

Genes, Environment and Sport Performance

Why the Nature-Nurture Dualism is No Longer Relevant

Keith Davids¹ and Joseph Baker²

1 School of Human Movement Studies, Queensland University of Technology, Kelvin Grove, Queensland, Australia

2 School of Kinesiology and Health Science, York University, Toronto, Ontario, Canada

Contents

Abstract	1
1. The Nature-Nurture Debate in Psychological Science	3
2. Environmental Constraints on Performance	4
2.1 Quantity and Quality of Training	5
2.2 Access to Resources	6
2.2.1 Coaches	6
2.2.2 Parents	7
2.2.3 Culture	7
2.2.4 Relative Age	7
2.2.5 Size of Birthplace	7
3. Genetic Constraints on Sports Performance	8
3.1 Psychological Research	8
3.2 Studies of Genetic Constraints on Skill Acquisition and Performance	9
3.3 Issues with Twin Studies	10
3.4 Physiological/Molecular Biological Research	10
3.5 Skeletal Muscle and Skeletal Muscle Energy Systems	11
3.6 The ACE Gene	11
3.7 Stochasticity in Cellular Regulation Processes	13
4. The Fallacy of a Dualist 'Debate': Alternative Approaches to Nature and Nurture	14
5. Where to from Here? The Future of the Nature-Nurture Debate	16
6. Conclusions	17

Abstract

The historical debate on the relative influences of genes (i.e. nature) and environment (i.e. nurture) on human behaviour has been characterised by extreme positions leading to reductionist and polemic conclusions. Our analysis of research on sport and exercise behaviours shows that currently there is little support for either biologically or environmentally deterministic perspectives on elite athletic performance. In sports medicine, recent molecular biological advances in genomic studies have been over-interpreted, leading to a questionable 'single-gene-as-magic-bullet' philosophy adopted by some practitioners. Similarly, although extensive involvement in training and practice is needed at elite levels, it has become apparent that the acquisition of expertise is not merely about amassing a requisite number of practice hours. Although an interactionist perspective has been mooted over the years, a powerful explanatory framework has been lacking. In this article, we propose how the complementary nature of degenerate

neurobiological systems might provide the theoretical basis for explaining the interactive influence of genetic and environmental constraints on elite athletic performance. We argue that, due to inherent human degeneracy, there are many different trajectories to achieving elite athletic performance. While the greatest training responses may be theoretically associated with the most favourable genotypes being exposed to highly specialised training environments, this is a rare and complex outcome. The concept of degeneracy provides us with a basis for understanding why each of the major interacting constraints might act in a compensatory manner on the acquisition of elite athletic performance.

We used to think our fate was in our stars. Now we know, in large measure, our fate is in our genes (James Watson, 1989 cited in Vitzthum^[1]) ((**Author: please provide full publication details for the references you have listed in the footnote so that they can be added to the reference list as per our housestyle**)).¹

What are sports scientists to make of this geocentric view of human behaviour? This article considers one of the most complex and enduring controversies in science and medicine: the 'nature-nurture debate'.^[1-5] Science has a number of such dualisms where strong theoretical arguments are presented for two opposing viewpoints and the nature-nurture issue is, arguably, the most pervasive in its history. For example, in psychology it is known as the 'nativism-empiricism issue', developmental science terms it the 'maturation versus learning debate' and physiology and medicine considers how heredity and environment account for variations in health and human performance.

Put simply, the nature-nurture debate concerns the extent to which an individual is a product of her/his genes or environment, generating questions over the role of genes and environmental influences and experience in a range of human behavioural contexts, including athletic, educational and musical performance and achievement. For this reason, in psychological medicine, behavioural geneticists are interested in human variations in key factors, including health, development, cognitive and movement abilities, perceptual skills, social attitudes, psychopathology and personality, related to functioning in a range of domains.^[6-9]

How environmental and genetic constraints correlate or interact to shape performance variations in sport and exercise is a question of increasing interest in sports medicine, sports pedagogy and sports psychology.^[10-12] February 2001 marked the publication of the draft human genome, signalling the arrival of biology in the genomic era. Whilst questions of the relative roles of nature and nurture in the past may have been addressed from the standpoint of academic interest, in recent times there have been increasing reports of medical interventions and attempts to use genetic knowledge for performance enhancement in sport.^[13,14]

In particular, there have been some efforts in molecular biology to identify single gene variants with the potential to profoundly impact on individual performance or the propensity to lead to a specific disease (e.g. a gene responsible for physical power, the propensity to exercise, or for breast cancer).

In sport, this 'single gene as magic bullet' philosophy, favoured by some molecular geneticists, has led to claims that elite performers are born to succeed. This approach is exemplified by attempts to identify sprinters and endurance runners on the basis of differing alleles (i.e. forms) of a single gene known as α -actinin-3.^[15,16] There have been similar claims on the roles of different variants of the ACE gene in endurance and power events such as mountaineering and running.^[17] In those responsible for managing elite sports performance, the belief in the potential impact of single genes is perhaps more prevalent. For example, in September 2000, *Scientific American* published a vision of the Olympic Games in the year 2012, predicting the widespread

¹ Although research reviewed in this section is restricted to sport performance, similar noteworthy developments have also been made in exercise psychology (e.g. Podewils et al., 2005; Schuit, Feskens, Launer, & Kromhout, 2001).

existence of gene-transfer technology (popularly known as gene or cell doping) whereby specified artificial DNA material is coupled to well understood viral delivery mechanisms and inserted directly into the nuclei of muscle cells^[18,19] (also see Miah^[13] and McCrory^[20]). More recently, it was widely reported that the Sea Eagles, a rugby football league team from Manly, Australia, tested 18 players for variations in 11 different exercise-related genes in order to enhance the specificity of training programme design.^[21] The same article highlighted the possibility of sports clubs genetically profiling athletes to understand susceptibility for certain injuries, map genetic suitability for specific team positions and roles, and to gain insights into player development into various sports or physical activities.

These alarming trends by some elite sport scientists to use the 'single-gene as magic bullet' philosophy as a platform for optimising performance places the spotlight again on the nature-nurture debate. Besides obvious ethical issues, reports of gene-profiling and gene-transfer technology raise more general theoretical and practical questions about the nature of genetic and environmental constraints on skill acquisition and performance, and propensity to participate in physical activities.^[22] Although most knowledge on the effects of genes on athletic performance has been gained from research in molecular biology, genetics, genomics and medicine, this research also has relevance for many areas of sports science and medicine, such as sport and exercise psychology.^[23]

Clearly, sports scientists need to understand the current state of the nature-nurture debate in science in order to make sense of the pending practical applications of gene-transfer technology. In this article, we begin by historically reviewing the nature-nurture debate in science, focusing specifically on psychological medicine in which it has flourished. Secondly, we evaluate evidence for both nurture and nature constraints on sport performance and achievement. There is growing awareness in science of 'the complementary nature', as Kelso and Engström^[24] so aptly entitled their critique of the historical tendency to attempt to explain phenomena on the basis of dualist positions and theoretical stances. Their thesis is that a systems biological approach

can help categorise natural phenomena as exhibiting strong cooperative tendencies to interact as well as tendencies to function separately, the emergence of which can characterise the relationship of genes and environments. Here we note how this is an apt description for sports medicine and sport science to understand the relationship between genes and environment. The 'complementary nature' of phenomena in the natural world suggests that it is highly important for geneticists to identify many single gene variants, although the role of these genes in regulating behaviour needs to be framed by their overarching tendencies to network and to cooperate or compete with environmental constraints. In this respect, our article highlights the need for sports scientists to adopt a multidisciplinary perspective in order to gain a detailed understanding of the molecular biological mechanisms of DNA transmission and gene expression, and we discuss how some molecular biological advances may have been 'over-interpreted' by scientists using the ACE gene research literature as an example. Finally, we evaluate the limitations of current understanding raising questions over the current relevance of the debate.

1. The Nature-Nurture Debate in Psychological Science

There is no escape from the conclusion that nature prevails enormously over nurture when the differences of nurture do not exceed what is commonly found among persons of the same rank of society and in the same country.^[25]

Although it was Francis Galton^[25] who first used the phrase 'nature and nurture' to describe the sources of individual differences in 1874 (and made the subsequent 'conclusion' outlined above in 1883),^[25] arguments over the role of environmental influences versus innate characteristics can be traced back to the Platonic dialogues and Aristotelian philosophy of ancient Greece. It is only in the past 130 years, however, that these issues have come to dominate scientific (as well as non-scientific) discussions.

Increased interest in this area was undoubtedly driven to a large extent by the publication of Darwin's *Origin of Species* in 1859, which informed Galton's^[25,26] contributions most notably, but also those of William James^[27] and Lewis Terman.^[28]

Much of this work was based on the conclusion that biology was the chief constraint to expertise and achievement, known as biological determinism. Indeed, Terman's appropriately titled *Genetic Studies of Genius*,^[28-30] one of the longest and most ambitious longitudinal studies in history, was based primarily around this notion. In 1918, Fisher introduced the statistic of 'heritability', which can be defined as "the proportion of the total phenotypic variance that is associated with genetic variance in a specific sample with a specific genetic composition and environmental context."^[1] The heritability statistic to describe individual variation is captured in a biometric model, which includes the influence of individual alleles, dominant alleles and environmental variance in a studied sample.

Conversely, work from the environmentalist camp during the same period also reinforced this dualist 'all or nothing' approach – the idea that individuals start as a '*tabula rasa*' (blank slate) with no innate traits or characteristics, and that all forms of learning and behaviour result from interactions with our environment. This social deterministic viewpoint is succinctly demonstrated by Watson's^[31] famous boast:

"Give me a dozen healthy infants and my own specified world to bring them up in, and I'll guarantee to take anyone at random and train him to become any kind of specialist I might select – doctor, lawyer, artist... regardless of his talents, penchants, tendencies, abilities, vocations and race of his ancestors."

