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Individual differences as the output of evolved calibration mechanisms: does the theory make sense in view of empirical observations?

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Evolutionary psychologists have traditionally focussed on understanding the evolutionary basis of species-typical or sex-typical behavioural features. Recently, though, the differences between individuals have received increasing attention. A major class of evolutionary explanations of individual differences views them as the output of specialised species-typical calibration mechanisms that evolved to optimise the level of a trait to relevant contextual factors, which may be other characteristics of the individual or aspects of their environment. In this article I describe recent evidence that casts doubt on evolved calibration hypotheses of two particular traits — facial masculinity preference and the personality dimension extraversion. I then question whether evolved calibration mechanisms fit with what we know about the genetic and environmental causes of complex behavioural variation in general.

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Recently interest has burgeoned in the evolutionary basis of individual differences — relatively stable differences among individuals in a population (e.g. [1–3,4•,5–9]). One popular trend involves explaining behavioural trait variation in terms of specialised species-typical calibration mechanisms, evolved to optimise the level of the trait to relevant contextual factors. These factors may be other characteristics of the individual, early environmental conditions, or stable aspects of the current environment. This calibration has been referred to by various terms, including facultative calibration, adaptive calibration, adaptive plasticity, context-dependence, condition-dependence, and reactive heritability (i.e. when a trait's heritability is due to its calibration to a different heritable trait). Individual differences that evolutionists have sought to explain by specialised calibration mechanisms include personality traits [10•,11], mate preferences [12], attachment styles [13], life-history strategies [8,14], and psychopathology [15].

These hypotheses are intuitively appealing and theoretically plausible. However, I argue that they become doubtful when considered in the context of empirical findings from behavioural genetics. I briefly describe recent evidence with regard to two examples: first, women's facial masculinity preference, and second, the extraversion–introversion dimension. I then discuss behavioural genetic observations more broadly and why these suggest that specialised evolved calibration mechanisms do not commonly explain individual differences in complex behavioural traits.

Example 1: women's facial masculinity preference

Women show wide between-individual variation in preference for masculine versus feminine male faces. This wide variability has been hypothesised to be caused by evolved calibration mechanisms that optimise individual women's facial masculinity preference to relevant contextual factors [12]. These factors include women's self-perceived attractiveness [16], short versus long term relationship orientation [17], pathogen disgust sensitivity [18], and stage of the menstrual cycle [19]. Note that cycle effects are within-individual and thus not relevant to the question of stable individual differences (though see Ref. [20]). Facial masculinity is thought to reflect good genes but poor parenting qualities, so that masculine faced men are more beneficial/less costly as mates when genetic benefits can be reaped (in fertile phases of the menstrual cycle), when genetic benefits are the only fitness benefits on offer (as in short-term mating when paternal investment is not on offer), when there is less need to make a trade-off (in more attractive women who may be able to attract and retain a mate with both good genes and good dad potential), and when genetic benefits (theorised to include higher immunocompetence) are relatively more important (e.g. in pathogen-sensitive individuals). In this theoretical model, genetic variation is not considered as an influence on preferences.

However, recent work [21•] in 2160 identical and nonidentical twins and siblings has shown that a large part (38%) of the variation in masculinity preference is due to genetic variation, whereas the aforementioned contextual factors accounted for a negligible amount of the variation (<1% combined). This suggests that the specialised calibration mechanisms that had been proposed are not a major reason for the large variability in women's facial masculinity preferences.

It should be noted that these results do not preclude other (unmeasured) contextual factors playing important roles, and that the relative contribution of environmental factors could be lower in the Western population that was used than in ancestral populations. Nonetheless, the results appear more compatible with nonadaptive explanations of variation in women's facial masculinity preferences. For example, the genetic component of the variation could be random (arising from mutation and drift), and the non-genetic component could be a combination of measurement error and general learning effects from positive and negative experiences with previous partners or other individuals.

Example 2: extraversion

Extraversion is a major dimension of personality, and around half of the between-individual variation is due to genes [22,23•]. Existing theories suggest that this genetic variation reflects reactive heritability [24]. Specifically, extraversion levels are thought to depend on individuals' relative bargaining power, defined as the ability to deliver benefits or costs to others. Relative bargaining power is hypothesised to be jointly determined by traits such as physical formidability and attractiveness, and intelligence. In theory, individuals who are formidable, attractive, and intelligent maximise their fitness by being extraverted, while those who are weak, unattractive, and unintelligent maximise their fitness by being introverted.

Under this theory, extraversion levels are not directly heritable, but instead only appear heritable because of their calibration to heritable variation in other traits. This of course raises the question of why formidability, physical attractiveness, and intelligence exhibit heritable variation in the first place. Lukaszewski *et al.* [10•,24] suggest it is because those traits have a large mutational target size — that is, they depend on a large proportion of the functional genome and thus have a relatively good chance of being affected by a random mutation. The implied assumption is that extraversion does not have a large mutational target size. However, given that extraversion encompasses a vast range of brain-driven behaviours and that 84% of human genes are expressed in the brain [25], extraversion seems likely to be as susceptible to random mutations as are the traits to which it is purportedly calibrated.

The primary evidence supporting evolved calibration of extraversion to relative bargaining power is a phenotypic correlation of extraversion with physical strength and attractiveness [24,26•,27•]. However, there are explanations for such a correlation that do not involve a specialised calibration mechanism. For example, people who are physically attractive are treated more favourably throughout childhood and adulthood [28] and so experience more positive reinforcement to their social overtures throughout their development.

Other evidence contradicts the evolved calibration hypothesis. Namely, in 1659 identical and nonidentical twins, extraversion did not correlate with height or BMI in either sex [26•], even though height is related to both attractiveness and strength in men and BMI is negatively related to attractiveness in women. Likewise, extraversion did not correlate with intelligence. Furthermore, genetic analysis showed that genetic variation in facial attractiveness did not account for a significant amount of the variation in extraversion, in contrast to the reactive heritability account of extraversion's genetic variation.

Evolved calibration more broadly

Evolved calibration mechanisms are invoked to explain a wide range of individual differences, and seemingly many evolutionary psychologists view such mechanisms as promising explanations for individual differences in general [8,10•,11–15]. My view is that these specialised mechanisms are uncommon, and explain very little of the stable behavioural variation between individuals. This view is based on the following observations.

1. Any complex behavioural trait depends on numerous aspects of brain function. Given that 84% of human genes are expressed in the brain [25], such traits probably have a large mutational target size and thus large mutational variance. Precisely how large may differ between traits, and this will become clearer as their genetic architecture is mapped. One of the clearest findings from the current genomics era, though, is that complex behavioural traits are invariably influenced by very large numbers of genetic variants each contributing miniscule portions of trait variation [4,29,41].
2. Twin studies show that complex behavioural traits exhibit substantial variability and heritability, with somewhere between 20% and 80% of the trait variation generally accounted for by genetic variation [23•] (note that measurement error always makes up part of the non-genetic component). As an explanation for this pervasive genetic variation, myriad specialised mechanisms calibrating trait levels to other trait levels is less parsimonious, simple, and feasible than pervasive genetic 'noise' originating as mutations.