CHAPTER 32

Individual differences

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32.1. **Introduction**

The enduring differences between individuals have been one of psychology's central concerns over the past 100 years or more. In the last 25 years, evolutionary thinking has begun to make a huge impact on psychological explanation, particularly in social and cognitive psychology. However, the integration of evolutionary thinking into the study of individual differences has been more uneven (for some of the few major reviews, see Buss, 1991; MacDonald, 1995; Buss and Greiling, 1999). Evolutionary psychologists were initially more concerned with explaining central tendencies, and species-typical or sex-typical patterns of cognition, than they were with the individual variation. Nonetheless, a wave of recent work on humans and other species, including both theory and empirical study, has shed considerable light on how evolution shapes inter-individual variation. This chapter outlines the key frameworks that we have for explaining distributions of individual differences from an adaptive perspective. The focus is primarily on heritable individual differences, that is, differences underlain by population polymorphisms of particular genes. Individual differences which are temporally stable but non-heritable are considered briefly in Section 32.4.

32.1.1. **Background**

Variation is a pervasive feature of biological populations, and indeed, it was the observation of variation that allowed Darwin to formulate his theory of natural selection. Despite this, some evolutionary psychologists have given the impression that variation is only to be found in functionally unimportant characteristics, and that those traits for which an adaptive explanation is appropriate are precisely those that show no variation. Tooby and Cosmides (1992) argue, for example that "selection interacting with sexual recombination … tends to impose near uniformity" in psychological mechanisms (p. 79). Variability, they argue "is so often limited in its scope to micro-level biochemical variation, instead of introducing design differences." They will concede at most a "thin film" of inter-individual variation of any functional significance (p. 80). Thus, in summary, they assert that:

> Human genetic variation … is overwhelmingly sequestered into functionally superficial biochemical differences, leaving our complex functional design universal and species typical. (Tooby and Cosmides, 1992)

The logic of this position is that natural selection uses up genetic variation, by increasing the frequency of the variant with highest fitness until it reaches fixation, whilst removing others from the gene pool. Selection then becomes stabilizing in character, constantly winnowing out mutations, which are usually deleterious, or have the additional disadvantage of disrupting developmentally coordinated suites of genes. Thus, traits or mechanisms with a history of

selection will, according to this view, tend to dis-
play little or no heritable variation. This position
has been referred to as 'Fisher's fundamental
theorem' (Fisher, 1930).

It is true that genes coding for basic struc-
tures, such as body plans, generally reach fixation,
and are thereafter conserved by stabilizing selec-
tion. However, the assertion that heritable varia-
tion is absent from all important characteristics
is certainly not correct. The 'thin film' may not
be nearly as thin as Tooby and Cosmides imply.
The effect of many genetic variants, especially
on behaviour, is to produce a large or small
increment of change in the calibration or timing
of a characteristic, and variation of this kind is
very common in natural populations. Indeed,
Lynch and Walsh (1998), in their textbook of
evolutionary genetics, state that "almost every
character in every species that has been studied
intensively exhibits nonzero heritability." Such
genetic variation sometimes produces a pheno-
typic continuum, such as that of size in many
animals, or the propensity to call in male crick-
ets (*Gryllus integer*; Cade, 1981), and sometimes
gives rise to a number of discrete morphs or
strategies underlain by one or a few genetic
switches (an example is independent versus satel-
lite mating in the ruff, *Philomachus pugnax*;
Lank *et al.*, 1995). Many heritable traits have
been demonstrated to be relevant to fitness.
Indeed, Houle (1992, 1998) has shown that coef-
ficients of genetic variation are often *higher* in
those traits that are fitness-relevant than those

which are likely to be neutral. Fitness itself can
even be substantially heritable (for further
discussion of this paradox, see Sections 32.1.2
and 32.1.3).

Genetic variation is just as common in
humans as would be expected from the study of
other species. For example, the genes coding for
the serotonin and dopamine transmitter–recep-
tor systems in humans are massively and ubiq-
uitously polymorphic in the human population
(Cravchik and Goldman, 2000). Given that
these systems seem to be intimately involved in
emotional responsiveness to the environment, it
is likely that such variation is highly relevant to
fitness (see Section 32.2, below). A few of the
traits which have been established to be signifi-
cantly heritable are listed in Table 32.1, along
with, where known, their relationships to fit-
ness-relevant outcomes. After an overview of
this table, it cannot possibly be argued that the
only traits which display genetic variation are
those which are functionally superficial.

