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

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Croston and colleagues (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 that trait can be assigned to genetic effects. If so, and if there is fitness variation associated with the (genetic) trait variation, the trait will be subject to natural 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 (Kruuk et al., 2000; Mousseau and Roff, 1987). 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 two things we need to consider when trying to detect this genetic variation.

1.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 non-genetic 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 socio-economic status: in affluent families, h^2 for IQ is much higher than in poor families (where it is near zero). 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 non-genetic 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 two measures can lead to very different conclusions (Kruuk et al., 2000), so careful consideration of the outcomes is needed.

2. Which trait is actually heritable?

For both behavioural 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 suggested by Croston et al.; see also (Smulders et al., 2010), while 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 non-zero additive genetic variance in (e.g.) the number of neurons in the hippocampus of food-hoarding birds may be due to many factors. These could be genetic variance in the hippocampal developmental programme, 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 like 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 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.

References

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