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RESEARCH ARTICLE

Does individual quality mask the detection of performance trade-offs? A test using analyses of human physical performance

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ABSTRACT

Why are performance trade-offs so rarely detected in animals when their underlying physiological basis seems so intuitive? One possibility is that individual variation in health, fitness, nutrition, development or genetics, or 'individual quality', makes some individuals better or worse performers across all motor tasks. If this is the case, then correcting for individual quality should reveal functional trade-offs that might otherwise be overlooked. We tested this idea by exploring trade-offs in maximum physical performance and motor skill function in semi-professional soccer players. We assessed individual performance across five maximum 'athletic' tasks providing independent measures of power, stamina and speed, as well as five soccer-specific 'motor skill' tasks providing independent measures of foot control. We expected to find functional trade-offs between pairs of traits (e.g. endurance versus power/speed tasks or specialist–generalist performance) – but only after correcting for individual quality. Analyses of standardised raw data found positive associations among several pairs of traits, but no evidence of performance trade-offs. Indeed, peak performance across a single athletic task (degree of specialisation) was positively associated with performance averaged across all other athletic tasks (generalist). However, after accounting for an individual's overall quality, several functional trade-offs became evident. Within our quality-corrected data, 1500 m-speed (endurance) was negatively associated with squat time (power), jump distance (power) and agility speed – reflecting the expected speed–endurance trade-off; and degree of specialisation was negatively associated with average performance across tasks. Taken together, our data support the idea that individual variation in general quality can mask the detection of performance trade-offs at the whole-animal level. These results highlight the possibility that studies may spuriously conclude certain functional trade-offs are unimportant or non-existent when analyses that account for variation in general quality may reveal their cryptic presence.

KEY WORDS: Soccer, Skill, Motor control, Agility

INTRODUCTION

The vertebrate body is multi-functional, with the same suite of traits used for activities as diverse as capturing prey, defending territories, acquiring mates and escaping predators; yet, maintaining function under such variable and potentially conflicting demands may lead to compromises in performance (Vanhooydonck et al., 2001; Van Damme et al., 2002). Quantifying these compromises – or trade-offs – is key to understanding the basis of morphological and physiological evolution in all animals, including humans. Studies of performance between conflicting tasks have revealed two main types of trade-offs in animal movement: (i) functional performance trade-offs and (ii) specialist–generalist trade-offs. Functional trade-offs occur between pairs of performance traits, where increases in one result in decreases in the other (Garland et al., 1995; Vanhooydonck et al., 2001; Van Damme et al., 2002). For example, greater expression of faster- than slower-type muscle fibres can be associated with greater power output of muscles and better sprint speed, but poorer fatigue resistance of muscles and lower endurance-based performance (Garland et al., 1995; Dohm et al., 1996; Wilson et al., 2002; Wilson and James, 2004; Wilson et al., 2004). The second class of trade-off is that between functional specialists and generalist phenotypes, where increases in the maximum performance of one trait occur at the expense of average performance across other performance traits, or vice versa (Van Damme et al., 2002).

Although the mechanistic bases of many performance trade-offs are well described and accepted (Komi, 1984; Esbjörnsson et al., 1993; Wilson and James, 2004; Wilson et al., 2004), evidence for their existence at the whole-animal level is far from convincing (e.g. Ford and Shuttlesworth, 1986; Garland and Else, 1987; Garland, 1988; Tsuji et al., 1989; Huey et al., 1990; Jayne and Bennett, 1990; Sorci et al., 1995; Wilson et al., 2002; Herrel and Bonneaud, 2012). Most studies exploring trade-offs at the whole-animal level find that high performers in one task are also high performers in other tasks, or find no trade-off between tasks at all (Garland and Else, 1987; Tsuji et al., 1989; Huey et al., 1990; Jayne and Bennett, 1990). Given the intuitive physiological basis of many performance trade-offs, the paucity of studies showing them in whole animals is puzzling.

One potential explanation for this paradox is that variation in overall 'quality' masks biologically driven differences in performance. Because individuals vary in health, fitness, nutrition, development or genetics, which is the underlying basis of individual quality, some individuals perform better or worse across all types of motor tasks than others. This means that when researchers try to understand intra-individual functional trade-offs using inter-individual variation in performance, then trade-offs that do occur within individuals can be masked. In a similar way, variation in individual quality driven by ageing, phenotypic plasticity and resource allocation is known to mask life-history trade-offs across many species (Vaupel et al., 1979; Reznick, 1985; van Noordwijk and Dejong, 1986; Forslund and Pärt, 1995). Correcting for individual quality could therefore make it possible to detect functional trade-offs between motor tasks such as speed, power and endurance that would otherwise be missed. A key study supporting this idea is the work of Van Damme and colleagues (Van Damme et al., 2002), which examined trade-offs in performance within the 10 sporting tasks of elite decathletes, including power-based and endurance events. Van Damme et al. (Van Damme et al., 2002) found that all performance traits were highly positively correlated – that is, some individuals were better at everything – suggesting that trade-offs in performance were absent; however, when the

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Table 1. Correlation matrix of the 10 performance traits – five athletic and five motor skill traits – using the raw standardised data from the 28 semi-professional soccer players

	1500 m speed	Squat time	Jump distance	Sprint speed	Agility	Dribbling	Juggling	Volley	Passing
Squat time	0.16								
Jump distance	0.18	**0.47**							
Sprint speed	**0.32**	0.29	**0.37**						
Agility	0.28	**0.50**	**0.63**	0.24					
Dribbling	**0.41**	0.09	0.15	0.30	0.06				
Juggling	0.14	−0.03	**0.34**	−0.03	0.20	0.25			
Volley	−0.02	0.09	−0.02	**0.35**	−0.24	0.22	0.09		
Passing	0.16	−0.07	−0.07	0.23	−0.02	**0.37**	0.08	**0.53**	
Heading	0.13	0.15	0.04	−0.08	0.27	0.10	0.24	**0.48**	**0.55**

Significant correlations between pairs of performance traits are indicated by bold text.

researchers corrected for overall quality among decathletes (via an amalgamated score over all 10 tasks), they found strong evidence of both functional compromises between pairs of events as well as a specialist–generalist trade-off. Taken together, it seems that inter-individual variation in overall quality could obscure important individual-level trade-offs in animal performance, but few studies have considered this issue further.