How does variation persist, when some of the
variants can clearly reduce fitness? Two main
classes of mechanism have been identified, and
the next two sections briefly review them in
turn. Both rest on the axiom that variation in a
biological population is the product of two
forces: mutation, which introduces polymor-
phism, and selection, which removes it. In the case
of a trait affected by a single gene where one allele
has consistently higher fitness than all others,
and mutations are rare, Fisher's fundamental

Table 32.1 A selection of characteristics in humans that display heritable variation, and effects on fitness where known

Trait	Fitness effects
Stature	Positive for men, may be sexually disruptive
Personality	Various effects on life expectancy, morbidity, mating success
Vulnerability to schizophrenia	Reduced life expectancy and reproductive success
Vulnerability to depression	Morbidity and effect on relationships
Intelligence	Increases marriage probability for men, but in modern populations decreases family size
Attitudes	Unknown
Handedness	Left-handedness reduces life expectancy, possible frequency-dependent combat advantage

theorem means that heritability will indeed drop to zero. However, if many genes, and thus many possible targets for mutation, are involved, or if the relative fitness of different alleles fluctuates, then considerable standing heritability can be maintained (Maynard Smith, 1998).

32.1.2. **Fluctuating selection**

Biological changes that have fitness benefits will very often have costs too. This is because organisms are generally engaged in compromising between different goals that are all relevant to fitness, but involve zero-sum trade offs. To give a classic example, growing large may lead to success in intra-specific competition, but it delays the onset of reproduction (for many other examples of trade-offs, see Roff, 1992). Where a genetic variant increases or prolongs the expression of a mechanism, such as growth, it will produce both the benefits of increased size and the costs of delayed maturity. Thus, alleles, if they have benefits, will often have costs too.

The fitness of a particular copy of an allele is a function of its immediate environment. Relatively small ecological changes are sufficient to affect allelic fitness, by either favouring the benefits of some allele, or disfavouring its costs. Nowhere has this been more clearly demonstrated than by Peter Grant and colleagues, in a long series of investigations of Darwin's finches (*Geospiza* spp.) in the Galapagos (Grant, 1986; Grant and Grant, 1989). Not only do different islands, by subtle ecological variations, produce different relationships of beak size to fitness, but the fitness optimum on any given island fluctuates dramatically over time. For example, a dry year in 1977 reduced food availability on the island of Daphne, favouring larger birds with deeper beaks who could open large hard seeds. Selection was so strong that by 1978, the average body size of a young finch on Daphne was 0.31 standard deviations higher than it had been in 1976, and beak depth had increased by 4% (Grant, 1986). However, with the return of the rains in 1978, smaller, soft seeds would have become abundant once more and this selection possibly reversed. Change on this order is far too rapid for Fisher's fundamental theorem to operate and drive a particular beak genotype to fixation. Instead,

finch populations maintain high levels of genetic diversity, as alleles that one year were becoming rarer flourish in the next. In general, the more ecological conditions fluctuate, the more diversity is retained (MacKay, 1981).

Trade-offs and fluctuating selection also affect behavioural dispositions. To give one example, in the Trinidadian guppy (*Poecilia reticulata*), there is heritable variation in behavioural traits that affect the probability of survival in the presence of a piscivorous fish (Dugatkin, 1992; O'Steen *et al.*, 2002). Guppies that come from populations living upstream of waterfalls, where there are no such predators, are bolder and less likely to survive in the presence of a pike, whereas those downstream show enhanced ability to do so. These effects are heritable, and thus not based on individual experience with predators. When predators are introduced into previously predator-free streams, change in the population distribution of behaviour in the presence of predators is rapid. However, when predators are removed, circumspection in the presence of predators is very rapidly lost, and within 20 years or so, the populations are like those with no history of predation at all (O'Steen *et al.*, 2002). This suggests that anti-predator vigilance is imposing costs—in terms, for example, of lost foraging or mating time—as well as providing benefits, so selection will move the population distribution around in response to local predation intensity. There is gene flow between different guppy populations, and so, if the population of guppies is considered *in toto*, there is a normal distribution, underlain by genetic polymorphism, of anti-predator vigilance, even though for any specific guppy, there may be a unimodal optimum.