The history of this debate in psychological medicine is marked by radical shifts in opinion, usually driven by social/cultural factors.^[32] For example, the Nazi atrocities of the Second World War were strongly rooted in biological determinism and after 1945, political and intellectual thought changed to endorse positions based on the concept that differences between individuals were the result of opportunities and experience, coinciding with the dominance of the Marxist ideology of Dialectical Materialism in the Eastern European block, while opposing ideology that sought to separate individuals on the basis of biology were met with derision and scorn. A similar social upheaval occurred with the publication of Herrnstein and Murray's^[33] *The Bell Curve* in 1994.

Despite the prominence of these extreme views in the history of psychological medicine, it has become clear that many researchers misunderstand the statistic of heritability and confuse it with the concept of heritability defined as the transmission of a trait from parent to progeny.^[1] Regardless, few researchers today would argue that neither environmental nor biological factors are important and there is very little to suggest the nature-nurture debate could be resolved in favour of one constraint to the complete exclusion of the other. More recent nature-nurture studies seem focused on questions like:

- What factor is most important?
- How much of the variability in condition 'x' can be accounted for by genetic (or environmental) variables?
- When, during the lifespan, is a genetic or environmental constraint more influential in shaping behaviour?

Despite continued attention to these issues and considerable advancement in the methods of examination, it is unlikely they will be resolved soon. This is not to say that understanding of genetic and environmental influence has not advanced. It certainly has; moreover, these advances have obvious importance for understanding the development of expertise and talent identification in sports and physical activities. Individual differences between performers remains a central issue in many areas of sports medicine and science, leading to crucial questions such as: why do some athletes benefit more from training and practice than others? How can specific athletic potential be identified and developed? To what extent can genetic testing provide information for specifically designing training and practice programmes to suit individual athletes? Is there an innate drive to exercise? Our aim in this article is to overview current understanding of the role of the environment and genes in constraining physical performance and the acquisition of expertise. Next, we review the current level of knowledge regarding these issues.

2. Environmental Constraints on Performance

While 'nature' refers to the innate characteristics an individual contributes to their performance, 'nur-

ture' makes up those qualities that result from one's experiences. That experiential or environmental factors have a tremendous influence on learning and performance is undeniable. In this section we provide a synopsis of the range of environmental factors that contribute to sport performance.

2.1 Quantity and Quality of Training

In behavioural science, there are few relationships as robust as the one between time spent practising and improvements in performance. Examinations of skills ranging from cigar rolling^[34] to reading inverted text^[35] have supported the strong positive relationship between these variables. Despite the strength of this relationship, the specific profile of this association is a topic of debate, with some arguing that it best fits a power curve^[36] or an exponential curve,^[37] while others^[38] argue that learning curves are varied and diverse due to the different rates at which individuals satisfy unique constraints on them during practice. Although practice eventually becomes asymptotic, longitudinal examinations of practice over time indicate that improvements can continue even after years of involvement.^[34]

Much of our understanding about environmental influences on performance comes from studies of sports expertise. In 1993, Ericsson et al.^[39] produced a seminal paper on the role of practice and expert development that shaped a great deal of the research that followed. Their position (based on the work of Ericsson et al.,^[40] Simon and Chase,^[41] and others) was that, with proper attention to what they called 'deliberate practice' (i.e. relevant, effortful activities done with the specific goal of improving performance), healthy individuals could prevent performance improvements from tapering off. Ericsson et al.^[39] advocated that the relationship between time spent in deliberate practice was monotonic (i.e. linear) rather than a power or exponential function. Their research with elite and non-elite musicians supported the conclusion that the primary factor distinguishing performers at different skill levels was the number of hours spent in deliberate practice. For example, in their examination of violinists, experts had accumulated >7400 hours of deliberate practice by 18 years of age, compared with 5300 hours for intermediate-level performers and 3400

hours for lower-level performers. Despite originating with musicians, Ericsson and his colleagues (for a recent review see Ericsson^[42]) have repeatedly concluded that the deliberate practice framework also applies to the development of expert athletes.

To date, psychologists examining the application of the theory of deliberate practice sport performance have investigated a range of sports. In general, these studies have encountered problems with applying the deliberate practice framework to the attainment of sport skill. For example, athletes tend to rate relevant practice activities as being very enjoyable and intrinsically motivating,^[43,44] which contrasts with a key component of Ericsson et al.'s^[39] definition of deliberate practice activities. Furthermore, there is some concern about which forms of athletic training constitute deliberate practice. In the original work of Ericsson et al.,^[39] only practice alone was seen as meeting the requirements for deliberate practice. In studies of deliberate practice in sport, there are few, if any, training activities that meet the original criteria in the definition set out by Ericsson and others.^[39] Helsen et al.^[44] suggested that the specifications regarding what constitutes deliberate practice in sport should be extended to include all relevant forms of training.

Despite these problems, the relationship between hours of training and level of attainment is typically consistent with the tenets of the deliberate practice framework. Expert athletes accumulate more hours of training than non-experts.^[43-45] Not only do experts spend more time overall in practice, they also devote more time to participating in activities deemed most relevant to developing the essential component skills for the highest level of performance.^[46,47] For example, Baker et al.^[46] found that expert athletes from basketball, netball and field hockey accumulated significantly more hours in video training, competition, organised team practices and one-on-one coach instruction than non-expert athletes.

The approach advocated by Ericsson and his colleagues,^[39] where expertise is simply the end result of amassing the requisite number of hours of training, has come under some criticism. For example, this approach reinforces the idea that specialisation during early stages of development is necessary in order to attain elite performance as an adult. The

early specialisation approach is associated with several negative consequences,^[48,49] and researchers^[48,50] have recently challenged the necessity of early specialisation in the development of elite performance as an adult. They proposed that a more diversified involvement during early development is equally beneficial for acquiring requisite abilities. Baker et al.^[50] studied experts from field hockey, basketball and netball and found that a wide range of sports was typically performed during early stages of development. This broad involvement was gradually decreased as the athletes developed until they 'specialised' into their main sport. Moreover, Baker et al.^[50] found a negative correlation between the number of other sports played and the number of sport-specific training hours required before making their respective national teams, suggesting that participation in other indirectly relevant activities may augment the physical and cognitive skills necessary in the athletes' primary sport. There is evidence to suggest that some general capacities are transferable across similar activities.^[51-54]

Furthermore, Côté et al.^[55] also suggest that play-like activities during the early stages of training are beneficial for skill development in many sports. In early development, activities that are inherently enjoyable and motivating may be necessary to provide an impetus to continue training during times when more diligent, effortful practice is required. Without this pleasurable involvement, athletes run the risk of dropping out of sport.^[56]

The notion that play may be equally beneficial to skill development during initial stages of involvement is not unsupported. During early development, progress comes rapidly and easily because there is so much room for performance improvements. During this period, it is likely that any form of relevant participation would provide improvement, regardless of whether this participation is in the form of direct involvement through sport-specific training or indirect involvement through sports that share common basic characteristics. However, as performance progresses, enhancements become increasingly difficult to achieve until a point where focused training on specific areas of weakness becomes the only means of advancement. At this point, highly structured practice becomes the most effective form of training. Although work in this area continues and

these results should not be seen as conclusive, the data suggest that the relationship between practice and proficiency is more complex than originally thought.

Considerable debate remains over the extent to which training alone determines an athlete's ultimate level of proficiency;^[57,58] however, there seems to be little doubt that attention to high-quality training is critical for promoting the development of expert performance. The only issue seems to concern the nature of the practice constraints that interact with and shape the quality of training processes in high-level sport. These constraints can be captured as environmental or organismic in nature,^[10] and we discuss several examples in section 2.2.

2.2 Access to Resources

In a recent review, Baker and Horton^[59] identified a number of critical secondary factors that moderate the influence of primary factors such as training. The availability of essential resources can significantly influence the ability to engage in the required amounts of high-quality training. We consider several of these resources in sections 2.2.1–2.2.5.

2.2.1 Coaches

Coaches play a critical role in optimising an athlete's training time, in some cases having complete control over the practice environment. Indeed, a key characteristic of expert coaches is meticulous planning.^[60] Researchers have dissected practices in sports ranging from individual sports such as wrestling and figure skating,^[47,61] to team sports such as volleyball^[47] and basketball.^[62,63] What seems clear is that the structure and content of expert athletes' practice is superior to that of non-experts.

In addition to the ability to maximise training time, proper coaching is critical for promoting adaptations to more advanced levels of learning and development. As learners advance in skill development, cognitive, physical and emotional needs change and the role of the coach changes accordingly. For example, Côté et al.^[55] suggested that, during early phases of development, coaches should emphasise opportunities to develop fundamental motor skills and general abilities that will form the basis for more advanced development in the future. Only

later in development should the focus change to more technical aspects of training and a greater attention to 'deliberate' types of practice. The ability of the coach to use domain-specific knowledge to optimally structure practice is essential to athlete progression and development.

2.2.2 Parents

Researchers have highlighted the critical role that parents play in promoting the athletic development of their children. In an examination of exceptional individuals across a range of sports and other activities, Bloom^[64] reported that parental resources, such as support, were imperative in nurturing talent. In a more recent examination, Côté^[65] corroborated Bloom's findings.

Both researchers noted that athletes go through stages of development and that the resources provided by parents shift as athletes mature. During early sport development, parents typically provide the initial opportunity to get involved in sports. In essence, parents play a leadership role by initiating sport involvement. As the athlete matures, parental involvement decreases and the performer takes greater control of the decision-making process regarding their future career. Parents continue to provide support in a background role, as providers of financial support and, more importantly, emotional support.^[65]

2.2.3 Culture

A significant and often overlooked factor in the development of athletes is culture,^[59] which some have argued evolves at a faster rate than genetic trait dispositions.^[66] The importance that a nation or community places on a particular sport can have a dramatic influence on any success achieved. For example, in Canada, the sport of ice hockey has become a fundamental component of the national identity.^[67] Recent estimates^[68] suggest that Canada has three times more children playing ice hockey than Russia, Sweden, Finland, the Czech Republic and Slovakia combined. Given these factors, Canada's international success is not surprising. Other countries have similar sport-related associations including Austria with skiing and Kenya with distance running. More research is needed to develop our understanding of how culture constrains the development of expertise in sport.