In our study, we explore whether individual variation in general quality masks the detection of performance trade-offs in human locomotion. In studies of life history, individual quality is well known to mask trade-offs between current and future reproductive fitness (Hamel et al., 2009; Wilson and Nussey, 2010). We expect that the detection of performance trade-offs should be similarly affected. To test this prediction, we assessed individual performance of semi-professional soccer players in five maximum 'athletic' tasks providing independent measures of power, stamina and speed, as well as five soccer-specific 'motor skill' tasks providing independent measures of football control. Numerous studies have examined trade-offs among maximum traits (e.g. speed, power, strength, endurance) (e.g. Huey et al., 1990; Jayne and Bennett, 1990; Sorci et al., 1995; Wilson et al., 2002; Herrel and Bonneaud, 2012); but movement depends both on these maximum traits as well as on the ability to successfully perform controlled, precision-based movements (e.g. accuracy of foot and hand placement). We believe that this ubiquitous focus on maximum performance and an absence of quantifying motor skill in ecological or evolutionary studies of performance has narrowed our view of locomotor trade-offs. A trade-off between maximum performance and motor skill is likely to have constrained the evolution of the vertebrate locomotor system because of the contrasting morphological and muscular bases of these traits – but this has not been previously tested. Soccer players are ideal subjects for studies of performance trade-offs because motor skill and athletic ability are vital for success in competition, and each type of performance can be readily identified, isolated and quantified (Reilly et al., 2000; Ali, 2011; Russell and Kingsley, 2011).

We expected to find that: (i) performance in endurance-related athletic tasks would be negatively correlated with performance in tasks related to speed and power (speed–endurance trade-off hypothesis); (ii) maximum athletic performance would be negatively associated with an ability to perform controlled, skilful movements (maximum–control trade-off hypothesis); and (iii) a high degree of specialisation for any athletic or motor skill task would be associated with poorer average performance across all other athletic or motor skill tasks (specialist–generalist trade-off hypothesis). Importantly, we expected that correcting for differences in overall quality among subjects would allow us to better observe functional trade-offs between pairs of traits and between specialist–generalist phenotypes.

RESULTS

Maximum athletic capacity

Based on analyses of standardised raw data, we found positive associations among several pairs of traits, but did not identify any significant negative correlations, or trade-offs (Table 1). Speed over 1500 m was positively associated with the composite measure of power performance (agility and maximum jump distance) (r_p=0.25; P=0.05) (Fig. 1A), and speed over 40 m (r_p=0.32; P<0.05) (Table 1). Maximum speed of individuals over 40 m was positively correlated with maximum jump distance (r_p=0.37, P<0.05) (Table 1). When we corrected for player quality, we found trade-offs among several pairs of performance tasks, as expected (Table 2). Quality-corrected 1500 m

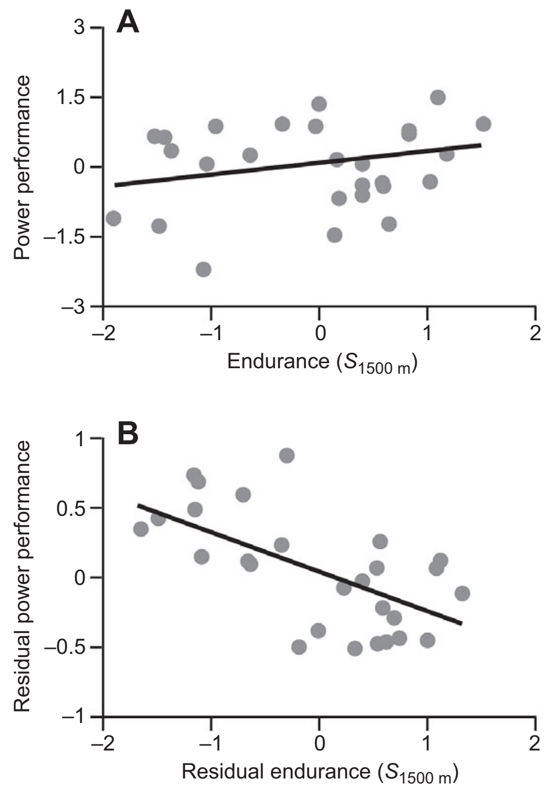

Fig. 1. The relationship between maximum 1500 m running speed (endurance) and power-based performance (agility speed and jump distance) for the human athletes. (A) Based on raw data, speed over 1500 m was positively associated with the composite measure of power performance (r_p=0.25; P=0.05), while (B) quality-corrected 1500 m speed was highly negatively correlated with power-based performance (r_p=–0.60; P<0.0001).

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Table 2. Correlation matrix of the 10 performance traits – five athletic and five motor skill traits – using the data corrected for individual general quality from the 28 semi-professional soccer players

	1500 m speed	Squat time	Jump distance	Sprint speed	Agility	Dribbling	Juggling	Volley	Passing
Squat time	**–0.52**								
Jump distance	**–0.41**	−0.20							
Sprint speed	0.05	−0.06	−0.25						
Agility	**–0.44**	0.15	−0.02	**–0.52**					
Dribbling	0.28	−0.03	−0.01	0.22	**–0.53**				
Juggling	0.01	−0.32	0.36	−0.23	0.12	0.04			
Volley	−0.16	0.14	−0.06	**0.46**	−0.23	−0.11	−0.31		
Passing	0.10	−0.13	−0.22	0.25	−0.18	−0.12	−0.40	0.09	
Heading	−0.02	0.01	−0.16	−0.39	**0.42**	**–0.50**	−0.07	0.06	0.15

Significant correlations between pairs of performance traits are indicated by bold text.

speed was highly negatively correlated with power-based performance (r_p=–0.60; P<0.0001) (Fig. 1B), including maximum squat time (r_p=–0.52; P<0.001), maximum jump distance (r_p=–0.41; P<0.01) and agility speed (r_p=–0.44; P<0.01) (Table 2). Maximum running speed through the agility course was negatively correlated with maximum sprint speed over a straight 40 m course (r_p=–0.52; P<0.01) (Table 2).

