in these different learning modalities, but do not formally test this possibility. A factor-analytic model applied to Finke et al. (2023) data revealed the presence of two perfectly congruent GCA factors (one for each stimulus condition). Both exhibited all-positive loadings, with the visual factor accounting for 46.8% of the performance variance and the olfactory factor accounting for 52.3%. Diagnostic statistics confirmed that in both stimulus conditions, the correlation matrices were adequate for factor analysis. These findings support extant hypotheses that GCA influences covariation between cognitive measures in honeybees, and constitute the first formal potential demonstration of GCA in an invertebrate. It is argued that GCA might be ubiquitous with respect to metazoans possessing organized nervous systems, perhaps because it convergently evolved multiple times in independent phylogenies, this being a key prediction of Christopher Chabris' *Law of General Intelligence*. Indeed, GCA has now been identified in insect, avian, mammal, and fish taxa. Some "primordial" aspects of GCA may even be basal to metazoans, and experiments employing *Caenorhabditis elegans* are suggested that could potentially shed light on such aspects. The findings are also strikingly inconsistent with evolutionary and comparative psychological theories positing a "modules first" understanding of cognitive evolution, such as one recent proposal that smaller brains cannot accommodate structures that give rise to GCA. Other theoretical implications of these findings are discussed.

## 1. Introduction

General cognitive ability (GCA) factors have been found in a large and growing number of animal (principally mammalian) taxa for several decades (for relevant reviews, see Burkart, Schubiger, & van Schaik, 2017; Chabris, 2007; Galsworthy, Arden, & Chabris, 2014). Meta-analyses of studies on mice (*Mus musculus*) and rats (*Rattus norvegicus*) dating back to the beginning of the 20th century find evidence that GCA factors account for 32.2% of the cognitive performance variance in the former ( $K = 28$  effect sizes) and 54.5% of the variance in the latter ( $K =$

11 effect sizes) (Woodley of Menie et al., 2022). A recent re-analysis and extension of meta-analytic data published by Poirier, Kozlovsky, Morand-Ferron, and Careau (2020) on 12 taxa (four mammals, seven avians, and one fish, the Trinidadian guppy; *Poecilia reticulata*) found that a GCA factor accounted for 30% of the variance across these taxa (Woodley of Menie et al., 2023). In the same study, a GCA factor among four cognitive tasks exhibiting all-positive loadings, and accounting for 19% of the variance, was identified in cleaner fish (*Labroides dimidiatus*) via re-analysis of data collected by Allen, Burkart, and Bshary (2022). Chabris (2007) has suggested that the apparent ubiquity of the GCA

\* Corresponding author.

E-mail address: [mpeaher@email.arizona.edu](mailto:mpeaher@email.arizona.edu) (M. Peñaherrera-Aguirre).<https://doi.org/10.1016/j.intell.2024.101856>

Received 1 February 2024; Received in revised form 6 August 2024; Accepted 7 August 2024

Available online 13 August 2024

0160-2896/© 2024 Elsevier Inc. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

factor among individual-differences measures of cognition be termed the *Law of General Intelligence*:

This law would state that measurements of cognitive ability tend to correlate positively across individuals, with a corollary that the first principal component or general factor extracted from any such correlation matrix - assuming a diverse battery of mental tests and a diverse sample of subjects - will account for a substantial fraction of the variance. (p. 452).<sup>1</sup>

On the basis of this law, Chabris (2007) predicted that GCA should be ubiquitously present across individual differences measures of cognition in non-human and even invertebrate taxa (effectively any taxon possessing a structured nervous system), noting that:

Hints of evidence for general intelligence have also emerged in recent studies of non-mammals, specifically insects. Honeybees were divided into two groups according to their performance on a test of latent inhibition (high or low inhibition); the offspring of these groups showed a similar difference on latent inhibition, and high-inhibition bees performed worse on a reversal learning task (Chandra, Hosler, & Smith, 2000; but see Ferguson, Cobey, & Smith, 2001 for inconsistent findings). While this study observed a positive association between just two tasks, it is intriguing that reversal learning is a test of executive function, which is related to fluid intelligence in humans ... The development of more diverse batteries of tests, as has been done for mice, could facilitate studies of general intelligence in suitable insect species, such as honeybees and fruit flies, as well as other species in which individual differences have been found at the single-neurone level, such as molluscs (Matzel & Gandhi, 2000). (p. 459).