2.2.4 Relative Age

Another factor that appears to influence the acquisition of expertise is the 'relative age effect' (see Musch and Grondin^[69] for a detailed review of this concept). Many sporting codes group children by age to moderate evaluation and competition; however, research indicates that older individuals in a given age cohort (i.e. that have a greater 'relative age'), report higher levels of proficiency. To date, this effect has been reported in various educational settings^[70,71] and in sports ranging from professional ice hockey and baseball^[72,73] to junior football.^[74]

Two main explanations have been offered to account for the relative age effect. The first is that older players are bigger, stronger, faster and better coordinated than the younger players and thus experience more success and rewards and are more likely to remain involved. Younger peers, on the other hand, experience failure and frustration and withdraw. A second hypothesis is that older players are more likely to be selected to higher competitive representational teams where they receive improved coaching, facilities and playing time compared with their peers. Each of these explanations have clear implications for the development of elite athletes.

2.2.5 Size of Birthplace

Preliminary research has indicated that the size of the city where an athlete spends their developmental years may also affect their likelihood of attaining elite-level performance.^[75,76] In an examination of birthplace size in professional baseball, basketball, ice-hockey players and golfers, Côté et al.^[77] found that the optimal city size for athlete development appears to be between 1000 and 500 000 people. What sets this study apart is that the effect was consistent across team and individual sports and across countries (Canada and US).

While the mechanisms for this 'birthplace effect' are not known, it is likely that a range of factors play a role. For example, adolescents in smaller communities receive more social support, have higher levels of self-efficacy, and experience fewer conflicts with others than those from larger cities.^[78] Furthermore, smaller cities may provide an environment that is more conducive to the development of sports skills by virtue of having more and safer recreational space.^[79] Further research is required to confirm the specific source(s) of this effect, but

these findings reinforce the role that contextual factors play in promoting sports achievement.

Although research on sports expertise has provided a wealth of information about the environmental constraints on the development of expert level performers, less is known about how these variables facilitate or impede performance at lower levels of ability. Further research is needed with intermediate-level performers to complete our understanding of the process of skill acquisition and the role of various environmental constraints.

3. Genetic Constraints on Sports Performance

This section examines evidence for genetic constraints on performance variability.^[1] We focus on the literature in psychological medicine and physiology/molecular biology, which take different approaches to this issue.

3.1 Psychological Research

The field of behavioural genetics in psychological medicine focuses on individual differences. Despite the, at times, acrimonious debate over the role of genes and environment in psychological medicine and related fields, it has been largely ignored in theoretical sport and exercise psychology where systematic research programmes on genetic constraints have been conspicuous by their absence. As with many other contentious issues in psychological research, the dualist approach has failed to capture the 'complementary nature' of the relationship between genetic and environmental constraints, that is, subtle nuances of the complex interrelations between genes and environment.

Although research in this area is still limited, requiring replication and validation, there is consistent evidence supporting the role of genes in determining intelligence (as measured by IQ tests) and personality. Behavioural genetics studies have placed the heritability of IQ at around 50%. Perhaps more interesting is the heritability of personality. Population examinations of a range of personality measures have reported that heritability ranges from 0.30 to 0.50, regardless of the instrument used or the personality trait being measured (for a review see Plomin et al.^[80]).

One of the most productive research programmes examining relationships between genetic factors and psychological outcomes has been MISTRA (Minnesota Study of Twins Reared Apart)^[81] In addition to examinations of general intelligence^[82] and personality,^[83,84] MISTRA has also considered the influence of genes on psychological measures such as attitudes towards work^[85] and job satisfaction,^[86] as well as score on the Stroop Color-Word Test.^[87] Without exception, genes account for a significant portion of the inter-individual variation in these measures. While the proportion of variance accounted for by genes varies depending on the measure and the study sample, no psychological measure has been found that has zero heritability.

A primary limitation of genetic studies of psychological variables is that their role in performance is relatively unknown. Physiological traits such as muscle fibre type and aerobic capacity have been clearly linked to performance by specific underlying mechanisms. However, the links between psychological traits and performance are not as clear (e.g. how does one's attitude towards work specifically affect performance?). This state of affairs may exist because (i) research in the field of sports medicine has not evolved to the point where there is a clear understanding of the mechanisms of psychological effects; or (ii) the mechanisms of effect are too complex for current levels of understanding. What is clear, however, is that without unambiguous understanding of how psychological factors affect performance, researchers will be unable to replicate the study designs used in population genetics and molecular biology.

Furthermore, while certain general traits have been linked to heritability, it is now widely accepted in behavioural genetics research that refinement of these traits into domain-specific abilities (e.g. pattern recognition, strategic thinking) occurs through exposure to optimal preparation in specific environments. Plomin and Colledge^[88] have argued that genetic research in psychological science is moving beyond heritability, especially beyond the dualist 'how much' issue (i.e. how much of the phenotype is predicted by either genetic or environmental constraints) towards a greater understanding of the 'how' question (i.e. focusing more clearly on the

mechanisms by which genes can be expressed in specific environments).

3.2 Studies of Genetic Constraints on Skill Acquisition and Performance

There have been some attempts to understand whether expertise, for example captured in the ability to recognise and perform a musical note or collection of notes when sounded, known as perfect or absolute pitch,^[89] has a genetic or environmental basis. Absolute pitch is over-represented in professional musicians, compared with the general population where its incidence has been estimated at 1 in 10 000.^[90] Using surveying techniques, investigators have shown strong familial^[91] and racial dispositions for the ability^[92] in expert musicians. Interestingly, Slonimsky^[93] pointed out that lacking perfect pitch did not hinder the careers of genius composers such as Wagner or Tchaikovsky.

Some early attempts to examine the genetic contributions to performance and acquisition of motor skills also did not support a genocentric view. For example, Williams and Gross^[94] studied the performance of 22 monozygotes (MZ; same genome twins) and 41 dizygotes (DZ; non-identical twins) on a stabilometer balance task over 6 days to examine the genetic contribution to performance and learning. It was expected that between-individual variation in performance and learning would be less in the MZ group compared with the DZ group. This prediction was supported by data indicating a greater intra-pair resemblance for the MZ group only when learning profiles of the twins were compared over time. Intraclass correlations were used to provide an estimate of the proportion of total phenotypic variance in performance and learning accounted for by heritability. Heritability effects were reported as low during the earliest stages of learning, but became increasingly influential later in practice. Moreover, the proportion of variance in performance accounted for by systematic variation of the environment, due to manipulation of constraints during learning by coaches and teachers, peaked early in practice. Although, heritability is made up of genetic and environmental components, these findings imply that there is some potential for influencing performance and learning by manipulating task constraints during practice.

Other work on motor learning and performance has been more ambitious. A study of pursuit rotor tracking performance from MISTRA^[95] examined performance and learning of MZ ($n = 64$ pairs) and DZ ($n = 32$ pairs) twins reared apart. The performance outcome score was time on target over 75 trials (expressed as a proportion of the perfect score of 20 seconds). Fox et al.^[95] observed that performance of the groups was highly similar with both showing substantial improvements over the five trial blocks of the first day. Patterns of variability for both groups were also similar. Over practice, some participants improved more than others leading to increases in the within-group variability by day 3 of the practice regime. However, it is important to note that statistical analysis did not reveal significant differences between the variances of the MZ and DZ twins over trials. The authors noted greater variability in correlations with task performance in the DZ group over trials, although this effect may have been due, in part, to the smaller number of DZ pairs studied. The slope of the regression line for the DZ intraclass correlations for the last 2 days was close to zero, implying a decreasing contribution of environmental factors as practice continued. Despite the large inter-group differences in participants, it was concluded that the consistently larger intraclass correlations for performance in the MZ group compared with DZ twins pointed to a significant genetic component of performance.

Fox et al.^[95] proposed that a model in which genetic and environmental effects were combined best fit the data. The influence of heritability (reflecting both genetic and environmental factors) was high from the first (proportion of performance variance explained = 0.66) to last trial block (0.69). The fact that the influence of heritability was high for the first of the initial five trial blocks (0.66, 0.53, 0.52, 0.55, 0.52, respectively) might be taken as evidence to imply that individuals rely on innate capacities when they attempt to perform a novel task for the first few practice trials. Conclusions of a clear MZ versus DZ distinction for dependent variables such as percentage time on target, rate of improvement of performance over trial block and improvement after a period of rest, were based on genetic influence.

This line of research could be most relevant for clinicians interested in motor learning and the acqui-

sition of expertise. However, more work is needed to clarify the influence of heritability, since in the study by Fox et al.^[95] it seems that motor performance was confused with skill acquisition. They only studied participants over 75 trials and it could be argued that the skill acquisition processes were not examined, but rather motor performance. Finally, more recent work has examined heritability in neuromuscular coordination.^[96] A twin model was used to investigate MZ-DZ variations in accuracy and economy of effort, assessed by analysing kinematic data and electromyographical records of muscle activity. Data showed that heredity accounted for the greatest proportion of MZ-DZ twin differences in movement accuracy and economy for fast elbow flexion movements, not slow velocity movements.