Such interactions can be even more complex, as Dingemanse *et al.* (2002, 2003, 2004) have shown in a series of exquisite recent experiments on the great tit, *Parus major*. Individuals of this species differ on a behavioural dimension called exploration, with high scorers being aggressive and bold in exploring the environment, and low scorers exploring less freely and showing low levels of aggression. Exploration is consistent within individuals and substantially heritable ($h^2 = 0.3–0.6$). Dingemanse *et al.* (2004) show that in poor years, when food resources are scarce, there is a linear positive

relationship between exploration score and the probability of survival for females. This is because the bolder individuals are more successful at locating and competing for what resources there are. However, in years of abundance, when there is mast seeding of beech trees, there is a strongly negative linear relationship between female survival and exploration score. The authors suggest this may be because high-scoring individuals become involved in dangerous and costly aggressive encounters which, with resources limitless, have no benefit. For males, the patterns are diametrically opposite. Males are generally dominant in this species, and much of their effort is directed to defending territories. In poor years, males lower in boldness do well. This is because, with higher overall mortality, competition for territories is relaxed, and thus aggressive interactions with other males are less important. However, in good years, more fledglings survive and compete for territories, and so there is increased male–male aggression. Here, males with a high exploration score fare better.

The great tit experiments show that levels of exploration have both costs and benefits: costs in terms of getting into aggressive encounters, with all the harm that can bring, and benefits in terms of holding resources or territories when these are limited. The optimal balance between these costs and benefits depends on exact local conditions and the sex of the individual. As these vary, the overall population maintains a normal distribution of exploratory tendencies, and genetic polymorphism underlying it.

Another mechanism that is often discussed as a possible reason for the maintenance of variation is negative frequency-dependent selection (e.g. in Buss and Greiling, 1999). This is the situation where the fitness advantage of an allele declines as it becomes more common in the population. However, because conspecifics are part of the environment, negative frequency-dependent selection is just a sub-case of fluctuating selection, where the relevant parameter is the distribution of surrounding individuals. It has long been recognized that negative frequency-dependent selection can in theory lead to the maintenance of polymorphism (Maynard-Smith, 1982), though it has been harder to demonstrate empirically that such a

mechanism is in operation. One such demonstration comes from the bluegill sunfish, *Lepomis macrochirus* (Gross, 1991). Males of this species can either be 'parental' or 'cuckolding', with the former delaying reproduction and building nests, and the latter maturing small and early, and sneaking into nests built by other males. Gross (1991) shows that the reproductive success of the cuckolding males is high when they are rare in a colony, but declines steeply as they become more common. Thus, selection must produce a dynamic equilibrium between the frequency of cuckolds and parentals.

In summary, then, fluctuating selection can maintain genetic diversity wherever there are costs and benefits to the phenotype associated with a particular allele, and varying local conditions (including the distribution of competitors) favour different balances between the costs and benefits. Possible human examples are discussed in Section 32.2.

32.1.3. **Fitness indicators**

Fitness itself can display heritable variation. This appears paradoxical given Fisher's fundamental theorem, since selection might be expected to winnow low fitness alleles. A related phenomenon is the so-called 'Lek paradox' (Rowe and Houle, 1996). Females of many species select the mates of highest phenotypic quality, which might be expected to quickly use up heritable variation in male quality, yet such variation is observed to persist. For example, male peacocks (*Pavo cristatus*) with elaborate trains have increased reproductive success, and their offspring have better physical condition (Petrie *et al.*, 1991; Petrie, 1994). Since train elaboration is heritable, non-elaborate trains might be expected to disappear very rapidly. Yet this does not happen.

A solution to this paradox is that variation in many genes—perhaps most of the genome—affects general condition, as expressed in characteristics like train elaboration. There are thus numerous targets for mutations affecting condition, and condition becomes an index of the mutational load that the individual is carrying. General condition related traits affected by numerous genes are known as 'fitness-indicator' traits. The most widely discussed non-human

example is physical symmetry (see Moller and Swaddle, 1997). To reiterate the difference between fluctuating-selection traits and fitness-indicator traits, in the former case there are trade-offs, whereas in the latter, there are no disadvantages associated with increasing the trait. Selection is directional and uniformly positive. However, mutation affecting multiple genes is constantly introducing variation, which selection takes time to remove. The trait thus serves as an index of mutational load, and may consequently be used in mate choice. Examples of possible fitness-indicator traits are discussed in Section 32.3.

