

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 non-identical 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.

3. Twin studies also allow estimation of the contribution of environmental factors shared by twins (e.g. 'risky' childhood family environment, socioeconomic status, parental support, etc.). These shared environmental factors by definition predict equal correlation in both twin types, whereas genetic influences predict double the correlation in identical twin pairs compared with nonidentical twin pairs, in accordance with their respective genetic similarity. Twin studies suggest that the proportion of trait variation accounted for by the shared environment is usually very small in comparison to genetic variation. For example, a meta-analysis of 630,304 twin pairs measured across 1134 traits related to temperament and personality found an average correlation of .47 for identical pairs and .23 for nonidentical pairs, which suggests a negligible (estimated at 0%) shared environmental contribution to trait variation compared with a genetic contribution of 47% ([23*]; see online MaTCH tool). The many hypotheses that explain trait variation by evolved calibration to family environmental factors during development must therefore contend with the evidence that such factors account for little variation in behavioural traits. For example, Lukaszewski [30] argues that the general factor of personality (GFP) is calibrated to parental support in childhood; however, earlier twin studies research showed that GFP variation is largely accounted for by genes (~50%) and not by shared environmental influences (0%) [31], which is inconsistent with the proposed calibration effect.
4. Apparent evidence for adaptive calibration to family environmental factors during development can disappear when familial (including genetic) confounding is controlled. For example, researchers have hypothesised that father absence causes early physical and behavioural sexual maturation (age-of-menarche, age at first intercourse) because of an evolved mechanism that strategically calibrates development to the riskiness of the environment [32]. However, Mendle *et al.* [33,34] showed that these effects were not present when familial confounds were controlled using the children-of-twins design: cousins discordant for father absence showed no differences in sexual maturation. This finding is inconsistent with the evolved calibration mechanism, but consistent with genetic or environmental factors that both predispose fathers to leave the family unit and predispose daughters to early sexual maturation. Familial controls should be standard in research on the lasting effects on environmental conditions during development, but such controls are rarely employed; when they are employed, confounding is often evident [35,36].
5. Evidence for conditional fitness-optimums of trait levels is scarce. In the extraversion example described above, the key assumption of the theory is that the optimal strategy for those high in relative bargaining power is extraversion while the optimal strategy of those low in relative bargaining power (e.g. physically unattractive) is introversion. There is no evidence for this assumption. One could even argue to the contrary that introversion compounds the disadvantages of being low in relative bargaining power — for example, a physically attractive man can rely on his looks to attract mates whereas a physically unattractive man must advertise his personal qualities through extroverted behaviour to attract female attention. The point is that speculation about conditional fitness optimums is an insufficient basis for a compelling model: empirical evidence is needed. Note, too, that where conditional fitness-optimums are demonstrated, it does not follow that a calibration mechanism has necessarily evolved to capitalise on them.
6. Behavioural calibration to one's own individual characteristics need not imply a specialised evolved mechanism — there are alternative explanations that must be eliminated before claiming evidence for special design [37]. These alternatives include general learning mechanisms (operant and classical conditioning), and reasoned behaviour. For example, the correlation in men between physical strength and aggression has been explained as a specialised evolved mechanism calibrating aggression levels to self-assessments of strength [38]. Alternatively, the correlation could be explained by (a) operant conditioning (aggressive solutions to conflicts are reinforced by success, and the tendency to opt for aggressive solutions is strengthened), and (b) reasoning (stronger individuals could reason that aggression is an effective strategy). Sell *et al.* [38] showed that reasoned behaviour is unlikely to explain the correlation of strength with aggression by additionally revealing a correlation of physical strength with endorsement of international military aggression (where an individual's physical strength is rationally irrelevant). However, the latter association does not pose a problem for a general learning explanation — conditioned responses are generalisable, so the conditioned tendency towards aggressive solutions (as per (a) above) could generalise to assessment of conflicts where the individuals' strength is not directly relevant. Another possibility is that the association between physical formidability and aggression is due to joint hormonal mediation. There are large evolved sex differences in both aggression and upper body strength, mediated at least in part by androgens, and individual differences in male androgen levels during development could cause corresponding individual differences in both aggression and upper body strength. Under this scenario, the covariation between aggression and strength is a side effect of androgen-mediated sex-differences in both traits. This possibility is consistent with the finding that boys' greater aggressive tendencies arise while they are still physically smaller than girls, and that more aggressive boys are not stronger than less

aggressive boys at age 11 but do become stronger later on in development [39]. This pattern of results is inconsistent with the specialised calibration mechanism proposed by Sell *et al.* [38].

7. Selection should increase the size of an adaptively important calibration effect while decreasing the background genetic variation (since minimal non-calibrated variation is optimal). This is difficult to reconcile with the observation that background genetic variation dwarfs the variation explained by proposed calibration effects (e.g. in large studies where they have been jointly estimated [21,26] and, by inference, in cases where the proposed calibration is to shared environmental factors that have been shown to account for little or no variation as per point #3 above). There may be constraints on the calibration effects that keep them small, but to my knowledge no such constraints have been proposed. Likewise there may be constraints on suppressing genetic variation, though such constraints would apply to genetic variation in the mechanism itself, which is assumed not to vary. Mathematical or empirical modelling is needed to properly elucidate the circumstances under which calibration effects are likely to evolve, and the size of calibration effects relative to background genetic variation that we should expect.

Concluding thoughts

I have argued above that empirical observations do not support the idea that specialised evolved calibration mechanisms account for large portions of variation in complex traits in general. This perspective need not preclude the existence of some such mechanisms. However, 'adaptation is a special and onerous concept that should not be used unnecessarily' [40]. Therefore, solid evidence is needed for the relevant conditional fitness optimums and that alternative explanations of the data (e.g. developmental constraint, general learning mechanisms, genetic/environmental confounding) are inadequate. Furthermore, the claims must be consistent with behavioural genetic research regarding the sources of variance in the trait of interest. Formal modelling may be needed to better understand the compatibility between wide genetic variation and small calibration effects, and to identify conditions under which the latter are most plausible.

Lastly, it is important to emphasise that even in the case that most between-individual variation is not the output of specialised adaptations, it is nonetheless invaluable for investigating evolutionary hypotheses. For example, as Zietsch *et al.* [4] explain: historical selection pressures on traits can be revealed by the number, frequency, and directional dominance of alleles causing variation; genetic correlations between traits, between the sexes, and between populations can test evolutionary predictions regarding mating structures, sexual selection, and modern vs. ancestral fitness; and genetic correlations between

traits and fitness can illuminate current selection pressures and predict future evolutionary change. As such, I urge evolutionists to continue to increase the focus on human individual differences while also adopting a critical perspective on adaptationist explanations thereof.

Conflict of interest statement

There are no conflicts of interest.

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