More recently, Finke et al. (2023) have conducted research on honeybees involving individual differences in performance on three distinct learning tasks (associative learning, reversal learning, and negative patterning) across two sensory domains: visual and olfactory. Two different samples of honeybees were used, one for each stimulus condition. In this study, a color (visual learning condition) or odor (olfactory learning condition) association task was used to evaluate associative learning (AL) efficiency, in which one stimulus was rewarded (with sucrose solution) and the other punished (with quinone solution, to which bees have a mild aversion). Subsequently reversal learning (RL) was evaluated by reversing the reward settings, and measuring the efficiency with which the bees could learn the new association pattern. The third learning task employed a negative patterning (NP) protocol. This task involved the use of three consecutive sets of trials, two of which were rewarded whereas a compounded third condition was non-rewarded. In this task, the bees had to learn to associate the reward with either of the single reinforced stimulus conditions, but not when the stimuli were presented jointly. Finke et al. (2023) note that NP problems “can only be solved if the compound stimulus is treated as being different from the sum of its components, which requires inhibiting stimulus summation and implementing different forms of processing such as configural processing” (p. 910). The three learning tasks capture domains related to *operant conditioning* (in the case of AL), *executive functioning-like ability* (in relation to RL, and as noted by Chabris, 2007), and *inhibition and configural processing* (in the case of NP; Devaud, Papouin, Carcaud, & Giurfa, 2015).

In interpreting the results of their correlational analysis, Finke et al. (2023) discuss the possibility that GCA might be responsible for positive correlations observed among these three tasks under both of the sensory conditions, noting that “it might ... be possible that a g-factor accounts for a small proportion of inter-individual variability across the three

learning tasks tested” (p. 923). Very similar experimental designs involving correlations among trios of learning measures have also yielded potential experimental evidence of GCA in other taxa. Prentice, Thornton, and Wilson (2022), for example, were able to identify a general factor (which they identified with GCA) accounting for 57% of the performance variance in an associative, reversal, and motoric learning task in the Trinidadian guppy.

Despite their initial speculation concerning a possible small effect of GCA, Finke et al. (2023) do not attempt to conduct a formal test for the presence of this factor. Instead, they simply suggest that “[GCA is] concealed by interindividual variability caused by other experimental or intrinsic factors and low sample sizes” (p. 923). In other words, they reject the idea that their samples would provide evidence of GCA if an effort to detect it were made, insofar as they assume that they are too small and that there are problematic confounders present. Nevertheless, these suspicions might be unfounded, and so the possibility of GCA factors in Finke et al.’s data should be statistically evaluated through the use of appropriate factor-analytic methods (specifically Parallel Analysis and Exploratory Factor Analysis), which is our aim in the current paper. If the presence of GCA can be formally and robustly established using the Finke et al. (2023) data, then major new evidence for the *Law of General Intelligence* would be found, as its key prediction—the universality of GCA in metazoans—would be supported through the first ever demonstration of this factor in an invertebrate.