Peak performance across all the athletic tasks (degree of specialisation) was positively associated with performance averaged across all other athletic tasks (generalist) (Fig. 2A) (r_p=0.79; P<0.01). Overall, individuals performing well in one task seemed to also perform well in other tasks, indicating variation in quality among players. The best-performing athletic trait was 1500 m speed for 36% of the participants (N=28). When we corrected for quality, we found that an individual's peak performance was negatively associated with their performance averaged across all other tasks, indicative of a specialist–generalist trade-off (Fig. 2B) (r_p=–0.61; P<0.001).

Motor skill function

As we observed with uncorrected athletic traits, standardised raw values for many motor skill traits were positively correlated. Passing accuracy was positively correlated with dribbling performance (r_p=0.37; P<0.05), volley accuracy (r_p=0.53; P<0.01) and heading accuracy (r_p=0.55; P<0.001) (Table 1). For quality corrected data, the only negative correlation detected between any pair of motor skill traits was that between dribbling performance and heading accuracy (r_p=–0.50; P<0.01) (Table 2). Dribbling ability was the highest performing trait for 29% of individuals while either juggling or heading was the best trait for 21% of individuals (N=28). Using standardised raw values, we found that a high degree of specialisation to one motor skill task (peak score) was positively associated with performance averaged across all other motor skill tasks (Fig. 2C) (r_p=0.67; P<0.001). When we corrected for individual quality, we found that peak performance across motor skill tasks was not associated with performance averaged across all other motor tasks (Fig. 2D) (r_p=0.034; P>0.10).

Athletic–motor skill trade-offs

We found no evidence of a trade-off between an individual's athletic performance and their ability in the motor skill tasks. Whether we investigated raw standardised data (r_p=0.22; P>0.05) (Fig. 3A) or

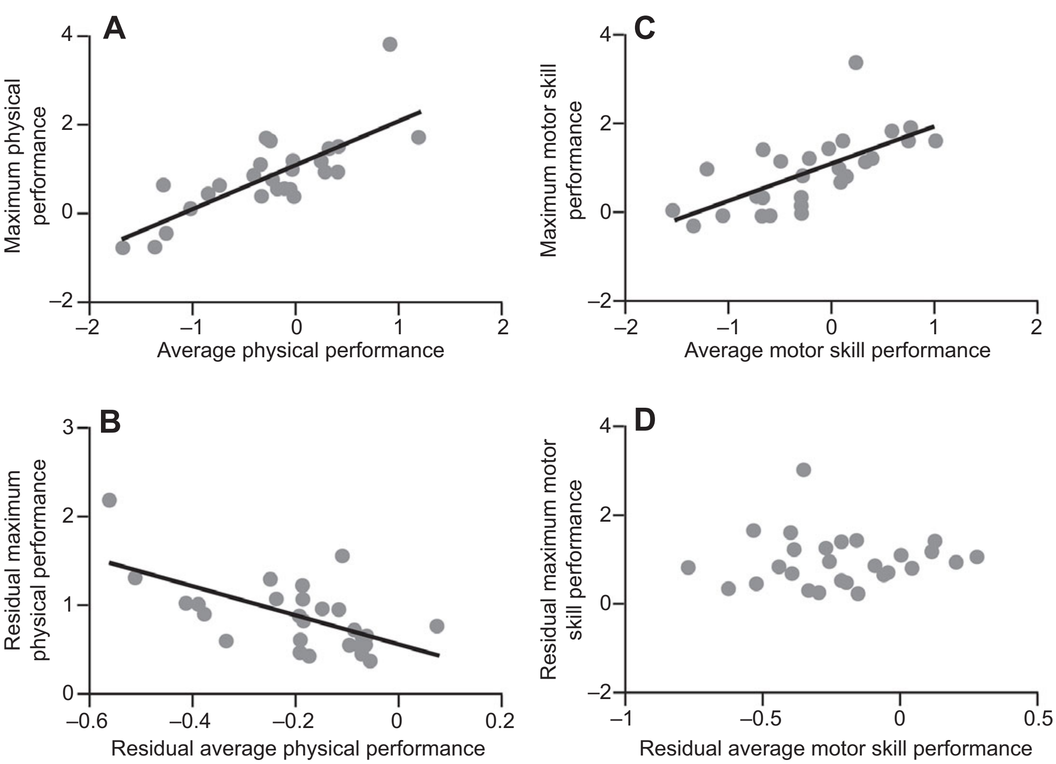

Fig. 2. The relationship between peak performance (specialisation) and performance averaged across all other performance tasks (generalisation) for the human athletes. (A) Peak performance across all the athletic tasks was positively associated with performance averaged across all other athletic tasks (r_p=0.79; P<0.01). (B) When corrected for quality, peak performance of athletic traits was negatively associated with their performance averaged across all other tasks (r_p=–0.61; P<0.001). (C) Peak performance across all motor skill tasks was positively associated with performance averaged across all other motor skill tasks (r_p=0.67; P<0.001). (D) When corrected for quality, peak performance for motor skill was not significantly associated with motor skill performance averaged across all other tasks (r_p=0.034; P>0.10).

