In search of the Darwinian Holy Trinity in cognitive evolution: a comment on Croston et al.

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In the last few years, the study of cognitive evolution has been reinvigorated by a renewed focus on the Darwinian Holy Trinity of necessary conditions for traits to respond to selection: 1) phenotypic variation that is 2) heritable and 3) affects fitness. Croston and colleagues highlight the need for studies of heritability, but of course progress in understanding both of the latter factors still depends on development of rigorous methods to quantify the former. Notwithstanding the challenge of characterizing among-individual cognitive differences in the first place (Rowe and Healy 2014; Thornton et al. 2014), we are certainly supportive of Croston et al.’s argument that more genetic studies of cognition are needed. It is notable that despite considerable interest among behavioral ecologists, our best evidence for individual and genetic cognitive differences comes not from this field but from laboratory studies of memory and intelligence in experimental psychology (references in Croston et al. 2015). Although the direct ecological and evolutionary significance of such domain-general processes may be less obvious than in the case of classic adaptive specializations (e.g., long-term spatial memory in food storing birds), they are among the few cognitive traits known to be heritable (at least in humans, chimpanzees, rodents, and insects). They are also likely to be crucial determinants of animals’ abilities to adapt to changing environments, exploit novel resources, and learn from one another (Sol et al. 2005; Leadbeater 2015).

Quantifying heritable variation in, for instance, learning, memory, generalization, and categorization is therefore a crucial step in helping to explain how cognitive traits evolve within species and diversify between species. However, it is vitally important to take on board the lessons learned from the wider field of evolutionary quantitative genetics. Importantly, heritability alone will be insufficient to predict selection responses in the presence of interlocus conflict, maternal effects, indirect genetic effects, and a host of other phenomena that are widely investigated in research on morphological, behavioral, and life history traits (Kruuk et al. 2008; Wilson 2014). Moreover, we suggest that an overemphasis on estimating heritability is problematic because natural selection does not act on traits in isolation. Consequently, evolutionary change (or lack thereof) in cognitive traits can only be fully understood by considering the genetic basis of associations between cognition, behavioral, life history, and even fitness itself (Walsh and Blows 2009).

Fully multivariate approaches are required, with the goal of determining the genetic variance–covariance matrix \( G \) among traits, not just the heritability of individual traits. Estimation of \( G \) would allow us to examine integration among cognitive domains (as argued for in the “general intelligence” or \( g \) model) at the genetic level. It might also permit alternative models of causal pathways between (genetic) variation in cognition and fitness to be tested (e.g., using structural equation modeling or related techniques (Valente et al. 2010). For instance, there is considerable interest in the hypothesis that cognitive variation is linked to differences in individual personality traits such that, for example, bold, “proactive” personality types are associated with speed in decision making, whereas shyer, “reactive” individuals exhibit greater accuracy (Sih and Del Giudice 2012). This idea remains controversial, and although there are a handful of studies pointing at links between personality and cognition (reviewed by Griffin et al. 2015), the direction of causation remains unclear. Future research examining the genetic architecture of suites of cognitive and personality traits, and the covariance between them is likely to be crucial in understanding whether personality generates differences in cognition or vice versa. Unlike researchers interested in morphological or behavioral evolution, students of cognitive evolution do not have the luxury of being able to observe and measure their traits of interest directly and there is no doubt this imposes additional challenges. However, by integrating psychologically grounded experiments with methods and insights from behavioral ecology and quantitative genetics, we can begin to piece together the puzzle of how and why cognition evolves.

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It may be important to know how much of the trait’s variance is likely to respond to natural selection in a given population, what one is trying to establish. If the question is how strongly a trait could respond to natural selection at all, it may be much more important to know whether there exists any additive genetic variance component, independent of the size of other components. For this, the Coefficient of Additive Genetic Variance has been recommended (Houle 1992; Kruuk et al. 2000). The 2 measures can lead to very different conclusions (Kruuk et al. 2000), so careful consideration of the outcomes is needed.

**WHICH TRAIT IS ACTUALLY HERITABLE?**

For both behavioral and neural aspects of cognition, the final outcome measurement depends on many factors. For example, the outcome of a spatial memory task depends both on the spatial memory abilities of the animals (if they are challenged enough) and on their motivation (Rowe and Healy 2014). Memory ability may well be a combination of traits (as mentioned by Croston et al.; see also Smulders et al. 2010), whereas motivation may be both positive (e.g., hunger) and negative (e.g., neophobia). Any additive genetic variance detected in task performance may therefore be due to any or all of these underlying traits. Similarly, significantly nonzero additive genetic variance in (for example) the number of neurons in the hippocampus of food-hoarding birds may be due to genetic variance in the hippocampal developmental program, but it is also possible that what is actually heritable is the motivation to hoard food, which could in turn stimulate the development of the hippocampus.

There is no easy solution to the problem of how to interpret heritability of complex traits such as brain structures and performance on cognitive tasks. Like in the estimates of cognitive abilities themselves, the (by no means simple) solution might be to measure the presumed cognitive abilities and/or confounding factors in a battery of carefully designed tasks (Kamil 1988; Rowe and Healy 2014). This might allow us to separate the different sources of variance.

In conclusion, Croston et al. (2015) set the field a challenging, but not impossible, task. I look forward to seeing some well-designed and carefully interpreted studies in this field in the (hopefully) not-too-distant future.

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