## 2. Methods

### 2.1. Reanalyzing Finke et al.’s (2023) correlational data

The results of Finke et al.’s (2023) analyses of the pattern of Spearman correlations among the three learning tasks, in each of the two stimulus conditions (see their Table 1, p. 914, experiments 1 and 2), were replicated using the raw individual-differences data that the authors have shared publicly (available from doi: <https://doi.org/10.6084/m9.figshare.20473113.v.>). Performance data are given in the form of the percentage of correct choices made by subjects across trials, learning modalities, and conditions, so performance with respect to each learning task is scaled equivalently, such that higher values always correspond to better subject performance. The Kaiser-Meyer-Olkin (KMO) and Bartlett’s tests were conducted on the correlation matrices using the *KMO* and *Cortest.Bartlett* function from the *psych* package (Revelle, 2015) to determine whether these matrices exhibited adequate statistical properties for use in latent variable models. As these Spearman correlations were estimated using slightly different sample sizes for each pair of abilities being correlated, to correctly specify model degrees of freedom for the tests, we estimated the harmonic mean sample size using the following equation:

$$n_h = \frac{k}{\frac{1}{n_1} + \frac{1}{n_2} + \dots + \frac{1}{n_k}}$$

Where  $n_h$  is the harmonic mean,  $k$  is the number of pair-wise correlations, and  $n_1, n_2, \dots, n_k$  are the sample sizes used for each correlation. In the case of the visual learning protocol experiment, the harmonic  $n$  is 28.74 (rounded to 29), and in the case of the olfactory learning protocol experiment, the harmonic  $n$  is 20.63 (rounded to 21).

Once sample adequacy was established, these correlations were then entered into Parallel Analyses (using the *fa.parallel* function in *psych*) to assess the most likely number of latent dimensions (based on maximum likelihood estimations involving 500 iterations) present in the case of each stimulus condition. Exploratory (Principal Axis) Factor Analyses (EFA) were also conducted using the correlation matrices with the *fa* function in the *psych* package, to determine the loading of each manifest variable (learning task) onto its latent variable in each stimulus condition. These analyses were conducted using R v4.0.1 (R Core Team, 2022).

<sup>1</sup> Note that Spearman (1927, pp. 197–198) used the term *indifference of the indicator* to refer to precisely the same tendency for any arbitrarily selected set of cognitive ability measures to correlate among themselves giving rise to GCA.

**Table 1**

Measurement models estimating the factor structure of GCA in bees in two samples (visual and olfactory).

Indicators	Factor loadings sample 1 (Visual)	Factor loadings sample 2 (Olfactory)
AL	0.944	0.997
RL	0.562	0.601
NP	0.445	0.461
<i>Measurement Model Parameters</i>	<i>Sample 1</i>	<i>Sample 2</i>
R <sup>2</sup>	0.468	0.523
MSA	0.59	0.52
Bartlett X <sup>2</sup>	13.74	12.69
Bartlett p-value	<0.01	<0.01
Harmonic N	29	21

A final robustness test involved fitting 95% confidence intervals (CIs) to the Eigenvalue associated with the first factor derived from the EFA. This involved the use of Eigenvalues derived from the experimental data associated with each stimulus condition and also simulated data. An Eigenvalue can be said to be statistically significantly different from 1.00 (a commonly used criterion for determining whether or not to retain a factor) if its lower 95% CI does not bisect 1.00. This analysis was carried out using macro in SAS 9.4.

### 3. Results

#### 3.1. Measurement models

In each stimulus condition (visual and olfactory), Parallel Analysis indicated the presence of a single latent dimension. The results of the EFA on this latent variable estimated for each stimulus condition, along with other measurement model parameters, are reported in Table 1.

For the visual stimulus condition, The KMO Measure of Sampling Adequacy (MSA) value was of mediocre magnitude (between 0.5 and 0.59; Field, 2013), but indicates sampling adequacy given that Bartlett's test of sphericity reached statistical significance ( $X^2 = 13.74$ ,  $p = .0033$ ). The latent variable estimated via EFA loaded positively onto all cognitive indicators with factor loadings ranging from 0.445 to 0.944. This latent dimension explained 46.8% of the variance. For the olfactory learning condition similar results were noted, with the MSA also being of mediocre, but acceptable, magnitude, as Bartlett's test of sphericity reached statistical significance ( $X^2 = 12.69$ ,  $p = .0054$ ). The EFA also yielded a single factor that loaded positively onto all three behavioral indicators, with factor loadings ranging from 0.461 to 0.997. This factor accounted for 52.3% of the variance.