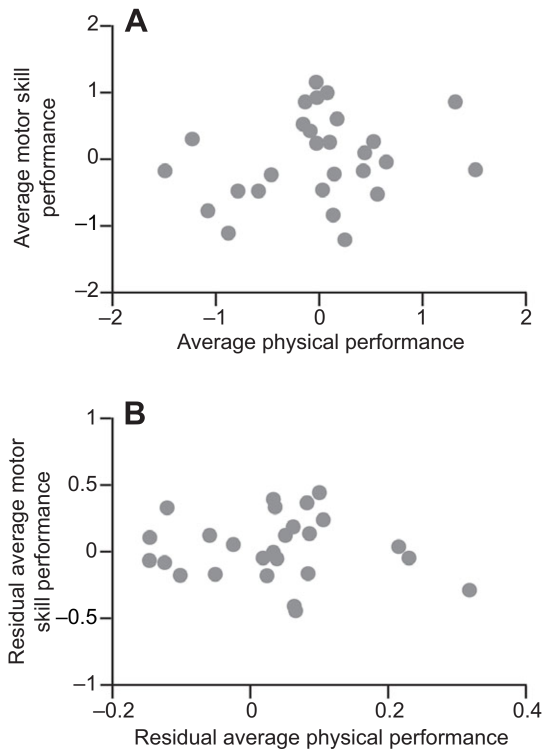

Fig. 3. The relationship between overall athletic performance and overall motor skill performance for the 28 human athletes. No significant correlations were detected between these two traits based on (A) raw data (r_p=0.22; *P*>0.05) or (B) individual quality-corrected data (r_p=–0.09; *P*>0.10).

those corrected for individual quality (r_p=–0.09; *P*>0.10) (Fig. 3B), no significant correlations were detected between overall motor skill and athletic performance. However, we found that maximum running speed through the agility course was negatively correlated with dribbling speed throughout the same circuit (r_p=–0.53; *P*<0.01) (Table 2).

DISCUSSION

Functional trade-offs are ubiquitous in nature but their role in shaping complex performance traits can be difficult to study. Problems arise because studies seek to understand intra-individual functional trade-offs by examining inter-individual variation in performance; when life-history trade-offs are examined in this way, variation in individual quality often masks the detection of expected trade-offs (Hamel et al., 2009; van Noordwijk and de Jong, 1986; Reznick et al., 2000). Accordingly, we expected that variation in individual quality would simultaneously affect the performance of all functional tasks, masking trade-offs between performance types. Consistent with this idea, we found no evidence for negative associations between speed and endurance capacity (speed–endurance trade-off) or between peak performance on singular tasks and average performance across all tasks (specialist–generalist trade-off) when analysing raw values of performance. Performance activities were either positively associated or not related at all, suggesting variation in quality among individuals.

When we accounted for individual quality – based on a multivariate analysis of performance across multiple tasks – we found significant trade-offs in individual performance across several activities. Quality-corrected analyses showed a strong trade-off between peak performance at one activity (specialisation) and average performance across all activities (generalisation), and a trade-off between performance in power- or speed-related tasks and endurance. Previous studies of whole-animal performance provide limited support for functional trade-offs, even those with a clear physiological basis (such as speed–endurance). Our work shows that individual quality may cloud the detection of within-individual functional trade-offs, and highlights the possibility that functional constraints on evolution could be more common than previously shown.

So, can correcting for quality tell us all we need to know about functional trade-offs? Certain functional trade-offs are logistically difficult to explore, yet many others remain open to manipulative experiments that enable one to establish causality. For example, males of many fish, bird or insect species produce extravagant ornaments used to show quality, and which augment mating opportunities (Andersson, 1994). However, greater attractiveness from increased ornamentation is expected to occur at a cost to an individual's viability; by altering ornament size, shape and mass, it is then possible to test the costliness of these signals to behaviour and locomotion. For example, a recent study was able to explore the trade-offs associated with the exaggerated fins of male threadfin rainbowfish (*Iriatherina werneri*); by experimentally manipulating fin length, it was shown that variation in fin size does not affect burst swimming speeds (Trappett et al., 2013). Clearly, testing for causality between many functional traits is difficult – if not impossible. For instance, we cannot (currently) engineer individuals with fewer or greater fast-type muscle fibres to observe for any subsequent changes in endurance, or establish ecological implications. To partially circumvent these experimental issues, biologists are beginning to define individual quality in a way that it can be measured (Wilson and Nussey, 2010; Lailvaux and Kasumovic, 2011) to enable practical analyses: from an evolutionary standpoint, 'individual quality' can be defined as 'a property of the phenotype that is positively, but not necessarily perfectly, correlated with fitness' (Wilson and Nussey, 2010). In the current study, we used Wilson and Nussey's method of quantifying individual quality as a 'scalar abstraction' of multiple phenotypic traits. In other words, we defined individual quality as the first dimension of a principal component analysis (PCA) of phenotypic variation across multiple traits, using traits associated with either maximum physical performance or motor skill function. In a similar way, Hamel and colleagues (Hamel et al., 2009) quantified individual quality using a species-specific combination of longevity, success in the last breeding opportunity before death, adult mass and social rank. Using longitudinal data from three ungulate populations, Hamel and colleagues (Hamel et al., 2009) explored how individual quality affects the probability of detecting life-history trade-offs between current reproduction and future reproduction for females. They found high-quality females consistently had a higher probability of reproduction that was independent of previous reproductive status (Hamel et al., 2009). However, they did detect a reproductive trade-off for female mountain goats after accounting for differences in individual quality; low-quality female goats were less likely to reproduce following years of breeding than following non-breeding (Hamel et al., 2009). In addition, offspring survival was lower in bighorn ewes after a successful breeding season than after those seasons when no lamb was produced – but this occurred only for low-quality females (Hamel et al., 2009).

