Invited Commentaries

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 heritable, and 2) 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 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, behavior, life history, and even fitness itself (Walsh and Blows 2009).

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**Interpreting measurements of heritability: a comment on Croston et al.**

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Croston et al. (2015) point out that in order to really understand the evolution of cognitive and brain traits, we need to know whether any of the variability in these traits can be assigned to genetic effects. If so, and if there is a significant genetic variation associated with the trait, the trait will be subject to evolutionary selection. They then review what is known about the heritability of some cognitive traits and their associated brain areas, and come to the conclusion that a lot of work remains to be done. I can only agree with their assessment.

Of course, it is possible that a trait has undergone natural selection in the past, and that it has become fixed in the population, resulting in zero genetic variance today (Mousseau and Roff 1987; Kruuk et al. 2000). However, this seems unlikely for most cognitive traits. In this commentary, then, I will go from the assumption that there is genetic variation in cognitive and/or brain traits, and discuss 2 things we need to consider when trying to detect this genetic variation.

**WHICH MEASURE OF HERITABILITY IS APPROPRIATE?**

The classic method of calculating heritability \( h^2 \) (additive genetic variance/total variance) has been suggested not to be the best measure of the evolvability of a trait (Houle 1992). This is because both (additive) genetic and nongenetic sources of variance influence this measure: for a constant genetic contribution to variance, \( h^2 \) goes down as environmental contributions to variance increase. Indeed, Turkheimer et al. (2003) showed that heritability estimates of IQ in humans vary tremendously with socioeconomic status: in affluent families, \( h^2 \) for IQ is much higher than in poor families (where it is near 0). It is unlikely that there are no genes influencing IQ in the poor families, but the environmental variation masks this.

Of course, which measure one should use depends crucially on what one is trying to establish. If the question is how strongly a trait is likely to respond to natural selection in a given population, it may be important to know how much of the trait’s variance in that population is due to nongenetic effects, as this may slow down natural selection. On the other hand, if the question is whether 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 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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