95% CIs were fitted to the Eigenvalues associated with each latent dimension in order to determine whether they were significantly >1.00. Simulated data were used in order to generate a null-contrasting condition (where Eigenvalues should exhibit values <1.00, with 95% CIs that include upper-bound values >1.00 and lower-bound values <1.00). The results of this analysis are presented in Table 2.

The Eigenvalues associated with the latent variables estimated using the real data were in each case "significantly" >1.00, with lower-bound 95% CIs that do not cross the 1.00 threshold in either case.

Finally, Tucker's coefficient of congruence (Lorenzo-Seva & Ten

**Table 2**

Eigenvalues, and their corresponding 95% confidence intervals, estimated using Horn's Parallel Analyses for samples 1 (visual) and 2 (olfactory), using real and simulated data.

Sample	Data Featured	Eigenvalues	95% LCI	95%UCI
1 (Visual)	Real data	1.40	1.03	1.77
	Simulated data	0.92	0.68	1.16
2 (Olfactory)	Real data	1.54	1.06	2.02
	Simulated data	0.99	0.68	1.30

Berge, 2006) was used to compare the visual and olfactory GCA factors. It revealed that their structures were statistically identical ( $r_c = 1.00$ ), indicating perfect congruence.

### 4. Discussion

Reanalysis of Finke et al.'s (2023) raw data and correlations offers clear indications of GCA factors accounting for close to half of the systematic variance in each of the two stimulus conditions. These estimates were generated from three learning tasks tapping aspects of *operant conditioning*, *executive-functioning-like ability*, and *inhibition plus configural processing*. The diagnostic tests indicated that, contrary to Finke et al.'s misgivings, their samples and their associated correlation matrices were adequate for use in formal factor analysis. Furthermore, perfect factorial congruence was observed between the two GCA estimates. Given the very substantial implications of these results (elaborated below), it must be stressed that independent efforts to replicate them are crucial.

The identification of the GCA factors in these learning domains is consistent with Chabris' (2007) *Law of General Intelligence*, which explicitly predicts a positive manifold among individual differences measures of cognition in metazoans exhibiting structured nervous systems, including those that are very far removed phylogenetically from humans, such as honeybees (and other insects). Notably, the GCA factor in honeybees is highly comparable in magnitude to meta-analytic estimates of GCA variance in studies of human intelligence. In one such (particularly broad and well-executed) meta-analysis—in instances where EFA presented initial indications of a general factor—GCA accounted for 45.9% (vs. 46.8% and 52.3% in the case of the two honeybee GCA factors) of the variance (Warne & Burningham, 2019).

The observation of similar magnitude GCA factors in humans and honeybees suggests that social complexity may be one source of convergent selection acting to integrate the components of cognition. This may also provide a basis for so-called swarm intelligence in such insects. In the biological sense, swarm intelligence encompasses the ability for organisms to solve problems (e.g., efficient foraging) collectively, via coordination among members of the swarm and interactions between the swarm and its environment (Tan & Zheng, 2013). It might be that the means and variances of GCA among honeybees impose constraints upon the global efficiency of the swarms in which they participate. As honeybee worker drones are sterile, their level of GCA cannot condition their individual-level fitness. Any genetic contributions to these individual differences must originate from the diversity present among spermatozoa from multiple males collected by queen bees during nuptial flights (Schlüns, Moritz, Neumann, Kryger, & Koeniger, 2005). GCA can therefore only payoff fitness-wise at the colony level through inclusive fitness dynamics. This situation differs from the basic assumption of swarm intelligence models, which is that the agents of a swarm can be treated as essentially equivalently "simple," their behavior being governed by basic sets of universal rules or biological "algorithms," which compound into intelligent behavior only at the level of swarm dynamics (Tan & Zheng, 2013).