Although there has been some recent interest in the evolutionary consequences of variation in motor skill (Byers and Kroodsma, 2009; Byers et al., 2010; Barske et al., 2011), there is still a paucity of knowledge on the repeatability and ecological importance of motor control traits. Most previous analyses of motor control have focused on the underlying mechanisms and neural pathways (Daley and Biewener, 2006; Kohlsdorf and Biewener, 2006; Toro et al., 2006). Prior studies of functional trade-offs have almost entirely focused on maximum performance traits (e.g. speed, strength, endurance), largely ignoring motor control traits (i.e. precision-based movement). We suggest this focus on maximum performance promotes a narrow view of the evolution of the locomotor system because an individual's success in all complex activities relies upon both an animal's maximum capabilities and its ability to perform fine motor skills. From our analysis of motor skill traits, we only identified one negative association: that between dribbling performance and heading accuracy. The underlying basis of this trade-off is not immediately obvious but could be associated with an agile, manoeuvrable phenotype that supports better foot coordination whilst a taller, long-limbed physique may enable better neck control. Although there is currently limited support, we expect that many motor skill trade-offs will be caused by the functional advantages and limitations imposed by stouter, shorter individuals versus taller, leaner physiques.

A trade-off between maximum performance and motor skill has relevance for understanding the evolution of form for all animals, as it suggests that increases in physical size, strength and speed will compromise precision-based motor function. We expected to find such a trade-off but we found no such negative association between maximum performance capacity and motor skill function, even after accounting for individual general quality. Functionally, a phenotypic design that allows strong, rapid movements should be at odds with a design facilitating accurate, precise movement. Our data suggests this may not the case – at least between overall maximum physical performance and motor skill performance. However, we did find a negative correlation between running speed through the agility circuit and dribbling speed (kicking speed) through the same circuit, suggestive of such a trade-off between leg-power and leg-control. Further analyses should explore the possibility of maximum performance/motor skill trade-offs and we suggest specialised features such as the human hand may be ideal for such analyses.

Using our multivariate analyses of individual quality, we identified functional performance trade-offs in our human subjects. But can this idea also be explored using non-human animals? To our knowledge, only one other study has explored the importance of individual quality in masking performance trade-offs – and it was also based on human athletes (Van Damme et al., 2002). Correcting for individual quality requires measurement of performance across multiple tasks – for example, our study measured performance over five athletic and five motor skill tasks, while the work of Van Damme and colleagues (Van Damme et al., 2002) compared performance among the 10 tasks associated with decathlon. Quantifying a large number of performance traits for non-human animals is likely to be difficult because of the limited repertoire of performances that can be elicited in animals. Most study animals can be encouraged to perform sprinting, endurance and biting tasks, but getting them to perform other tasks – including motor skill-related tasks – may be quite difficult. Work in this area might begin with animal models such as rodents, which are already used in studies of speed (Garland et al., 1995; Dohm et al., 1996), endurance (Billat et al., 2005), swimming (Dohm et al., 1996), cognitive function (Kitsukawa et al., 2011), motor skill (Song et al., 2006) and gripping strength (Abdelmagid et al., 2012).

MATERIALS AND METHODS

We recorded parameters associated with athletic performance and motor skill in semi-professional soccer players (*N*=28) within the premier division of Brisbane Men's Football. The average age for participants was 24.5 years (s.d.=2.8 years; range 20–33 years).

Maximum athletic capacity

For each individual, we measured the following athletic performance traits: (i) maximum speed over 1500 m, (ii) total squat time, (iii) maximum jumping distance, (iv) fastest sprint speed over 40 m, (iv) and fastest speed through an agility circuit. To determine 1500 m speed for each individual, we recorded the total time taken to complete a 1500 m circuit around a grassed oval on two separate occasions (1 week apart). We used the fastest time recorded for each individual and converted it into a measure of average speed over the 1500 m. Total squat time was recorded as the maximum single wall-squat time when an individual had their back flat against a concrete wall and both thighs were kept parallel to the ground, while the lower legs were at right angles to the ground. Maximum lower body power was quantified by recording each individual's maximum static jump distance over four trials, with 1 min rest between each test; only those jumps that were performed with both feet hip-width apart and starting from a crouched position (full knee bend) were used, and the single best jump for each individual was taken as his maximum jump distance. To determine maximum sprint speed, we recorded the total time taken to complete a 40 m straight-line distance on grass on five separate occasions. Each sprint was separated by a rest period of 2 min, and the fastest single time recorded for individuals was used as their maximal sprint speed. This fastest time was converted into a measure of average speed over the 40 m. To determine the maximum agility speed, we recorded the total time to complete a 44.8 m agility circuit (Fig. 4A) on grass on three separate occasions. Each sprint was separated by a rest period of 2 min, and the fastest single time recorded for each individual was used as his measure of agility speed. We converted the time taken to complete the sprint into a measure of average speed over the 44.8 m.

For data analyses, we first standardised all raw values of athletic performance so that each of the five traits possessed the same mean (mean=0) and standard deviation (s.d.=1). To do this we subtracted the mean value for each particular task from each individual's score for that same task and then divided it by the overall standard deviation for the task. This ensured that each of the tasks was comparable in mean and standard deviation, and we refer to these as the standardised raw values of performance. Following this, we conducted a PCA on all five measures of athletic performance using the standardised raw values. The first component of the PCA of athletic performance ($PCA_{Ath}1$) explained 49% of the variation observed in athletic performance (Table 3). All vectors of $PCA_{Ath}1$ loaded in the same direction; thus, it represented a measure of overall athletic performance (general athletic quality). The second component, $PCA_{Ath}2$, explained 20% of the variation and this was indicative of a negative correlation between acceleration–power with maximum sprinting speeds (Table 3). Positive values of $PCA_{Ath}2$ were representative of faster speeds through the agility circuit and longer jump distances (rapid acceleration and high leg power), while negative values were associated with high performance in the 40 and 1500 m run (high maximal running speeds).