32.2. **Fluctuating selection models**

An explicit application of fluctuating selection and trade-off ideas to human personality variation is advanced by Nettle (2005, and in press a). Nettle argues, drawing comparisons with animal research, that the variation in the major personality continua described by psychologists such as Costa and McCrae (1992) has both positive and negative effects on different components of fitness. For example, extraversion represents sensitivity to rewards available in the environment.

Increasing extraversion increases the number of sexual partners, including extra-pair copulations. On the other hand, those scoring highly in extraversion, since they are drawn to risky activities, have an elevated probability of hospitalization through accidents (Nettle, 2005).

Similar hypotheses can be advanced for the other 'Big Five' personality domains (Table 32.2). The argument is that varying levels of the traits produce particular behavioural strengths and weakness, and the optimal combination of these in terms of fitness depends on very precise characteristics of the local environment, including the surrounding population. Thus, the human population considered *in toto* retains a normal distribution. For the cases other than extraversion, many of the behavioural costs or benefits have already been demonstrated empirically by psychologists not working within an explicitly evolutionary framework, and so the adaptive significance of the trade-offs has not been spelled out. Agreeableness, for example, is positively associated with harmonious interpersonal relationships, but negatively associated with status gain amongst male executives (Caprara *et al.*, 1996; Suls *et al.*, 1998; Boudreau *et al.*, 2001). Agreeableness is sexually dimorphic, with females having a higher level than males on average (Budaev, 1999; Heaven *et al.*, 2000). This finding

Table 32.2 The 'Big Five' personality domains, along with possible advantages and disadvantages of increasing levels, and relevant references

Domain	Benefits	Costs
Extraversion	Mating success; social allies; exploration of environment	Physical risks; reduced family stability
Neuroticism	Vigilance to dangers; striving and competitiveness	Stress and depression, with interpersonal and health consequences
Openness	Creativity, with effect on attractiveness	Unusual beliefs, depression, psychosis
Conscientiousness	Attention to long-term fitness benefits; enhanced life expectancy	Missing of immediate fitness gains; obsessionality; rigidity
Agreeableness	Harmonious interpersonal relationships; valued coalitional partner	Failure to maximize selfish advantage; disadvantageous in status competition

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From Nettle (in press). For references see text.

is robust across several cultures, and might be argued to reflect differing influences of status and social connection on fitness in the two sexes over evolutionary history. Perhaps an extreme case of the low-agreeableness life-history strategy is sociopathy. Mealey (1995) argues that sociopathy is maintained as a frequency-dependent variant, since sociopaths require a majority of trusting individuals to exploit.

Conscientiousness is associated with increased life expectancy (Friedman *et al.*, 1995), probably through more careful and hygienic behaviours, but negatively associated with taking short-term mating opportunities (Schmitt, 2004), and may even be associated with obsessive–compulsive type traits (Austin and Deary, 2000). Openness to experience is associated with artistic creativity (McCrae, 1987), and this in turn has been argued to be linked to attractiveness (Miller, 2000a). For example, in a vignette study, women find men described as creative attractive, especially at the most fertile phase of the ovulatory cycle (Haselton and Miller, in press). Poets and visual artists of both sexes also have more sexual partners than non-producers in these domains (Nettle and Clegg, 2006). However, artistic groups are also distinguished by high rates of mental illness (Andreasen, 1987; Jamison, 1989), and reduced life expectancy, especially through suicide (Kaufman, 2003). Openness to experience is elevated in groups of patients with affective disorder (Nowakowska *et al.*, 2004), and the Unusual Experiences schizotypy scale, which is elevated in schizophrenia patients as well as poets and artists (Nettle, in press b), is correlated with Openness to Experiences (Rawlings and Freeman, 1997). Nettle (2001) thus argues that the openness to experience spectrum is subject to trade-offs. Increasing it increases the probability of socially valued, sexually attractive creative output, but also increases the risk of damaging psychopathology.