An intriguing parallel exists with so-called "collective intelligence" in human populations: while it has been claimed that this emergent swarm-like problem-solving capability is independent of the level of GCA of the individuals comprising such collectives (Woolley, Chabris, Pentland, Hashmi, & Malone, 2010), this finding has not replicated, with a more recent study finding that 100% of the variance in latent "collective" intelligence can be accounted for by individual-level GCA (Bates & Gupta, 2017).

The theory that the mean and variance in GCA may contribute more broadly to group-level outcomes involving competition between human biocultural groups (such as competition between countries and even empires; Woodley of Menie et al., 2017) would seem to complement Bates and Gupta (2017) observation, and suggests an even broader evolutionary analogy between humans and honeybees in terms of inclusive fitness processes among differentially "swarm intelligent"

competing honeybee colonies composed of genetically and phenotypically heterogeneous workers exhibiting different means and variances in GCA.

Another complementary possibility is that as honeybees are a human domesticate, artificial selection pressures may have served to amplify the coherence of GCA in this taxon as a means of adapting it to the contours of the human cognitive niche, including those aspects that relate to social complexity, which may co-contribute along with other behavioral factors that make them more amenable to management (see Bogнар et al., 2023 for similar arguments in relation to the potential origin of the human-like structure of canine cognition under domestication).

One additional hypothesis is that certain aspects of GCA might be in some sense basal to metazoans, with GCA in neurologically less complex animals such as insects (Knebel & Rigosi, 2021), whose brains are primarily composed of neuronal cells (Raji & Potter, 2021), being more reflective of factors that might affect basic global neurological quality among individuals. When neuronal differentiation is low, global sensitivity to the adverse effects of a given mutation or environmental insult might reasonably be expected to be higher given their more systemic effects in such conditions. For example, sensitivity to a virus that targets, or the presence of a deleterious mutation in, one kind of nerve cell will lead to more damage when an organism's nervous system is dominated by that one cell type, rather than a plurality of such cell types. Another source of quality differences among the nervous systems of relatively less complex organisms might be raw variability in neuronal count, which would either directly constrain or enhance the amount of neural-substrate available to an organism for the purposes of executing problem solving irrespective of domain.

This situation might contrast with that of generally more recently evolved and complex organisms exhibiting highly structured nervous systems, and very specialized neuron types (such as the von Economo neuron; Bruton, 2021). In such organisms, the GCA factor may be in part reflective of both the basic neurological quality axis outlined immediately above and a novelty-adapted system, related to executive functioning, which facilitates the coordination and combination of inputs associated with lower-level dedicated cognitive systems for the purpose of solving phylogenetically irregularly occurring problems (for similar arguments on the latter source of GCA, see Geary, 2005). Rather than GCA reflecting only the "primordial"/"quality" or "coordination-combination" dimension, in highly neurologically complex species, it may involve both GCA dimensions, which should be phenotypically discriminable (Sarraf, Woodley of Menie, M.A, Peñaherrera-Aguirre, & Figueredo, forthcoming, develop a more detailed theoretical and empirical case for this theory). This is contrary to the standard evolutionary psychology paradigm, in which simple and discrete modules evolved first, with GCA merely reflecting the action of many such modules that have been forced into functional coordination through some process, such as the action of highly pleiotropic mutations (e.g., Houle, 2000; Miller, 2000), or selection favoring recruitment of multiple "dedicated modules" to "improvise" solutions to certain "large bandwidth" problem types (Cosmides & Tooby, 2002).

Theorizing of this type appears in the comparative psychology literature, in which it has been recently claimed that the apparent absence of a coherent GCA factor in one taxon (the cleaner fish) is evidence that small brains cannot accommodate the coordinating structures necessary for the formation of GCA, and that specialized cognitive modules must therefore instead compete among one another yielding trade-off patterns (Aellen et al., 2022). The presence of a much stronger GCA factor in honeybees (which have very small and much less complex brains compared with fish) is strikingly inconsistent with models of this kind. In the case of honeybees, we expect that both proposed sources of GCA covariance are likely to be in effect, as the presence of specialized structures such as mushroom bodies and a central complex in this taxon (Plath et al., 2017), along with the ability to engage in RL, suggests the presence of an executive functioning-like faculty (as argued by Chabris,

2007), and therefore some level of "coordinating" GCA.