To calculate an individual's performance in each athletic task relative to their overall quality (i.e. correcting for individual quality), we calculated the residuals for each performance trait when regressed upon an individual's overall measure of athletic performance ($PCA_{Ath}1$). Thus, values above the line of best fit were then indicative of a high level of performance for that task relative to an individual's overall athletic ability. As such, residual values were then referred to as an individual's quality-corrected performance.

Motor skill function

For each player, we measured performance in the five soccer-specific motor skill tasks: (i) maximum dribbling speed, (ii) average juggling (i.e. keep-up) ability, (iii) static ball passing accuracy, (iv) volley-kick accuracy, and (v) heading accuracy. Maximum dribbling speed was quantified by recording the total time taken for an individual to dribble (i.e. kick) the football through the 44.8 m agility course (Fig. 4A) without making any mistakes (i.e. knocking

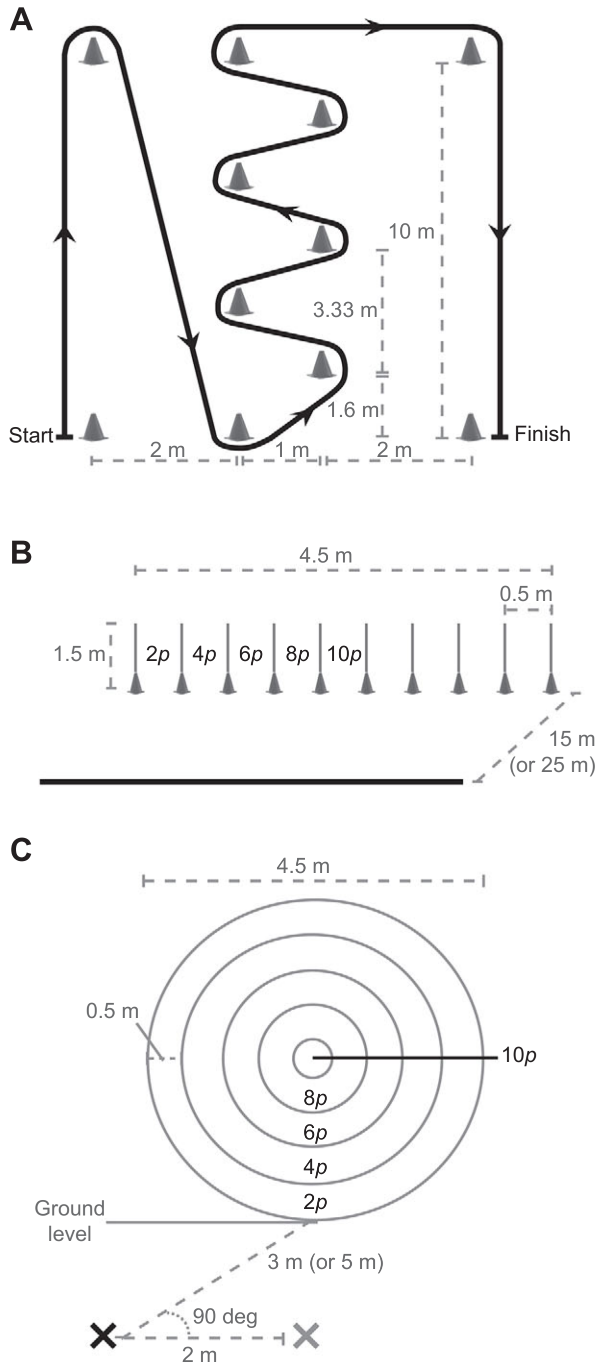

Fig. 4. The dimensions and set-up for the different tests. (A) Agility and dribbling performance task; the solid line with arrows indicates the path taken by the athletes; (B) static passing tests; and (C) volley-kick and heading test. See text for more details about set-up. *p*, points.

over cones or going along the wrong path). Each individual was given three attempts at the dribbling task, with 2 min rest between each attempt, and the fastest time was taken as their peak performance. We converted the time taken to complete the dribbling circuit into a measure of average speed over the 44.8 m. Average 'juggling' performance was determined by recording the total number of times an individual could kick a size 1 football (smallest size) without it touching the ground. This trial was repeated for each individual on 10 separate occasions, with his average score across all 10 attempts used as a measure of juggling ability. Static ball passing accuracy was assessed by giving each individual five attempts to kick a stationary ball at a target from both 15 and 30 m, using their left and right feet (total of 10 kicks from 15 m, and 10 kicks from 30 m). The target consisted of a series of 50 cm wide scoring zones demarcated by 1 m high posts. The central scoring zone was worth 10 points, the next two 50 cm areas on either side were worth 8 points, and these scoring zones decreased accordingly. The total target area was 4.5 m wide and 1 m high, with any part of the ball falling within this zone scoring the relevant points (Fig. 4B). Any balls that hit the posts and did not go through the scoring zone were scored as intermediates between the scoring zones; for example, if the ball hit the post between the 8 and 6 point scoring zones, then that kick was scored as 7 points. Volley-kick accuracy was assessed by giving each individual five attempts to kick an aerially served ball at a target from both 5 and 10 m, using their left and right feet (total of 10 kicks from 5 m and 10 kicks from 10 m). The target consisted of a series of concentric circles with each larger circle represented by a 0.5 m increase in diameter (Fig. 4C). The central scoring zone was worth 10 points and consisted of an area 0.5 m in diameter, with each outer circle decreasing by 2 points for a 0.5 m increase in diameter. Thus, the entire scoring zone was 2.5 m in diameter and the centre of the scoring zone was 1.25 m off the ground. Each individual's total accumulated score across the 20 volleys was used as their measure of volley accuracy. Heading accuracy was assessed using an identical methodology as that outlined above for volley accuracy, except that players were required to use their heads to move the ball toward the target. The total accumulated score was based on all 20 headers, which was then used as their measure of heading accuracy. For both volley and heading tasks, serving of the football in the air could occasionally lead to a poor delivery that prevented the player from obtaining good contact with the football. To minimise the effects of server error on a player's score, we used one server for all tasks. In addition, only balls served at a height that was below mid-thigh and above mid-shin were counted towards a player's overall volley score, and only balls served at a standing height below the top of the head and above the shoulders were counted towards a player's overall heading score. Any misdirected serves were immediately repeated.