3.3 Issues with Twin Studies

In the literature on genetic variations and performance, there are a number of substantial methodological concerns with twin and adoption studies.^[1,10,97] Classical twin research methodology compares the correlation or concordance rates with the same measures from same sex DZ twins reared together and MZ twins reared together. Identical (MZ) twins share 100% of the same genes and fraternal or non-identical (DZ) pairs only 50% on average. Greater MZ similarity is taken as evidence of the powerful influence of genetic constraints. A popular method has been to study identical twins separated at birth (MZA: monozygotic, reared apart; e.g. MISTRA), and raised under different socioeconomic and cultural constraints. Such a comparison is believed to provide an ideal analysis of nature and nurture effects. Genetic inferences from separated twin studies are based on the assumption that their shared environments were not systematically more similar than a group of unrelated and randomly selected paired individuals, the so-called 'unequal environment assumption'. The problem, according to Joseph,^[97] is that these comparisons are almost impossible to achieve in reality. It is a daunting task to obtain 'pure' separated twin samples that fit the stringent criteria needed for a good test of genetic and environmental constraints. This is because separated twins are often reared by different parts of the same extended family, or are brought up in highly similar cultures and socioeconomic contexts. Some-

times separation was not at birth and intermittent contact was maintained during upbringing.^[1,97] These design weaknesses have led to questions whether there have been strong and clear demonstrations of behavioural similarities between MZAs reared in uncorrelated environments. According to Joseph^[97] "... significant MZA personality and behavioural correlations can be explained plausibly on the basis of the various environmental similarities shared by separated identical twins and by inflated figures resulting from bias and error in the various studies."

3.4 Physiological/Molecular Biological Research

Research in the disciplines and sub-disciplines of biological psychology, medicine, physiology and cell biology has favoured a molecular approach in attempting to identify the genetic influence on individual differences in human behaviour, rather than relying on the twin study methodologies favoured by psychologists. As highlighted in the introduction, a number of candidate genes that contribute to performance variability continue to be identified in the molecular biology and exercise and sports physiology literature (for a review see Davids et al.^[98]). The molecular search for the genetic bases of human capacities, such as physical performance, has engendered strong rhetoric in some quarters, with some molecular biologists calling it the 'biological counterpart' to the holy grail,^[99] and some sport scientists asserting that genes are responsible for up to half the variation in physical performance between individuals within a population.^[100] But does current scientific understanding support the philosophy of biological determinism? Is the 'single gene as magic bullet' rationale a valid basis for investigating the complexities of genetic and environmental constraints on performance in sport? In this section we examine some evidence for the genetic bases of physical performance in humans showing that the bio-deterministic viewpoint is not supported.

There has been an ongoing, concerted endeavour to produce a human gene map for physical performance and health-related fitness.^[101] Most effort to identify single gene variants influencing the genetics of fitness and physical performance has been conducted on ACE insertion/deletion (I/D) poly-

morphisms in different groups of exercisers including elite athletes and non-exercisers. However, the ACE gene is one of a number of candidate genes researchers have associated with inter-individual variability in physical performance.^[101,102] Other studies have examined the relationship between the insulin-like growth factor-1 (IGF-1) genotype and responses to muscle training.^[103] Some research has attempted to determine mitochondrial DNA and α 3-actinin (ACTN3) genotypes in elite national-level athletes in endurance events ($n = 52$) and sprints ($n = 89$). A trend towards higher ACTN3 X/X genotype frequency was observed in the endurance athletes.^[104] A detailed overview of all the work on single gene variants for fitness and performance is beyond the scope of this article. Instead, we shall focus on research in key areas of skeletal muscle and muscle energy systems in humans as well as the ACE gene to exemplify the benefits of a model of nature and nurture interactions to explain fitness and performance variations in humans.

3.5 Skeletal Muscle and Skeletal Muscle Energy Systems

The effects of various environmental factors on gene expression in fibre typology of striated muscle have been studied in humans and animals, with many studies reporting interactive effects between expression of single gene variants and a number of environmental factors including microgravity conditions, training, illness, obesity and aging.^[105,106] In particular, onset of sarcopenia with aging has stimulated increased effort to study the inter-individual variability in adaptation to muscle strength training, causing some researchers to seek a genetic explanation for the individual variations.^[107] Other work has demonstrated how environmental constraints such as training or enforced immobilisation (simulating injury or illness) interact with gene expression in muscle fibre type. Adaptation to environmental constraints appears to mediate gene expression in muscle fibre and myofibril, although the interaction effects can differ extensively. Myosin heavy chain is a highly significant protein, with three functionally distinct forms, and research has attempted to understand how its expression in muscle is affected by environmental constraints such as diet, training and rest.^[105] For example, enforced immobilisation and

exercise training down- and upregulated expression of type I myosin heavy-chain messenger RNA (mRNA), respectively, whereas both environmental factors upregulated expression of type IIx myosin heavy-chain mRNA.^[108]

Twin-based research has revealed for some time that at least 50% of variance in baseline strength and lean body mass is accounted for by genetic factors,^[109,110] with muscle adaptation to strength training also long considered to be high in heritability.^[111,112] Genes that constrain production of proteins are believed to be influential in regulating muscle strength and muscle mass.^[103] For this reason, IGF-1 is believed to be a prime candidate genetic marker for these purposes, although the environmental influence of training is clearly implicated in its effect on muscle mass and strength gains.^[113] In research on muscle fibre gene expression, calcineurin has been proposed to stimulate the slow and fast muscle fibre-type phenotype. This is important given the role of intracellular calcium levels in regulation of slow twitch fibres.^[114,115] In more health-related research, the influence of environmental factors on gene expression has also been demonstrated on different muscle fibre types. For example, dietary regulation of fat oxidative gene expression has been examined for type I (soleus) and type II (extensor digitorum longus) muscle fibres in humans.^[116] Evidence showed that the expression of an array of genes was increased regardless of muscle fibre type.

Finally, the role of the enzyme adenosine monophosphate deaminase (AMPD) has been identified in regulating muscle energy metabolism during intense endurance exercise, with the skeletal muscle-specific isoform of AMPD encoded by the gene *AMPD1*, located on chromosome 1p13-p21.^[117] Although a deficiency of AMPD was considered to be responsible for exercise limitation and decrements in functional capacity, reports suggest that this was not the case, as long as training and experience to an elite level had occurred.^[117]

3.6 The ACE Gene

Over the last decade, the role of ACE gene variants has received considerable attention in the exercise physiology, molecular biology and sports medicine literature bases.^[118-121] Significant inter-

individual variations in response to training of the cardiovascular system have led investigators to question the extent to which genetic diversity may be responsible for the data.^[122,123] In muscle, ACE has the role of degrading vasodilators (i.e. bradykinin and tachykinin) and stimulating production of the vasoconstrictor angiotensin II during physical performance.^[124] Three variants of the polymorphism of the human ACE gene have been found. The presence or absence of a 287 bp fragment, characterises the I (insertion) and D (deletion) allele respectively, leading to three variants (II, ID and DD).

Increasing ACE activity has been linked with the D allele, affecting the degradation of bradykinin and synthesis of angiotensin II. DD participants show increased conversion of angiotensin I to angiotensin II, the latter having a vasoconstriction effect. However, since the conviction of early research, there has been less certainty in the outcomes of studies on ACE gene polymorphisms on endurance performance. For example, work on Kenyan elite middle- and long-distance runners, compared with non-athlete controls, found no differences in genotype frequencies between the groups.^[119] Clearly more work is needed in this area since Rankinen et al.^[101] noted that three cross-sectional association studies published in 2005 reported a positive performance effect for endurance-related phenotypes in the ACE gene.

Angiotensin II seems to have a stimulatory influence on endogenous factors for muscle cell growth, contributing to a hypertrophic training response useful for power development.^[125] Degradation of bradykinin results in lower substrate metabolism and less efficient vasodilation. Therefore, lower levels of ACE activity may be associated with increased half-life bradykinin, which alters substrate metabolism. Increased angiotensin II is associated with the DD genotype and may facilitate muscle bulk for power sport performance. It is estimated that 25% of the population have the II genotype, 50% the ID genotype and 25% the DD genotype.^[102]

Do particular variants of the ACE gene genotype occur more frequently in specific populations (e.g. endurance or power athletes) compared with controls? Early work with army recruits found that the II form of the gene was associated with lower activity

levels of ACE in muscle than the DD allele, and an increased response to physical training.^[126] Recruits with ACE genotype II differed by as much as 1100% in response to repetitive upper-arm exercises compared with DD genotype peers. Individuals with a heterogeneous genotype (DI) were associated with levels of performance between both homozygous genotypes. In sport, a higher prevalence of the II genotype has been found in elite endurance athletes including mountaineers able to resist effects of hypoxia and climb to 7000m without the aid of oxygen, as well as Olympic-standard endurance runners and elite rowers.^[126-128] In their compendium of all genes and markers associated with health-related fitness and performance, Rankinen et al.^[101] revealed six studies reporting a positive relationship between power performance and muscle strength-related phenotypes.

Do these data imply that athletes are born and not made? Despite the rhetoric in the popular science literature, it seems that there is currently no clear evidence to support that implication. The appropriateness of this conclusion in the face of claims that human physical performance is 'strongly' influenced by genetic factors^[128] was underscored in a study by Bouchard et al.^[129] who attempted to establish the proportion of influence attributable to genetic and environmental constraints on familial resemblance for maximal oxygen uptake during exercise on a cycle ergometer in sedentary individuals.^[129] Exercise performance of fathers, mothers, sons and daughters was measured in 86 nuclear families. Maximum heritability including genetic and non-genetic causes for physical performance accounted for 51% of the total adjusted phenotype variance. Several models of interacting constraints were tested and results showed that there was 2.6–2.9 times more variance between families than within families.

Yet again, difficulty in disambiguating the specific constraints of genes and environments was apparent in that study. Genetic and familial environmental influences could not be 'fully quantified separately' although 'inferences about their respective contributions to the phenotype variance could be made by inspection of the pattern of familial correlations'. Of course correlations do not imply causation. The emphasis on the constraints imposed

by the shared familial environment is also important to note. While this explanation may hold, it does not preclude influence of 'wider' environmental constraints such as sociocultural changes in society, including the impact of media images, 'stereotype threat',^[130] government education programmes and peer group pressure.