#### 4.1. Limitations

Although the three learning tasks captured a range of learning modalities, more tasks would be highly desirable in future experiments of this kind to determine the extensiveness of the positive manifold in honeybees. Such tasks might include tests designed to identify individual differences in spatial memory and navigation, which in honeybees involve the encoding of spatially relevant information with reference to a variety of cues, including landmarks and celestial bodies for the purpose of optimizing foraging routes (Dyer, 1996). Larger sample sizes in future studies would also increase the power with which GCA factors can be identified. A final important limitation raised by a reviewer is that the source of the covariance among the learning tasks may have an origin that is independent of GCA. For example, a general influence of motivation across tasks could potentially create a positive manifold (Finke et al., 2023 did in fact select bees for inclusion in their experiments on the basis of motivation to complete tasks). Lower-level motor abilities may also generally co-influence performance across the three tasks. Separating these alternate potential non-GCA sources of learning task covariance would doubtless require a novel experimental study in which the potential influence of these on GCA (if any) can be properly evaluated.

## 5. Conclusions

Clearly, more insect taxa should be investigated experimentally with a view to testing for the presence of GCA in the correlations among different learning modalities. Chabris (2007) suggests that *Drosophila melanogaster* may be one such organism in which the chances of detecting GCA are high. Eusocial insects that are relatively well experimentally characterized, such as ants, termites, and other members of the Hymenopteran order (the order to which honeybees belong), would also be good targets for expanding observations of GCA in insect taxa.

More broadly, a solid candidate taxon for exploring the possible existence of a discrete "primordial" GCA is the nematode and model organism *Caenorhabditis elegans*, which exhibits a minimally differentiated nervous system (being composed of a longitudinal nerve cord and ring, and both head and tail ganglia) and does not have a capacity for RL (Becerra, Calixto, & Orio, 2023), but does possess a capacity for various forms of more "primitive" learning, such as AL (Amano & Maruyama, 2011). Microfluidics-based experimental platforms (e.g., Qin & Wheeler, 2006) could be used for the identification of potentially correlated individual differences in performance on different forms of AL (e.g., appetitive vs. aversive) and spatial navigation tasks (e.g., being able to efficiently navigate a basic maze, which may be dependent on long-term AL). Such experiments should use genetically heterogeneous (wild-type) strains of this taxon, in order to maximize genetic diversity and therefore potential individual differences. Given the aforementioned, it is interesting to note that AL exhibited the strongest loading of the three learning modalities examined in the honeybees ( $\lambda = 0.944$  in the visual condition, and 0.977 in the olfactory condition) a finding suggesting that "primordial" GCA may be the dominant "flavor" of GCA in this taxon.

The finding of a GCA factor among such simple organisms will require scientists to fundamentally rethink the way in which nervous systems give rise to general problem-solving ability, and would provide exceptionally strong evidence for the *Law of General Intelligence*.

#### Funding for this project

None.

## Code availability

The R code will be made available upon request.

## Ethics approval

Due to the archival nature of this study, using data taken from online sources, human subjects' approval from the Institutional Review Board at the University of Arizona was not needed.

## CRediT authorship contribution statement

**Mateo Peñaherrera-Aguirre:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Matthew A. Sarraf:** Writing – review & editing, Writing – original draft, Conceptualization. **Michael A. Woodley of Menie:** Writing – review & editing, Writing – original draft, Conceptualization. **Aurelio-Jose Figueredo:** Writing – review & editing, Writing – original draft.

## Declaration of competing interest

None.

## Data availability

The authors provided sources to the original data sources in the Methods section.