Finally, neuroticism, which relates to the ease of elicitation of negative emotions, has clear negative effects on psychological and physical health, probably due to the chronic activation of stress mechanisms (Neeleman *et al.*, 2002). However, those high in neuroticism are also more achievement-striving and competitive than those lower in the dimension (McKenzie *et al.*, 2000;

Ross *et al.*, 2001). If animal analogies are any guide (e.g. Dugatkin, 1992), they may also have been better at avoiding physical dangers such as predators in the ancestral environment. Thus it is not obvious that even this most personally damaging of characteristics has a uniformly negative effect on fitness.

Another trait that has been given a fluctuating-selection explanation is handedness (Billiard *et al.*, 2005). Right-handedness is the modal pattern across all cultures, but there is a minority of variable size that shows a left-hand advantage. Left-handedness is associated with health costs, leading to reduced life expectancy among left-handers (Coren and Halpern, 1991). On the other hand, there is strong evidence that left-handers, as long as they are rare, have an advantage in adversarial sports (Raymond *et al.*, 1996). It has thus been argued that left-handed individuals under ancestral conditions would have a frequency-dependent advantage in hand-to-hand combat. Billiard *et al.* (2005) produce a model with a fixed fitness cost to left-handedness, through health disadvantages, and a frequency-dependent benefit expressed in combat. The model predicts, at equilibrium, a level of left-handedness that is less than 50% and proportional to the rate of violent combat in the society. In keeping with this prediction, Faurie and Raymond (2005) find that the rate of left-handedness across a sample of traditional societies is proportional to estimates of the homicide rate. This intriguing work awaits further replication.

A final example of a fluctuating-selection explanation of heritable variation comes from work on stature. Pawlowski *et al.* (2000) and Mueller and Mazur (2001) had shown that taller-than-average men have increased reproductive success, apparently due to the enhanced ability to attract mates. This would appear to constitute directional selection. However, Nettle (2002) shows that amongst British women, those with the highest probability of marriage and children are actually below average height. It may be that relatively tall women are found less attractive, or that women growing less tall develop more feminine body shapes. It is certainly the case that growing tall delays puberty (Nettle, 2002). Thus, for stature, selection can be sexually disruptive, tending to increase it in men

and decrease it in women. Since the mechanisms of inheritance of height are not sex-linked, the result is the maintenance of variation.

32.3. **Fitness-indicator models**

The most obvious example of a fitness-indicator trait is physical symmetry. The achievement of symmetry during development reflects a good genotype and benign developmental conditions. Symmetry in humans is associated with physical attractiveness (Hume and Montgomery, 2001; Simmons *et al.*, 2004) and mating success (Gangestad *et al.*, 2001). It is likely that the psychology of attraction has become responsive to cues of symmetry precisely because symmetry is condition-dependent in the manner required. As physical symmetry is such a clear example of a fitness-indicator trait, one way of identifying other such traits is finding that they correlate with physical symmetry.

Geoffrey Miller has argued, for example, that general intelligence is a fitness-indicator trait (Miller, 2000a,b). The basis of variation in general intelligence is not well understood, though it is significantly heritable (Bouchard and McGue, 1981) and probably reflects a number of systemic properties of the central nervous system (MacKintosh, 1998). Not only is IQ positively correlated with physical symmetry (Furlow *et al.*, 1997), but those measures of IQ which load most heavily on the general factor of intelligence, *g*, are precisely those with the highest physical symmetry correlations (Prokosch *et al.*, 2005). Intelligence is also correlated with perceived attractiveness (MacIntyre and West, 1991).

There are relatively few studies of achieved fitness and general intelligence. Increasing intelligence increases probability of marriage for men in modern populations (Taylor *et al.*, 2005), at least partly because it is associated with gain in social status. However, for women, both intelligence and social status actually decrease probability of marriage (Taylor *et al.*, 2005). Moreover, because higher socio-economic groups have smaller family sizes, the effect of intelligence on overall reproductive success tends to be negative (see MacKintosh, 1998). It seems likely, though, that these patterns are a specific product of highly developed, post-demographic transition societies. It has plausibly been more common in

human history for there to be a manifold of positive relationships between intelligence, status and reproductive success.