Other research on human behaviour has revealed that genes work in combined networks to influence biological function, refuting the idea of successful athletes being differentiated on the presence of a single gene variant (for a similar argument in developmental theory see Johnston and Edwards^[131]). Rankinen et al.'s^[101] record on the progress in molecular biology towards a human gene map, noted that although 165 autosomal entries, 5 X chromosome assignments and 17 mitochondrial markers were obtained in 2005 alone, there is still little understanding of the role that such genes might play in individual differences in health-related fitness and physical performance. Therefore, whilst research may be capable of identifying single gene variants believed to be involved in variations in fitness and physical performance, many scientists have moved away from an extreme biologically deterministic stance. Despite this, there has been inadequate progress in understanding how single gene variants may interact with different environmental constraints, such as enforced bed rest, illness, aging, space travel and sports training.^[119] These more complex research investigations are precisely what are needed with respect to understanding how practical interventions may interact with distinctive genotypical profiles.

3.7 Stochasticity in Cellular Regulation Processes

The arguments against a biologically deterministic view of processes of gene transmission are important to note because of the prevalence of the implicit assumptions underlying the 'single-gene as magic bullet' philosophy held by some sport practitioners. Somehow over the years, the view of DNA as information bearer has been replaced with the mechanistic fallacy of DNA as blueprint, plan, or master molecule.^[5] Fortunately, the 'gene as blueprint' traditional rationale is giving way to better understanding of the mechanisms and processes

of genetic transmission, including transcription and translation, revealing that expression levels of single genes or networks of genes are far more open to stochastic fluctuations in constant environments than previously thought.^[132] It is now proposed that molecular interactions are inherently random leading to stochasticity in the biochemical processes of transcription, protein synthesis and the basis of gene transmission.^[133] Intracellular processes involve thousands of chemical interactions and a high level of random fluctuations has been identified in RNA levels and expressed proteins with the potential for considerable unpredictability in molecular events.^[134] As Kauffman^[132] noted, random chemical-electrical fluctuations are a serious issue in genetic networks since cellular regulatory processes in biological systems are inherently noisy. The use of negative feedback loops helps to stabilise system dynamics against effects of perturbing fluctuations.^[134] Simulation modelling of the gene transmission process has shown that deterministic views of protein concentration and synthesis, the basis of gene expression, are untenable due to the potential for fluctuations in these critical variables, both linked with population heterogeneity.^[133] Traditional views hold that stochasticity is an index of cellular noisiness, disruptive to cell regulation processes. Some more recent interpretations of stochasticity suggest that it is a mechanism for cellular and phenotypic diversification, providing an evolutionary advantage for organisms that benefit from it.^[133]

Although some geneticists have pointed to the propensity of some physiological processes for destabilising the phenotype, the main argument proposed is that there is a 'redundancy and reserve capacity'^[120] in the design of neurobiological systems to cope with these perturbations. Later in this article we argue that a more accurate characterisation in neurobiology may be that genetic regulatory systems are 'degenerate' and not replete with redundancy.^[135,136] This is because the propensity for re-entrant trajectories between network states has provided valuable insights into the functional role of stochasticity in stabilising diversified cell types as attractors within cellular networks.^[132]

What are the implications of this new knowledge from molecular biology for sport scientists interested in individual differences between performers? It

is critical that scientists and clinicians understand the biological significance of this previously unobserved stochasticity in gene expression. Furthermore, other data mitigating against the blueprint conceptualisation of genetic transmission processes can be observed in evidence that identical twins are not actually identical. Evidence from the study of phenotypically identical twins showed that their fingerprints differ and the shape of their brains can differ by as much as 40%.^[137] This is important for sport clinicians to note because typically they are exposed to research findings from behavioural genetics, which are concerned with explanations of hereditary influences at the level of populations, not individuals. Heritability estimates are specific to a sample studied, and changes to the environment can change the heritability estimate from the same sample of individuals with the same genotypes.^[1]

Clearly, therefore, as sequencing of genomes in biological organisms gathers pace, it is becoming apparent that genes should not be viewed as a blueprint for success in sport. As Johnston and Edwards^[131] have pointed out, it is “a very long step from polypeptide sequences to behaviour – a step that covers much incompletely understood territory.” Attempts to see genes as building plans are one of the great artificialisms of human conceptualisations of nature.^[138] It has become a ‘central dogma’ of how people think about the process of evolution.^[139] Genes simply contain the information to synthesise proteins with properties leading them to cluster together. Lewontin^[5] criticised the stance of ‘biological determinism’, the medical model’s rejection of polymorphism and the implicit notion of variability as deviation from a ‘perfect ideal’. Genetic diversity is the norm and biological systems are not DNA-determined. There is no single, standard, normal DNA sequence that human beings share and it is estimated that DNA sequencing in individuals varies by 0.1% (~3 million nucleotides) including inherited sequences from parents. It takes more than DNA to produce a living organism, which cannot be computed from DNA sequences. According to Lewontin,^[5] “A living organism at any moment of its life is the unique consequence of a developmental history that results from the interaction of and determination by internal and external forces.”

The shift in understanding of the cellular mechanics of gene expression should lead to a correction in the relentless advance to find the ‘single gene as magic bullet’. Some molecular biologists are leading the way in advocating a less deterministic view of gene expression based on their research findings. For example, Jones et al.^[102] have noted that “The ACE I/D polymorphism should not be considered a ‘gene for human performance’, but a marker for modulation such that one would expect an excess of the I allele in the truly elite endurance athlete, with a concordant excess of the D allele represented in the more power-oriented events.”

With respect to understanding the nature of genetic constraints on variability in sport performance, it is not clear how useful this information could be for sport practitioners designing specific training and selection programmes. Jones et al.^[102] also stated that “The ACE genotype has never been associated with endurance performance in the untrained state. Any effect appears to require a period of gene-environment interaction. A high level of aerobic fitness is an essential, but not sole, requirement for elite endurance.” A final point to note according to Jones et al.^[102] is that “There will always be elite endurance athletes who are of the ACE DD genotype, and many champions in anaerobic sports of the II genotype. Whatever the data may conclude, elite athletes are still made and not born, though perhaps some may be made elite in one discipline more easily than others.”

4. The Fallacy of a Dualist ‘Debate’: Alternative Approaches to Nature and Nurture

Our review of the strengths and weaknesses of theoretical ideas and empirical research for theories of learning and performance has revealed major implications for understanding how environmental and genetic constraints function. It can be concluded that neither specific approach provides enough explanatory power to account for all the data on performance variability. There is now clear evidence rejecting the idea that single gene variants can predispose an athlete to superior performance manifested in a specific domain, without clear and detailed consideration of the performance context (e.g. a gene for soccer performance). Edelman and Gal-

ly^[135] have highlighted the fallacy of this view by arguing that "All observable properties of an organism are determined by the workings of a degenerate network of many genes." Degeneracy exists at all levels of biological movement systems and is technically defined as non-isomorphic components producing isofunctional outcomes, effects or solutions.^[136] Degeneracy in gene networks promotes evolutionary fitness of a species by ensuring that genetic diversity supports functional adaptation to variable environments. Neurobiological degeneracy provides the basis for gene expression as an inherently stochastic process.^[133] We also noted that the implicit basis of the deliberate practice perspective is the adage 'all healthy individuals are created equal'. Analysis of the literature on genetic constraints on variability of performance does not support this conclusion, but this interpretation of the literature should not be taken to imply that physical performance is biologically determined. Rather, effects of interacting constraints on acquisition of skill, expertise, health and physical performance have been noted, since despite variations in genetic structure, maximal heritability of particular traits includes strong environmental components. The presence of dynamically varying environments interacts with an inherent property of human movement systems, degeneracy, to signal a new view on variability. Degeneracy is an omnipresent property of many complex, neurobiological systems that facilitates achievement of functional movement outcomes in variable environments through diversity of processes.^[136] This new perspective on variability reveals that compensatory adaptation in performance achievement occurs as the result of system trade-offs between specificity and diversity of behaviours.^[135]

Research considered in this article has shown that, in the development of individuals, biological dispositions and environments should not be conceptualised as separately evolving, static entities, but rather as dynamically yoked. Biological dispositions and environmental influences are responsive to each other as exemplified in research on the changing structure of the CNS with learning experiences.^[140] Determining the impact of neurobiological degeneracy on achievement of elite sport per-

formance remains an important focus for future research on genetic and environmental constraints.

These ideas on the dynamic relationships between genes and environment and the functional role of degeneracy in the human nervous system are harmonious with a dynamical systems theoretical perspective on the influence of interacting constraints. In this regard, science needs to move beyond a characterisation of natural phenomena in 'dualisms' to understand the 'complementary nature'.^[24] The application of dynamical systems theory to the study of neurobiological performance can provide a substantial theoretical framework for interpreting the complementary nature of genetic and environmental constraints on each individual performer.^[10,98] From this theoretical standpoint, genetic diversity may be responsible for a small part of training or performance response differences between individuals, and only when there is a favourable interaction with important environmental constraints are performance benefits observed. For example, there is growing consensus in the study of human obesity that the contribution of genetic factors is exacerbated in environments that differ in caloric availability.^[141] Genetic propensity towards adiposity has less of a constraining influence on individuals in environments where caloric availability is lower, whereas these same individuals would be at greater risk in caloric-rich environments. Such environments can be categorised as high or low risk, depending on prevalence of other significant cultural constraints including lack of training facilities, work patterns imposed on traditional meal times, and the fall in popularity of physically active pastimes, leading to a greater emphasis on more static activities such as playing computer games and TV watching.