## References

- Aellen, M., Burkart, J. M., & Bshary, R. (2022). No evidence for general intelligence in a fish. *Ethology*, *128*, 424–436.
- Amano, H., & Maruyama, I. N. (2011). Aversive olfactory learning and associative long-term memory in *Caenorhabditis elegans*. *Learning & Memory*, *18*, 654–665.
- Bates, T. C., & Gupta, S. (2017). Smart groups of smart people: Evidence for IQ as the origin of collective intelligence in the performance of human groups. *Intelligence*, *60*, 46–56.
- Becerra, D., Calixto, A., & Orío, P. (2023). The conscious nematode: Exploring hallmarks of minimal phenomenal consciousness in *Caenorhabditis elegans*. *International Journal of Psychological Research*, *16*, 87–104.
- Bognár, Z., Turcsán, B., Faragó, T., Szabó, D., Iotchev, I. B., & Kubinyi, E. (2023). The hierarchical structure of canine cognition: Two domains and a general cognitive factor. *bioRxiv*. <https://doi.org/10.1101/2023.02.07.525704>
- Bruton, O. J. (2021). Is there a “g-neuron”? Establishing a systematic link between general intelligence (g) and the von Economo neuron. *Intelligence*, *86*, Article 101540.
- Burkart, J. M., Schubiger, M. N., & van Schaik, C. P. (2017). The evolution of general intelligence. *Behavioural & Brain Sciences*, *40*, Article e192.
- Chabris, C. F. (2007). Cognitive and neurobiological mechanisms of the law of general intelligence. In M. J. Roberts (Ed.), *Integrating the mind: Domain general vs domain specific processes in higher cognition* (pp. 449–491). Psychology Press.
- Chandra, S. B. C., Hosler, J. S., & Smith, B. H. (2000). Heritable variation for latent inhibition and its correlation with reversal learning in honeybees (*Apis mellifera*). *Journal of Comparative Psychology*, *114*, 86–97.
- Cosmides, L., & Tooby, J. (2002). Unraveling the enigma of human intelligence: Evolutionary psychology and the multimodular mind. In R. J. Sternberg, & J. C. Kaufman (Eds.), *The evolution of intelligence* (pp. 145–198). Erlbaum.
- Devaud, J.-M., Papouin, T., Carcaud, J., & Giurfa, M. (2015). Neural substrate for higher-order learning in an insect: Mushroom bodies are necessary for configural discriminations. *Proceedings of the National Academy of Sciences*, *112*, E5854–E5862.
- Dyer, F. C. (1996). Spatial memory and navigation by honeybees on the scale of the foraging range. *Journal of Experimental Biology*, *199*, 147–154.
- Ferguson, H. J., Cobey, S., & Smith, B. H. (2001). Sensitivity to a change in reward is heritable in the honeybee, *Apis mellifera*. *Animal Behaviour*, *61*, 527–534.
- Field, A. (2013). *Discovering statistics using IBM SPSS statistics*. Sage.
- Finke, V., Scheiner, R., Giurfa, M., & Avarguès-Weber, A. (2023). Individual consistency in the learning abilities of honey bees: Cognitive specialization within sensory and reinforcement modalities. *Animal Cognition*, *26*, 909–928.
- Galsworthy, M. J., Arden, R., & Chabris, C. F. (2014). Animal models of general cognitive ability for genetic research into cognitive functioning. In D. Finkel, & C. A. Reynolds (Eds.), *Behavior genetics of cognition across the lifespan* (pp. 257–278). Springer Science + Business Media.
- Geary, D. C. (2005). *The origin of mind: Evolution of brain, cognition, and general intelligence*. American Psychological Association.
- Houle, D. (2000). Is there a g factor for fitness? In G. R. Bock, J. A. Goode, & K. Webb (Eds.), *The nature of intelligence* (pp. 149–170). Wiley Ltd.
- Knebel, D., & Rigosi, E. (2021). Temporal and structural neural asymmetries in insects. *Current Opinion in Insect Science*, *48*, 72–78.