Table 3. Principal components analysis matrix of the five athletic performance traits (*N*=28) showing the factor loadings of each measured variable and the direction in which they contribute towards the components

Principal component	$PCA_{Ath}1$	$PCA_{Ath}2$	$PCA_{Ath}3$
%Variance	48.6	19.6	14.2
1500 m speed	−0.48	−0.73	0.46
Squat time	−0.73	0.30	−0.055
Jump distance	−0.81	0.26	−0.07
Sprint speed	−0.60	−0.47	−0.63
Agility	−0.81	0.25	0.31

PCA_{Ath}, principal components analysis of the athletic performance traits. See Materials and methods for a description of each trait.

As per our analyses of athletic performance, we standardised all raw values of motor skill performance so that each of the five traits possessed the same mean (mean=0) and standard deviation (s.d.=1). Based on these standardised raw values of motor skill, we conducted a PCA on the data. The first component of the PCA_{skill} based on measures of motor skill performance explained 48% of the variation observed in the data (Table 4). All vectors of $PCA_{skill}1$ loaded in the same direction; thus, it represented a measure of overall skill performance. The second component of the PCA for measures of motor skill performance explained 22% of the variation and this described the negative correlation between juggling and dribbling ability with volley and heading ability (Table 4).

To calculate an individual's performance in each motor skill task relative to their overall quality (i.e. correcting for individual quality), we also calculated the residuals for each performance trait when regressed upon an individual's overall measure of motor skill performance ($PCA_{skill}1$). These residual values were then referred to as an individual's quality-corrected motor skill performance.

Statistical analyses

All correlations among pairs of athletic and motor skill performance traits were conducted using Pearson's product moment correlations. These analyses

Table 4. Principal components analysis matrix of the five motor skill performance traits (*N*=28) showing the factor loadings of each measured motor skill trait and the direction in which they contribute towards the three components

Principal component	$PCA_{skill}1$	$PCA_{skill}2$	$PCA_{skill}3$
%Variance	48.0	22.1	18.8
Dribble	−0.52	0.69	−0.33
Juggles	−0.36	0.55	0.71
Volley	−0.78	−0.24	−0.16
Pass	−0.82	−0.09	−0.29
Heading	−0.60	−0.50	0.46

PCA_{skill}, principal components analysis of the motor skill traits.
See Materials and methods for a description of each trait.

were conducted on both the standardised raw data and those data corrected for individual quality. To correct for multiple statistical comparisons, we used a Bonferroni correction factor that divided the significance value of 0.05 by the number of comparisons being conducted. This supplied a new value for statistical significance for the multiple correlations. To test the speed–endurance (or power–endurance) trade-off hypothesis, we also conducted a correlation between 1500 m speed and performance averaged across the two power-based performance traits of maximum jump distance and agility speed. We used both standardised raw values and quality-corrected data for these analyses. To test the specialist–generalist trade-off hypothesis, we calculated the peak individual score for an individual across all athletic performance traits and correlated this with each individual's performance averaged across all other performance tasks. This meant that an individual's peak performance could be taken from any of the performance tasks. Tests of the specialist–generalist trade-off were repeated using the motor skill traits and conducted using both raw standardised data and those corrected for individual quality. Finally, we tested for a possible trade-off between motor skill function and athletic performance using correlation analyses of average athletic performance against average motor skill performance. This correlation was performed using both raw standardised data and those corrected for individual quality. All statistical analyses were performed using the software package R.

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Competing interests
The authors declare no competing financial interests.

Author contributions
R.S.W., A.C.N., G.D., A.H. and M.S. conceived, designed and executed experiments, interpreted the findings, and drafted the article.