Miller also extends his fitness-indicator argument to the cover verbal and artistic creativity more generally (Miller, 2000a). He notes that creative output in artistic domains tends to peak during the years of highest reproductive competition [Miller, 1999; this is also true of output in the fields of science and criminal endeavour (Kanazawa, 2000, 2003), and output is generally diminished by marriage]. As discussed above, creative activity appears to increase attractiveness and mating success (Nettle and Clegg, 2006; Haselton and Miller, in press). Furthermore, Clegg (2006) has shown, in a sample of non-artists, that female raters are able to judge with some accuracy the IQ of a man from an artwork that he has made under experimental conditions. These considerations all suggest that creative activity is functioning to display an underlying fitness-indicator trait of mental ability.

Note, however, that in the case of artistic creativity, there is an overlap of fluctuating selection and fitness-indicator accounts. Nettle (2001) argues that the artistically creative temperament is subject to trade-offs, since increasing creativity is associated with increased mating success on the one hand, but increased risk of psychiatric disorder and reduced life expectancy on the other (see Section 32.2). Miller, on the other hand, sees creativity as a fitness-indicator trait. It is possible to reconcile these two perspectives. Increasing levels of creative temperament does indeed have the costs and benefits proposed by Nettle, but what determines whether an individual reaps the benefits of successful creative activity, or the costs of psychopathology, is general condition. In support of this view, schizophrenia patients and poets score in very similar ways on measures of unusual thought and experience, but differ drastically on measures of social withdrawal and negative affect (Nettle, in press b). Schizophrenia patients have decreased physical symmetry (Yeo *et al.*, 1999), and increased rates of perinatal and developmental disturbances (Kunugi *et al.*, 2001). This suggests that where general condition is poor, a schizotypal temperament is converted into psychopathology, whereas where it is good,

it is converted into creativity and mating success (Shaner *et al.*, 2004).

32.4. **Non-heritable variation**

This chapter has focused on the maintenance of genetically based heritable variation relevant to phenotypic traits. However, stable individual differences are by no means wholly attributable to genetic polymorphisms. Behaviour genetic studies of a wide variety of traits, mainly in developed, Western populations, produce heritabilities of around 0.5, which means that 50% of the variance in the trait is not associated with genetic variation in these populations.

The design of behaviour genetic studies generally allows variation to be partitioned into three categories: that due to heredity, that due to the shared environment, and that due to the unique environment. Shared environmental factors are those parameters which are constant within a given family environment, such as general parenting practices and socio-economic background. Both biological and adoptive siblings have the same shared environment as each other. The unique environment is those factors that differ—or whose effects differ—across individuals in the same household. For example, a child might have an early illness, or premature birth, or obstetric complications, that obviously would not characterize his or her siblings.

One of the most striking findings has been that the shared environment seems relatively unimportant in many cases, whereas unique aspects of the environment can be very influential (Plomin and Daniels, 1987). One interpretation of these findings is that our developing nervous systems have evolved to be sensitive to certain kinds of early cues which lead to the calibration of development. Such effects are very common in other species. For example, in rats, administering glucocorticoid stress hormones to pregnant females has a suite of effects on the offspring. This includes lower birthweight, metabolic differences, and, crucially, an apparently permanent up-rating of the glucocorticoid response to environmental stressors (see Weinstock, 2005, for a review). Although the effects of these phenotypic shifts lead to pathologies such as Type II diabetes in the long term, they can none the less be interpreted as

adaptive (Worthman and Kuzara, 2005). The foetus may be detecting cues that the local environment is hostile, and calibrating the trade-off of investment between immediate and long-term survival appropriately. The stress system in general is an allocation mechanism for switching effort from long- to short-term somatic maintenance, and thus making it more reactive would favour immediate survival. The long-term costs in terms of impaired growth, reduced immune competence and excessive anxiety may simply be irrelevant in a local context where the rate of mortality is very high.

Theory predicts that such developmental calibration mechanisms can evolve where the environment fluctuates, such that selection cannot fix the optimal genotype, but where these fluctuations are not so fast as to require radical recalibration many times during an individual's life. If environmental change were too rapid, then early-life conditions would be no guide to the conditions to be faced later, and a permanent calibration would be maladaptive.

