

Behavioral and Brain Sciences

Measuring heritability: why bother?

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Abstract:	Uchiyama et al. rightly consider how cultural variation may influence estimates of heritability by contributing to environmental sources of variation. We disagree however with the idea that generalisable estimates of heritability are ever a plausible aim. Heritability estimates are always context-specific, and to suggest otherwise is to misunderstand what heritability can and cannot tell us.

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2 Ryutaro Uchiyama, Rachel Spicer, and Michael Muthukrishna

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36 **10. ABSTRACT**

37 Uchiyama et al. rightly consider how cultural variation may influence estimates of
38 heritability by contributing to environmental sources of variation. We disagree however
39 with the idea that *generalisable* estimates of heritability are ever a plausible aim.
40 Heritability estimates are always context-specific, and to suggest otherwise is to
41 misunderstand what heritability can and cannot tell us.

42

43 **11. MAIN TEXT (with paragraphs separated by full blank lines, NOT tab indents)**

44

45 ***Measuring heritability: why bother?***

46 Uchiyama et al. address the role cultural variation may play in influencing estimates of
47 the quantitative genetic parameter of heritability, h^2 . They argue, rightly in our view,
48 that cultural differences among human groups can contribute an important component
49 of environmental variation in human behaviour. Indeed, given the preponderance of
50 social learning in human populations, it is right to consider how this source of variance
51 may influence our estimates of heritability, by shaping the relationship between genetic
52 and non-genetic sources of variation in behaviour and other traits.

53

54 Where we depart from Uchiyama et al.'s view is in terms of their emphasis on the
55 generalisability of heritability estimates. Heritability estimates are *always* context
56 specific (Falconer & Mackay 1996; Visscher et al. 2008). Even if one is able to identify,
57 and then control for, components of environmental variance (as those studying
58 quantitative genetic parameters in the wild often do: Charmantier et al. 2014), one is
59 still left with a context-specific estimate. Importantly, this context specificity is not just
60 in terms of the role of gene-by-environment (GxE) interactions – emphasised in the
61 context of culture by Uchiyama et al. – but also in terms of *all* the components of
62 variance that go into the heritability calculation, including other sources of
63 environmental variance, and population genetic parameters such as the frequencies of
64 causal alleles segregating in the population. This means that it is a mistake, and a
65 misunderstanding, to expect a *generalisable* estimate of heritability for any given trait,
66 an aim stated more than once by Uchiyama et al.

67

68 The interpretation of heritability is crucial. Uchiyama et al. provide many reasons for
69 not over-interpreting heritability, but these are at odds with imagining that there could
70 be such a thing as a “true” heritability. Heritability only speaks to the sources of
71 variance expressed by a trait in a given sample. In terms of environmental sources of
72 variation, if these are large then additive genetic effects may be swamped, but it does
73 not necessarily mean that they are absent. Behavioural traits are often thought to be
74 contaminated with large sources of environmental variation for example (for discussion
75 see Stirling et al. 2002; Dochtermann et al. 2019). Likewise, if environmental sources of
76 variation are small, then heritabilities may be high, but again this tells us rather little
77 about the additive genetic variance itself. It is worse than that though, as additive and
78 residual sources of variance may be non-independent (Houle 1992; Hansen et al. 2011).
79 One alternative is the coefficient of additive genetic variation, CV_A , which may be more
80 comparable across contexts (Houle 1992).

81

82 As such, differences in heritability can be due to both differences in environmental and
83 additive genetic components (bundling away non-additive effects for brevity), but of

84 course the same is true for similarities: heritabilities may be alike, but for different
85 causal reasons. Uchiyama et al. talk about techniques such as polygenic scores in terms
86 of unpicking the quantitative genetic basis of traits, but as they note recent work has
87 shown that the causal variants identified by polygenic score methods do not replicate
88 well across populations (including for intensively studied human populations and traits
89 such as height, which are highly heritable across populations: Mathieson 2021). This
90 means that even if there was a “true” heritability, repeatable across populations (which
91 there isn’t), and we could unpick the cultural influences, it would not necessarily mean
92 that we were looking at the same underlying genetics. And if we are not looking at the
93 same underlying genetics, then what is the purpose of trying to generalise heritability
94 estimates? It is after all uncontroversial that most traits exhibit heritable variation
95 (Lynch & Walsh 1998; but see Blows & Hoffman 2005 for complications).

96

97 Heritability is a useful statistic, particularly coming into its own in comparative studies
98 across traits and organisms (Mousseau & Roff 1987; Weigensberg & Roff 1996).
99 Hundreds of studies across animals have told us that morphological, life-history, and
100 behavioural traits typically vary in their h^2 estimates, going from higher to lower
101 respectively. Moreover, within a species, variation in heritabilities with age, for
102 example, can give us hypotheses about (a) how selection acts at different ages, or (b)
103 how developmental processes, and the genes and environments they influence and call
104 upon, change over the lifetime (Wilson et al. 2005). But there is no generalisable,
105 canonical h^2 waiting to be discovered. Developmental processes, via the moment-to-
106 moment interactions of organisms in their environments, do not call on genes in such a
107 way that could generate such a canonical measure; put simply, the whole genome is not
108 scrutinised moment-to-moment by an organism, in its environment. Instead, if one
109 wants such an over-arching genetic perspective, then the molecular basis of traits of
110 interests needs to be considered more directly, one that embraces changes in gene
111 expression, within- and across-tissues, across time, as the organism lives its way
112 through its social, cultural, and other environments.

113

114 Why the emphasis on h^2 ? Given our clarification that a given h^2 estimate says rather
115 little without understanding the underlying sources of variance, and indeed given much
116 of Uchiyama et al.'s discussion, why view h^2 as potentially generalisable at all? We are
117 not sure. Heritability is a fundamentally flawed way of arguing that some traits are more
118 or less "genetic" in origin than others. *All phenotypes*, including culturally inherited
119 behaviours and artefacts, have a genetic component to them, because the bodies and
120 brains that produce those phenotypes are built by genes living in environments.
121 Heritability does not speak to that aspect of the genetic basis of traits though, it only
122 speaks to the variance in those traits. So, what are we trying to generalise?

123

124 For humans, culture is in the environmental mix in terms of sources of phenotypic
125 variance. As such, controlling for cultural exposure may help reveal patterns in
126 variation in h^2 that can lead to interesting hypotheses and further tests. But to over-
127 emphasise heritability, and to imagine that it can be meaningfully generalised, is to
128 misunderstand what it can, and cannot, tell us about the evolution of humans and other
129 organisms.

130

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132 We have no conflicts of interest to report.

133

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