Strong interaction effects on endurance performance of amphibians have been clearly demonstrated in evolutionary physiology studies manipulating diet. A high initial heritability component (0.40) for locomotory endurance capacity (running time to exhaustion just after birth) was altered with dietary changes, showing how expression of genetic tendencies for physical performance is dependent on environmental contexts.^[142] Although this work needs to be replicated with humans, it appears that phenotypic expression of exercise behaviours might be best

understood at the level of individual interactions with key environmental constraints and associated risk, rather than as defective behaviour in a 'medical model'.^[98] This is particularly relevant when considering effects of time spent in practice in sport. Given differences in genetic contributions, performance variations are more likely to assert themselves under intensive practice regimes.

An implication of these findings and of other data reviewed in this article for understanding individual variations in physical performance is that there may be diverse ways for neurobiological systems to achieve similar performance outcome levels. For example, athletes of a putatively less favourable genotypic disposition might succeed as long as they are exposed to appropriate training environments. However, it can be concluded that performers with a more favourable genotype, who interact with appropriate training environments, are more likely to receive a greater training response. Current data on genetic constraints on motor skill acquisition are unclear due to a number of methodological weaknesses and conflicting findings, and there is a need for more work to identify genetic mechanisms underlying performance variations. Moreover, the greater emphasis on constraints in the dynamical systems perspective implies that the nature-nurture argument can be superseded, as we note in section 5.

5. Where to from Here? The Future of the Nature-Nurture Debate

Based on evidence reviewed, one of the most likely reasons the nature-nurture debate has not been resolved is that it cannot be resolved using current dualist paradigms that separate influences into distinct categories (i.e. either nature or nurture). At its root, behavioural research will never predict events with the same level of certainty as fields like biology, physics and chemistry. Dynamic neurobiological systems, such as athletes, are dramatically affected by any uncertainty (or chaos) in the behaviour of performance-related variables. According to Gollub and Solomon,^[143] "any uncertainty [in a complex system]... no matter how small, will lead to rapidly growing errors in any effort to predict the future behaviour." The behaviour of complex systems is only completely predictable when the components of performance are known to an infinite degree of

accuracy. Given these constraints on performance and behaviour, prediction of athletic performance will always be limited by uncertainty and compounded by degeneracy. However, understanding the range of influences that affect sports performance is within our grasp, provided we ask the right questions.

In contrast to the bullish search by some molecular biologists for the single gene variant that characterises elite performance in specific sports and physical activities, psychologists generally seem to have accepted the idea of co-action of genes and environment, preferring to highlight the view that no psychological measure shows zero heritability.^[88] Furthermore, it is possible to interpret existing data on inter-individual variability in the health and physical activity domain based on the interaction of genetic and environmental constraints. For example, an interesting issue concerns the relationship between propensity to engage in daily physical activity and inter-individual differences in resting metabolic rate. The heritability estimate of the tendency to exercise and participate in sports and physical activity has been provided^[22] and this issue was considered with groups of five different types of twins differing on MZ-DZ and male-female dimensions in adolescents aged 15 years.^[144] Although, the original biometric model traced to Fisher in 1918 for estimating the heritability statistic did not include a component for interaction of genotype and environment, recent evidence suggests that an interactionist model exhibiting the co-influence of genetic factors, as well as unique and shared environments provides a best fit with the data on time spent in physical activity. In females, the genetic component contributed 44% of the variance explained, with shared environmental factors mainly contributing the rest. For males, the genetic component was more dominant, contributing 83% of the variance. The authors explained this major difference in the data as emanating from the importance of the social environment for female members of twins and physical morphological factors for males at the age studied. Other evidence has found that genes may influence the disposition towards higher intensity exercise in physical activity choices, although attempts to implicate marker genes with individual differences in resting metabolic rate have found only weak and

inconclusive support.^[144] The implication is that the genes-environment interaction may have different dimensions for males and females, which could have important implications for planning physical activity participation programmes.

6. Conclusions

Frans de Waal, in his address to the 2001 conference of the American Psychological Association, advocated for an approach to human behaviour that integrated the effects of learning and the environment with Darwinian perspectives of biology and genetics.^[145]

Allied to this recommendation, the literature reviewed in this article suggests that many clinicians and sports scientists may be expecting more from quantitative molecular studies than can be delivered. A requisite step forward would be to discard both the dualist approach to nature versus nurture and the 'gene as magic bullet' philosophy. It is becoming clear that sports performance is the result of interactions among a host of genes and environmental constraints. There are important implications for advising clinicians, teachers, coaches, administrators and athletes on the seductive, but highly simplistic, myths surrounding 'single-gene-as-magic-bullet' approaches, which have become more prevalent in sports medicine. These implications relate to the uncritical acceptance of general models for talent identification and development programmes across the world. For example, there is no single gene for 'hand-eye' or 'hand-foot' coordination in children. But there are nervous system thresholds and differences in children's opportunities to exploit critical maturational phases in developing timing behaviour in interceptive actions.^[146] Sport researchers are encouraged to consider interactionist designs when investigating the range of influences on the development of skilled performance. Nevertheless, establishing the validity of moderating and mediating relationships will be a long-term process due to the complexity of the relationships suggested and the difficulties associated with identifying interactive relationships of this nature (for a review see Wahlsten^[147]). Cronbach^[148] stated, "serious interaction research ought to be a program of several years' duration, although there are few examples in behavioural science." Although challenging, an in-

teractive approach for analysing relative contributions of genes and environment in degenerate neurobiological systems may shed light on a number of significant issues in sports science and medicine related to the acquisition of expertise in sport.

Acknowledgements

No sources of funding were used to assist in the preparation of this review. The authors have no conflicts of interest that are directly relevant to the content of this review. The authors wish to acknowledge the help of Pam Smith of the School of Human Movement Studies, Queensland University of Technology, in preparing this manuscript for publication.

References

1. Vitzthum VJ. A number no greater than the sum of its parts: the use and abuse of heritability. *Hum Biol* 2003; 75: 539-88
2. Wilson EO. *Sociobiology: the new synthesis*. Cambridge (MA): Harvard University Press, 1975
3. Hellman H. *Great feuds in science: ten of the liveliest disputes ever*. New York: Wiley, 1998
4. Ceci S, Williams W. *The nature-nurture debate: the essential readings*. New York: Blackwell Publishing Co., 2000
5. Lewontin RC. It ain't necessarily so: the dream of the human genome and other illusions. London: Granta Books, 2000
6. De Geus EJC, Boomsma DI. A genetic neuroscience approach to human cognition. *Eur Psychologist* 2001; 6: 241-53
7. Bouchard Jr TJ, McGue M. Genetic and environmental influences on human psychological differences. *J Neurobiol* 2003; 54: 4-45
8. Kimble GA. Evolution of the nature-nurture issue in the history of psychology. In: Plomin R, McClearn GE, editors. *Nature, nurture and psychology*. Washington, DC: American Psychological Association, 1993: 3-25
9. Petrill SA, Lipton PA, Hewitt JK, et al. Genetic and environmental contributions to general cognitive ability through the first 16 years of life. *Dev Psychol* 2004; 40: 805-12
10. Baker J, Davids K. Genetic and environmental constraints on variability in sport performance. In: Davids K, Bennett SJ, Newell KM, editors. *Variability in the movement system: a multidisciplinary perspective*. Champaign (IL): Human Kinetics, 2006: 129
11. Brutsaert TD, Parra EJ. What makes a champion? Explaining variation in human athletic performance. *Resp Physiol Neurobiol* 2006; 151: 109-23
12. Pitsiladis Y, Bale J, Sharp C, et al., editors. *East African running: towards a cross-disciplinary perspective*. London: Routledge, Taylor & Francis, 2006
13. Miah A. *Genetically modified athletes: biomedical ethics, gene doping and sport*. London: Routledge, Taylor & Francis, 2004
14. Tamburrini C, Tansjö T, editors. *Genetic technology and sport: ethical questions*. London: Routledge, Taylor & Francis, 2005
15. Coghlan A. Elite athletes born to run. *New Scientist* 2003; 30: 4-5
16. Yang N, MacArthur DG, Gulbin JP, et al. ACTN3 genotype is associated with human elite athletic performance. *Am J Hum Genetics* 2003; 73: 627-31
17. Coghlan A. How the right genes may get you off to a flying start. *New Scientist* 1998; May 23: 4
18. Anderson JL, Schjerling P, Saltin B, et al. Muscle, genes and athletic performance. *Scientific Am* 2000; 283: 31-7