There are a few human phenomena which are suggestive of early-life calibration effects. For example, birth weight is related to basal salivary cortisol levels in human adults, and is also predictor of the amplitude of the cortisol response to an experimental stressor (Wust *et al.*, 2005). Several studies have linked self-reported maternal anxiety or stress during pregnancy with later anxiety, emotional disorders or hyperactivity in the child (see O'Connor *et al.*, 2002; Weinstock, 2005). The effect is found even when controlling for post-natal maternal depression, which suggests that a direct endocrine mechanism is at work rather than genetic transmission or post-birth learning. There is also evidence that early-life sexual abuse can permanently affect the regulation of the stress hormone system (Heim *et al.*, 2000).

One area where there appears to be strong evidence of perinatal programming effects is season of birth. In high-latitude environments, season of birth is related to birth weight, and historically at least, it has been related to long-term survival and reproductive success (Doblhammer and Vaupel, 2001; Lummaa and Tremblay, 2003). It is likely that winter-gestated babies experience cues of environmental hostility such as lowered energy availability from the

mother, or maternal hormonal or immune changes. Several studies have found that people gestated in winter in temperate latitudes display, as adults, higher levels of sensation or novelty seeking (Chotai *et al.*, 2003; Joinson and Nettle, 2005). These are personality dimensions similar to extraversion and characterized by elevated risk-taking. Season of birth is also a risk factor for several psychiatric disorders, which suggests that it might be associated with elevated neuroticism or stress susceptibility (Castrogiovanni *et al.*, 1998). Thus, it would not be implausible to speculate that winter gestation, by introducing cues of environmental hostility, calibrates the developing offspring towards a shorter-term survival strategy of increased risk-taking and greater harm-avoidance. This calibration would appear to be lifelong.

Such effects may be quite numerous, and their study is just beginning. It is not yet clear what the relevant critical periods and cues are. It is, however, clear that they can be post-birth as well as perinatal. One post-birth calibration effect that is well-studied in humans is that of either father absence, family conflict or childhood stress on sexual maturation in women. Girls who have been abused, stressed or have no father figure present reach puberty more quickly, begin sexual behaviour earlier, become pregnant earlier, and have greater interest in infants, than controls (Belsky *et al.*, 1991; Hoier, 2003; Maestripieri *et al.*, 2004; Vigil *et al.*, 2005). This is consistent with a calibration model in which stress or father absence is a cue of an environment in which survival may be curtailed, and so reproduction should be brought forward (Belsky *et al.*, 1991; Belsky, this volume, Chapter 18; Bereczkei, this volume, Chapter 19). A recent extension of this model links relatively hostile early conditions to reduced agreeableness and conscientiousness in adulthood as well as to sexual behaviour changes (Figueredo *et al.*, 2005).

Many of these calibrational cues, such as season of birth, or father absence, will not be shared by siblings, and so their effects on long-term individual differences such as personality would show up in the unique environment rather than the shared environment in behaviour genetic studies. Thus, a suite of developmental calibration effects may well explain the bulk of the non-heritable variation in individual difference traits.

32.5. Conclusions

In conclusion, we have seen that there is abundant evidence that the 'film' of individual differences that overlays our shared psychological architecture is not really that thin. In fact, the enduring differences between individuals are quite marked, and relevant to fitness. This situation is not unique to humans; it is the norm in all animal populations.

Differential traits tend to exhibit non-zero heritabilities in all the human populations that have been studied so far. I have argued that there are two classes of explanation which may account for the maintenance of such genetic variation. On the one hand, there are trade-offs between different classes of response, and the optimum fluctuates with local conditions, such that a spectrum of different strategies is maintained in the population. Trade-off accounts seem particularly relevant to personality traits, which represent continua of adaptive strategies.

On the other hand, there are fitness-indicator traits, where selection is directional, but such a large number of genes contribute to the trait that a level of variation is maintained. It was suggested that variation in intelligence might be maintained this way.

Finally, there is abundant evidence of non-genetic effects, mostly from unique early-life factors. In at least some cases, such calibration may represent the functioning of adaptive mechanisms designed to optimize the phenotype to its local setting.

Empirical research in the evolutionary psychology of individual differences is still in its infancy, and it is yet to be seen how developmental calibration, fluctuating selection, fitness-indicator traits, and other mechanisms all interact in maintaining the levels of individual differences that we observe in the human population.

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