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References
Abdelmagid, S. M., Barr, A. E., Rico, M., Amin, M., Litvin, J., Popoff, S. N., Safadi, F. F. and Barbe, M. F. (2012). Performance of repetitive tasks induces decreased grip strength and increased fibrogenic proteins in skeletal muscle: role of force and inflammation. *PLoS ONE* **7**, e38359.
Ali, A. (2011). Measuring soccer skill performance: a review. *Scand. J. Med. Sci. Sports* **21**, 170-183.
Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.
Barske, J., Schlinger, B. A., Wikelski, M. and Fusani, L. (2011). Female choice for male motor skills. *Proc. R. Soc. B* **278**, 3523-3528.
Billat, V. L., Mouisel, E., Roblot, N. and Melki, J. (2005). Inter- and intrastrain variation in mouse critical running speed. *J. Appl. Physiol.* **98**, 1258-1263.
Byers, B. E. and Kroodsma, D. E. (2009). Female mate choice and songbird song repertoires. *Anim. Behav.* **77**, 13-22.
Byers, J., Hebets, E. and Podos, J. (2010). Female mate choice based upon male motor performance. *Anim. Behav.* **79**, 771-778.
Daley, M. A. and Biewener, A. A. (2006). Running over rough terrain reveals limb control for intrinsic stability. *Proc. Natl. Acad. Sci. USA* **103**, 15681-15686.
Dohm, M. R., Hayes, J. P. and Garland, T. (1996). Quantitative genetics of sprint running speed and swimming endurance in laboratory house mice (*Mus domesticus*). *Evolution* **50**, 1688-1701.
Esbjörnsson, M., Hellsten-Westing, Y., Balsom, P. D., Sjödin, B. and Jansson, E. (1993). Muscle fibre type changes with sprint training: effect of training pattern. *Acta Physiol. Scand.* **149**, 245-246.
Ford, N. B. and Shuttlesworth, G. A. (1986). Effects of variation in food-intake on locomotory performance of juvenile garter snakes. *Copeia* 999-1001.
Forslund, P. and Pärt, T. (1995). Age and reproduction in birds – hypotheses and tests. *Trends Ecol. Evol.* **10**, 374-378.
Garland, T. (1988). Genetic-basis of activity metabolism. 1. Inheritance of speed, stamina, and antipredator displays in the garter snake *Thamnophis sirtalis*. *Evolution* **42**, 335-350.
Garland, T., Jr and Else, P. L. (1987). Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *Am. J. Physiol.* **252**, R439-R449.
Garland, T., Jr, Gleeson, T. T., Aronovitz, B. A., Richardson, C. S. and Dohm, M. R. (1995). Maximal sprint speeds and muscle fiber composition of wild and laboratory house mice. *Physiol. Behav.* **58**, 869-876.
Hamel, S., Côté, S. D., Gaillard, J. M. and Festa-Bianchet, M. (2009). Individual variation in reproductive costs of reproduction: high-quality females always do better. *J. Anim. Ecol.* **78**, 143-151.
Herrel, A. and Bonneaud, C. (2012). Trade-offs between burst performance and maximal exertion capacity in a wild amphibian, *Xenopus tropicalis*. *J. Exp. Biol.* **215**, 3106-3111.
Huey, R. B., Dunham, A. E., Overall, K. L. and Newman, R. A. (1990). Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiol. Zool.* **63**, 845-872.
Jayne, B. C. and Bennett, A. F. (1990). Selection on locomotor performance capacity in a natural-population of garter snakes. *Evolution* **44**, 1204-1229.
Kitsukawa, T., Nagata, M., Yanagihara, D., Tomioka, R., Utsumi, H., Kubota, Y., Yagi, T., Graybiel, A. M. and Yamamori, T. (2011). A novel instrumented multipeg running wheel system, Step-Wheel, for monitoring and controlling complex sequential stepping in mice. *J. Neurophysiol.* **106**, 479-487.
Kohlsdorf, T. and Biewener, A. A. (2006). Negotiating obstacles: running kinematics of the lizard *Sceloporus malachiticus*. *J. Zool. (Lond.)* **270**, 359-371.
Komi, P. V. (1984). Biomechanics and neuromuscular performance. *Med. Sci. Sports Exerc.* **16**, 26-28.
Lailvaux, S. P. and Kasumovic, M. M. (2011). Defining individual quality over lifetimes and selective contexts. *Proc. R. Soc. B* **278**, 321-328.
Reilly, T., Williams, A. M., Nevill, A. and Franks, A. (2000). A multidisciplinary approach to talent identification in soccer. *J. Sports Sci.* **18**, 695-702.
Reznick, D. (1985). Costs of reproduction – an evaluation of the empirical-evidence. *Oikos* **44**, 257-267.
Reznick, D., Nunney, L. and Tessier, A. (2000). Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol. Evol.* **15**, 421-425.
Russell, M. and Kingsley, M. (2011). Influence of exercise on skill proficiency in soccer. *Sports Med.* **41**, 523-539.
Song, Y. N., Li, H. Z., Zhu, J. N., Guo, C. L. and Wang, J. J. (2006). Histamine improves rat rota-rod and balance beam performances through H(2) receptors in the cerebellar interpositus nucleus. *Neuroscience* **140**, 33-43.
Sorci, G., Swallow, J. G., Garland, T. and Clobert, J. (1995). Quantitative genetics of locomotor speed and endurance in the lizard *Lacerta vivipara*. *Physiol. Zool.* **68**, 698-720.
Toro, E., Herrel, A. and Irschick, D. J. (2006). Movement control strategies during jumping in a lizard (*Anolis valencienni*). *J. Biomech.* **39**, 2014-2019.
Trappett, A., Condon, C. H., White, C., Matthews, P. and Wilson, R. S. (2013). Extravagant ornaments of male threadfin rainbowfish (*Iriatherina werneri*) are not costly for swimming. *Funct. Ecol.* **27**, 1034-1041.
Tsuji, J. S., Huey, R. B., Vanberkum, F. H., Garland, T. and Shaw, R. G. (1989). Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*) – quantitative genetics and morphometric correlates. *Evol. Ecol.* **3**, 240-252.
Van Damme, R., Wilson, R. S., Vanhooydonck, B. and Aerts, P. (2002). Performance constraints in decathletes. *Nature* **415**, 755-756.
van Noordwijk, A. J. and Dejong, G. (1986). Acquisition and allocation of resources – their influence on variation in life-history tactics. *Am. Nat.* **128**, 137-142.
Vanhooydonck, B., Van Damme, R. and Aerts, P. (2001). Speed and stamina trade-off in lacertid lizards. *Evolution* **55**, 1040-1048.
Vaupel, J. W., Manton, K. G. and Stallard, E. (1979). The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography* **16**, 439-454.
Wilson, R. S. and James, R. S. (2004). Constraints on muscular performance: trade-offs between power output and fatigue resistance. *Proc. R. Soc. B* **271**, S222-S225.
Wilson, A. J. and Nussey, D. H. (2010). What is individual quality? An evolutionary perspective. *Trends Ecol. Evol.* **25**, 207-214.
Wilson, R. S., James, R. S. and Van Damme, R. (2002). Trade-offs between speed and endurance in the frog *Xenopus laevis*: a multi-level approach. *J. Exp. Biol.* **205**, 1145-1152.
Wilson, R. S., James, R. S., Kohlsdorf, T. and Cox, V. M. (2004). Interindividual variation of isolated muscle performance and fibre-type composition in the toad *Bufo viridus*. *J. Comp. Physiol. B* **174**, 453-459.