19. Friedmann T, Koss JO. Gene transfer and athletics: an impending problem. *Mol Ther* 2001; 3: 819-20
20. McCrory P. Super athletes or gene cheats. *Br J Sports Med* 2003; 193
21. Dennis C. Rugby team converts to give genes test a try. *Nature* 2005; 434: 260
22. Stubbe JH, Boomsma DL, De Geus EJC. Sport participation during adolescence: a shift from environmental to genetic factors. *Med Sci Sports Exerc* 2005; 37: 563-70
23. Unal M, Unal DO. Gene doping in sports. *Sports Med* 2004; 34: 357-62
24. Kelso JAS, Engström DA. The complementary nature. Cambridge (MA): MIT Press, 2006
25. Galton F. Inquiries into human faculty and its development. London: Macmillan, 1883
26. Galton F. On men of science: their nature and their nurture. *Nature* 1874; 9: 344-5
27. James W. Principles of psychology. New York: Holt, 1890
28. Terman L. Genetic studies of genius. Stanford (CA): Stanford University Press, 1925
29. Terman LM, Oden MH. The gifted child grows up. Stanford (CA): Stanford University Press, 1947
30. Terman LM, Oden MH. The gifted group at mid-life. Stanford (CA): Stanford University Press, 1959
31. Watson JB. Behaviorism. New York: Norton, 1924
32. Pinker S. The blank slate: the modern denial of human nature. New York: Viking, 2002
33. Herrnstein RJ, Murray C. The bell curve: intelligence and class structure in American life. New York: Free Press, 1994
34. Crossman ERFW. A theory of the acquisition of speed-skill. *Ergonomics* 1959; 2: 153-66
35. Kolers PA. Memorial consequences of automatized encoding. *J Exper Psychol Hum Learn Memory* 1975; 1: 689-701
36. Newell A, Rosenbloom PS. Mechanisms of skill acquisition and the law of practice. In: Anderson JR, editor. Cognitive skills and their acquisition. Hillsdale (NJ): Erlbaum 1981: 1-55
37. Heathcote A, Brown S, Mewhort DJK. The power law repealed: the case for an exponential law of practice. *Psychonomic Bull Rev* 2000; 7: 185-207
38. Newell KM, Liu Y-T, Mayer-Kress G. Time scales in motor learning and development. *Psychological Rev* 2001; 108: 57-82
39. Ericsson KA, Krampe RT, Tesch-Römer C. The role of deliberate practice in the acquisition of expert performance. *Psychol Rev* 1993; 100: 363-406
40. Ericsson KA, Chase WG, Faloon S. Acquisition of a memory skill. *Science* 1980; 208: 1181-2
41. Simon HA, Chase WG. Skill in chess. *Am Sci* 1973; 61: 394-403
42. Ericsson KA. Development of elite performance and deliberate practice: an update from the perspective of the expert performance approach. In: Starkes JL, Ericsson KA, editors. Expert performance in sports: advances in research on sport expertise. Champaign (IL): Human Kinetics, 2003: 49-83
43. Starkes JL, Deakin J M, Allard F, et al. Deliberate practice in sports: what is it anyway? In: Ericsson KA, editor. The road to excellence: the acquisition of expert performance in the arts, sciences, sports and games. Mahwah (NJ): Erlbaum, 1996: 81-106
44. Helsen WF, Starkes JL, Hodges NJ. Team sports and the theory of deliberate practice. *J Sport Exerc Psychol* 1998; 20: 12-34
45. Hodge T, Deakin J. Deliberate practice and expertise in the martial arts: the role of context in motor recall. *J Sport Exerc Psychol* 1998; 20: 260-79
46. Baker J, Côté J, Abernethy B. Learning from the experts: Practice activities of expert decision-makers in sport. *Res Q Exerc Sport* 2003; 74: 342-7
47. Deakin JM, Cogley S. An examination of the practice environments in figure skating and volleyball: a search for deliberate practice. In: Starkes JL, Ericsson KA, editors. Recent advances in the study of sport expertise. Champaign (IL): Human Kinetics, 2003:115-35
48. Baker J. Early specialization in youth sport: a requirement for adult expertise? *High Ability Stud* 2003; 14: 85-94
49. Wiersma LD. Risks and benefits of youth sport specialization: perspectives and recommendations. *Pediatr Exerc Sci* 2000; 12: 13-22
50. Baker J, Côté J, Abernethy B. Sport specific training, deliberate practice and the development of expertise in team ball sports. *J Appl Sport Psychol* 2003; 15: 12-25
51. Abernethy B, Baker J, Côté J. Transfer of pattern recall skills as a contributor to the development of sport expertise. *Appl Cognitive Psychol* 2005; 19: 705-18
52. Flynn MG, Carroll KK, Hall HL, et al. Cross training: indices of training stress and performance. *Med Sci Sports Exerc* 1998; 30: 294-300
53. Millet GP, Candau RB, Barbier B, et al. Modelling the transfers of training effects on performance in elite triathletes. *Int J Sports Med* 2002; 23: 55-63
54. Mutton DL, Loy SF, Perry DM, et al. Effect of run vs combined cycle-run training on aerobic capacity and running performance. *Med Sci Sports Exerc* 1993; 25: 1393-7
55. Côté J, Baker J, Abernethy B. From play to practice: a developmental framework for the acquisition of expertise in team sports. In: Starkes J, Ericsson KA, editors. Expert performance in sports: advances in research on sport expertise. Champaign (IL): Human Kinetics, 2003: 89-110
56. Petlichkoff LM. Coaching children: understanding the motivational process. *Sport Sci Rev* 1993; 2: 49-61
57. Abernethy B, Farrow D, Berry J. Constraints and issues in the development of a general theory of expert perceptual-motor performance. In: Starkes JL, Ericsson KA, editors. Expert performance in sports: advances in research on sport expertise. Champaign (IL): Human Kinetics, 2003: 349-69
58. Sternberg RJ. Costs of expertise. In: Ericsson KA, editor. The road to excellence: the acquisition of expert performance in the arts and sciences, sports and games. Mahwah (NJ): Lawrence Erlbaum Associates, 1996: 347-53
59. Baker J, Horton S. A review of primary and secondary influences on sport expertise. *High Ability Stud* 2004; 15: 211-28
60. Voss J, Green T, Penner B. Problem-solving in social sciences. In: Bower G, editor. The psychology of learning and motivation: advances in research theory. New York: Academic Press, 1983:165-213
61. Starkes JL. The road to expertise: is practice the only determinant? *Int J Sport Psychol* 2000; 31: 431-51
62. Bloom GA, Crumpton R, Anderson JE. A systematic observation study of the teaching behaviors of an expert basketball coach. *Sport Psychologist* 1999; 13: 157-70
63. Tharp RG, Gallimore R. What a coach can teach a teacher. *Psychol Today* 1976; 9: 74-8
64. Bloom BS. Developing talent in young people. New York: Ballantine Publishing Group, 1985
65. Côté J. The influence of the family in the development of talent in sports. *Sport Psychologist* 1999; 13: 395-417
66. Ehrlich PR. Human natures: genes, cultures, and the human prospect. Washington, DC: Island Press, 2000
67. Russell S. Ice time: a Canadian hockey journey. Toronto: Viking, 2000
68. Robinson L. Crossing the line: violence and sexual assault in Canada's national sport. Toronto: McClelland & Stewart Inc., 1998