- Lorenzo-Seva, U., & Ten Berge, J. M. (2006). Tucker's congruence coefficient as a meaningful index of factor similarity. *Methodology*, *2*, 57–64.
- Matzel, L. D., & Gandhi, C. C. (2000). The tractable contribution of synapses and their component molecules to individual differences in learning. *Behavioural Brain Research*, *110*, 53–66.
- Miller, G. F. (2000). Sexual selection for indicators of intelligence. In G. R. Bock, J. A. Goode, & K. Webb (Eds.), *The nature of intelligence* (pp. 260–275). Wiley Ltd.
- Plath, J. A., Entler, B. V., Kirkerud, N. H., Schlegel, U., Galizia, C. G., & Barron, A. B. (2017). Different roles for honey bee mushroom bodies and central complex in visual learning of colored lights in an aversive conditioning assay. *Frontiers in Behavioral Neuroscience*, *11*, 96.
- Poirier, A. A., Kozlovsky, D. Y., Morand-Ferron, J., & Careau, V. (2020). How general is cognitive ability in nonhuman animals? A meta-analytical multi-level reanalysis approach. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20201853.
- Prentice, P. M., Thorton, A., & Wilson, A. J. (2022). A multivariate view of cognitive performance reveals positive correlation in the Trinidadian guppy (*Poecilia reticulata*). *bioRxiv*. <https://doi.org/10.1101/2021.11.04.467320>
- Qin, J., & Wheeler, A. R. (2006). Maze exploration and learning in *C. elegans*. *Lab on a Chip*, *7*, 186–192.
- R Core Team. (2022). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raji, J. I., & Potter, C. J. (2021). The number of neurons in *Drosophila* and mosquito brains. *PLOS ONE*, *16*, Article e0250381.
- Revelle, W. (2015). *psych: Procedures for psychological, psychometric, and personality research*. Illinois: Northwestern University.
- Sarraf, M.A., Woodley of Menie, M.A., Peñaherrera-Aguirre, M., & Figueredo, A.J. (Forthcoming). The g paradox: The pattern of affinity for g of crystallized and fluid abilities reverses at different levels of psychometric aggregation.
- Schlüns, H., Moritz, R. F. A., Neumann, P., Kryger, P., & Koeniger, G. (2005). Multiple nuptial flights, sperm transfer and the evolution of extreme polyandry in honeybee queens. *Animal Behavior*, *70*, 125–131.
- Spearman, C. (1927). *The abilities of man*. Macmillan.
- Tan, Y., & Zheng, Z.-Y. (2013). Research advance in swarm robotics. *Defence Technology*, *9*, 18–39.
- Warne, R. T., & Burningham, C. (2019). Spearman's g found in 31 non-Western nations: Strong evidence that g is a universal phenomenon. *Psychological Bulletin*, *145*, 237–272.
- Woodley of Menie, M.A., Figueredo, A. J., Sarraf, M. A., Hertler, S. C., Fernandes, H. B. F., & Peñaherrera-Aguirre, M. (2017). The Rhythm of the West: A Biohistory of the Modern Era 1600 CE to the Present. *Journal of Social Political and Economic Studies, Monograph Series, No. 37. Council for Social and Economic Studies*.
- Woodley of Menie, M.A., Peñaherrera-Aguirre, M., & Sarraf, M. A. (2022). Signs of a Flynn effect in rodents? Secular differentiation of the manifold of general cognitive ability in laboratory mice (*Mus musculus*) and Norwegian rats (*Rattus norvegicus*) over a century—results from two cross-temporal meta-analyses. *Intelligence*, *90*(101), 700.
- Woodley of Menie, M.A., Peñaherrera-Aguirre, M., & Sarraf, M. A. (2023). Do cleaner fish (*Labroides dimidiatus*) have general cognitive ability? A reanalysis of individual differences data and consideration of phylogenetic context. *Evolutionary Psychological Science*, *9*, 309–316.
- Woolley, A. W., Chabris, C. F., Pentland, A., Hashmi, N., & Malone, T. W. (2010). Evidence for a collective intelligence factor in the performance of human groups. *Science*, *330*, 686–688.