69. Musch J, Grondin S. Unequal competition as an impediment to personal development: a review of the relative age effect in sport. *Dev Rev* 2001; 21: 147-67
70. Barnsley RH, Thompson AH. Gifted or learning disabled? The age of entering school may make the difference. *Early Childhood Educ* 1985; 18: 11-4
71. Hauck AL, Finch AJ. The effect of relative age on achievement in middle school. *Psychol Schools* 1993; 30: 74-9
72. Barnsley RH, Thompson AH. Birthdate and success in minor hockey: the key to the NHL. *Can J Behav Sci* 1988; 20: 167-76
73. Thompson AH, Barnsley RH, Steblelsky G. 'Born to play ball': the relative age effect and major league baseball. *Sociol Sport J* 1991; 8: 146-51
74. Barnsley RH, Thompson AH, Legault P. Family planning: football style - the relative age effect in football. *Int Rev Sociol Sport* 1992; 27: 77-87
75. Carlson RC. The socialization of elite tennis players in Sweden: an analysis of the players' backgrounds and development. *Sociol Sport J* 1988; 5: 241-56
76. Curtis JE, Birch JS. Size of community of origin and recruitment to professional and olympic hockey in North America. *Sociol Sport J* 1987; 4: 229-44
77. Côté J, MacDonald D, Baker J, et al. When 'where' is more important than 'when': birthplace effects on the achievement of sporting expertise. *J Sports Sci* 2006; 24: 1065-73
78. Elgar FJ, Arlett C, Groves R. Stress, coping, and behavioural problems among rural and urban adolescents. *J Adolesc* 2003; 26: 574-85
79. Kytta M. Affordances of children's environments in the context of cities, small towns, suburbs, and rural villages in Finland and Belarus. *J Environ Psychol* 2002; 22: 109-23
80. Plomin R, DeFries JC, McClearn GE, et al. Behavioural genetics. 4th ed. New York: Freeman, 2001
81. Bouchard Jr TJ, Lykken DT, McGue M, et al. Sources of human psychological differences: the Minnesota Study of Twins Reared Apart. *Science* 1990; 250: 223-8
82. Bouchard Jr TJ. IQ similarity in twins reared apart: findings and response to critics. In Sternberg RJ, Grigorenko E, editors. *Intelligence, heredity, and environment*. Cambridge (MA): Cambridge University Press, 1997: 126-60
83. DiLalla DL, Carey G, Gottesman II, et al. Heritability of MMPI personality indicators of psychopathology in twins reared apart. *J Abnormal Psychol* 1996; 105: 491-9
84. Tellegen A, Lykken DT, Bouchard Jr TJ, et al. Personality similarities in twins reared apart and together. *J Personality Social Psychol* 1988; 54: 1031-9
85. Keller LM, Bouchard Jr TJ, Arvey RD, et al. Work values: genetic and environmental influences. *J Appl Psychol* 1992; 77: 79-88
86. Arvey RD, Bouchard Jr TJ, Segal NL, et al. Job satisfaction: environmental and genetic components. *J Appl Psychol* 1989; 74: 187-92
87. Johnson W, Bouchard Jr TJ, Segal NL, et al. The Stroop Color-Word Test: genetic and environmental influences: reading, mental ability, and personality correlates. *J Educ Psychol* 2003; 95: 58-65
88. Plomin R, Colledge E. Genetics and psychology: beyond heritability. *Eur Psychologist* 2001; 6: 229-40
89. Schlaug G, Jancke L, Huang Y, et al. In vivo evidence of structural brain asymmetry in musicians. *Science* 1995; 267: 699-701
90. Sacks O. Musical ability [letter]. *Science* 1995; 268: 621
91. Baharloo S, Service SK, Risch N, et al. Familial aggregation of absolute pitch. *Am J Hum Genet* 2000; 67: 755-8
92. Gregerson PK, Kowalsky E, Kohn N, et al. Absolute pitch: prevalence, ethnic variation, and estimation of the genetic component. *Am J Hum Genet* 1999; 65: 911-3
93. Slonimsky N. Perfect pitch. New York: Oxford University Press, 1998
94. Williams L, Gross JB. Heritability of motor skill. *Acta Genet Med* 1980; 29: 127-36
95. Fox PW, Hershberger SL, Bouchard TJ, et al. Genetic and environmental contributions to the acquisition of a motor skill. *Nature* 1996; 384: 356-8
96. Missitzi J, Geladas N, Klissouras V. Heritability in neuromuscular coordination: implications for motor control strategies. *Med Sci Sports Exerc* 2004; 36: 233-40
97. Joseph J. Separated twins and the genetics of personality differences: a critique. *Am J Psychol* 2001; 114: 1-30
98. Davids K, Glazier P, Araújo D, et al. Movement systems as dynamical systems: the role of functional variability and its implications for sports medicine. *Sports Med* 2003; 33: 245-60
99. Kevles DJ, Hood L. The code of codes: scientific and social issues in the human genome project. Boston (MA): Harvard University Press, 1992
100. Hopkins WG. Genes and training for athletic performance [online]. Available from URL: <http://www.sportssci.org/jour/0101/wghgene.htm> [Accessed 2005 Sep 17]
101. Rankinen T, Bray MS, Hagberg JM, et al. The human gene map for performance and health-related fitness phenotypes: the 2005 update. *Med Sci Sports Exerc* 2005; 38: 1863-88
102. Jones A, Montgomery HE, Woods DR. Human performance: a role for the ACE genotype? *Exerc Sport Sci Rev* 2002; 30: 184-90
103. Kostek MC, Delmonico MJ, Reichel JB, et al. Muscle strength response to strength training is influenced by insulin-like growth factor 1 genotype in older adults. *J Appl Physiol* 2005; 98: 2147-54
104. Niemi AK, Majaama K. Mitochondrial DNA and ACTN3 genotypes in Finnish elite endurance and sprint athletes. *Eur J Hum Genet* 2005; 13: 965-9
105. Allen DL, Harrison BC, Sartorius C, et al. Mutation of the IIB myosin heavy chain gene results in muscle fibre loss and compensatory hypertrophy. *Am J Physiol Cell Physiol* 2001; 280: C637-45
106. Mitch WE, Price SR. Transcription factors and muscle cachexia: is there a therapeutic target? *Lancet* 2001; 357: 734-375
107. Ivey FM, Roth SM, Ferrell RE, et al. Effects of age, gender, and myostatin genotype on the hypertrophic response to heavy resistance strength training. *J Gerontol A Biol Sci Med Sci* 2000; 55: 641-8
108. Hortobágyi T, Dempsey L, Fraser D, et al. Changes in muscle strength, muscle fibre size and myofibrillar gene expression after immobilization and retraining in humans. *J Physiol* 2000; 524: 293-304
109. Calvo M, Rodas G, Vallejo M, et al. Heritability of explosive power and anaerobic capacity in humans. *Eur J Appl Physiol* 2002; 86: 218-25
110. Forbes GB, Sauer EP, Wetkamp LR. Lean body mass in twins. *Metabolism* 1995; 44: 1442-6
111. Thibault M, Simoneau J, Côté C, et al. Inheritance of human muscle enzyme adaptation to isokinetic strength training. *Hum Heredity* 1986; 36: 341-7
112. Thomis MA, Bennen GP, Maes HH, et al. Strength training: importance of genetic factors. *Med Sci Sports Exerc* 1988; 30: 724-31
113. Chagnon YC, Rice T, Perusse L, et al. Genomic scan for genes affecting body composition before and after training in Caucasians from HERITAGE. *J Appl Physiol* 2001; 90: 1777-87
114. Naya FJ, Mercer B, Shelton J, et al. Stimulation of slow skeletal muscle fibre gene expression in Calcineurin in vivo. *J Biol Chem* 2005; 275: 4545-8

115. Swoap SJ, Bridge Hunter R, Stevenson EJ, et al. The calcineurin-NFAT pathway and muscle fibre-type gene expression. *Am J Physiol Cell Physiol* 2000; 279: C915-24
116. McAinch AJ, Lee JS, Bruce CR, et al. Dietary regulation of fat oxidative gene expression in different skeletal muscle fiber types. *Obesity Res* 2003; 11: 1471-9
117. Rubio JC, Martín MA, Rabadán M, et al. Frequency of C34T mutation of the AMPD1 gene in world-class endurance athletes: does this mutation impair performance? *J Appl Physiol* 2005; 98: 2108-12
118. Cam FS, Colakoglu M, Sekuri S, et al. Association between the ACE I/D gene polymorphism and physical performance in a homogenous non-elite cohort. *Can J Appl Physiol* 2005; 30: 74-86
119. Scott RA, Moran C, Wilson RH, et al. No association between angiotensin converting enzyme (ACE) gene variation and endurance athlete status in Kenyans. *Comp Biochem Physiol* 2005; 141 Pt A: 169-75
120. Silva GJ, Moreira ED, Pereira AC, et al. ACE gene dosage modulates pressure-induced cardiac hypertrophy in mice and men. *Physiol Genomics* 2006; 27: 237-44
121. Sayed-Tabatabaei FA, Oostra BA, Isaacs A, et al. ACE polymorphisms. *Circ Res* 2006; 98: 1123-33
122. Feitosa MF, Gaskill SE, Rice T, et al. Major gene effects on exercise ventilatory threshold: the HERITAGE Family Study. *J Appl Physiol* 2002; 93: 1000-6
123. Williams AG, Day SH, Folland JP, et al. Circulating angiotensin converting enzyme activity is correlated with muscle strength. *Med Sci Sports Exerc* 2005; 37: 944-8
124. Sonna LA, Sharp MA, Knapik JJ, et al. Angiotensin-converting enzyme genotype and physical performance during US Army basic training. *J Appl Physiol* 2001; 91: 1355-63
125. Pescatello LS, Kostek MA, Gordish-Dessman H, et al. ACE ID genotype and the muscle strength and size response to unilateral resistance training. *Med Sci Sports Exerc* 2006; 38: 1074-81
126. Montgomery HE, Marshall R, Hemingway H, et al. Human gene for physical performance. *Nature* 1998; 393: 221-2
127. Gayagay G, Yu B, Hambly B, et al. Elite endurance athletes and the ACE I allele: the role of genes in athletic performance. *Hum Genet* 1998; 103: 48-50
128. Myerson S, Hemingway H, Budget R, et al. Human angiotensin I-converting enzyme gene and endurance performance. *J Appl Physiol* 1999; 87: 1313-6
129. Bouchard C, Daw EW, Rice T, et al. Familial resemblance for $\dot{V}O_{2\max}$ in the sedentary state: the HERITAGE family study. *Med Sci Sports Exerc* 1998; 30: 252-8
130. Baker J, Horton S. East African running dominance revisited: a role for stereotype threat? *Br J Sports Med* 2003; 37: 553-5
131. Johnston TD, Edwards L. Genes, interactions and the development of behaviour. *Psychol Rev* 2002; 109: 26-34
132. Kauffman S. Understanding genetic regulatory networks. *Int J Astrobiol* 2003; 2: 131-9
133. Kaerns M, Elston TC, Blake W, et al. Stochasticity in gene expression: from theories to phenotypes. *Nature Rev Genet* 2005; 6: 451-64
134. Gardner T, Collins JJ. Neutralizing noise in gene networks. *Nature* 2000; 405: 520-1
135. Edelman GM, Gally JA. Degeneracy and complexity in biological systems. *Proc Natl Acad Sci* 2001; 98: 13763-8
136. Tononi G, Sporns O, Edelman GM. Measures of degeneracy and redundancy in biological networks. *Proc Natl Acad Sci* 1999; 96: 3257-62
137. Yates FE. Self-organizing systems. In: Boyd C, Noble D, editors. *Logic of life*. Oxford: Oxford University Press, 1993: 189-218
138. van Geert P. Dynamic systems of development: change between complexity and chaos. New York: Harvester Wheatsheaf, 1994
139. Oyama S. The ontogeny of information: developmental systems and evolution. 2nd ed. Durham (NC): Duke University Press, 2000
140. Dodge KA. The nature-nurture debate and public policy. *Merrill-Palmer Q* 2004; 50: 418-27
141. Barsh GS, Farooqi IS, O'Rahilly S. Genetics of body-weight regulation. *Nature* 2000; 404: 644-51
142. Le Gaillard J-F, Clobert J, Ferrière R. Physical performance and Darwinian fitness in lizards. *Nature* 2004; 432: 502-5
143. Gollub J, Solomon T. Chaos theory. In: Ranson KA, editor. *Academic American encyclopedia*. Danbury (CT): Grolier Incorporated, 1996
144. Beunen G, Thomis M. Genetic determinants of sports participation and daily physical activity. *Int J Obes Relat Metab Disord* 1999; 23: Suppl. 3: S55-63
145. Carpenter S. Psychology is bound to become more Darwinian, says eminent primatologist [letter]. *Monitor Psychol* 2001; 32: 4
146. Rosengren KS, Savelsbergh G, Van der Kamp J. Development and learning: a TASC-based perspective of the acquisition of perceptual-motor behaviours. *Infant Behav Dev* 2003; 26: 473-94
147. Wahlsten D. Insensitivity of the analysis of variance to heredity-environment interactions. *Behav Brain Sci* 1990; 13: 109-62
148. Cronbach LJ. Emerging views on methodology. In: Wachs TD, Plomin R, editors. *Conceptualization and measurement of organism-environment interaction*. Washington, DC: American Psychological Association, 1991

Correspondence: Prof. Keith Davids, School of Human Movement Studies, Queensland University of Technology, Victoria Park Road, Kelvin Grove, QLD 4059, Australia.