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Abstract

Running speed in animals depends on both genetic and environmental conditions. Maximal speeds were here analysed in horses, dogs and humans using data sets on the 10 best performers covering more than a century of races. This includes a variety of distances in humans (200–1500 m). Speed has been progressing fast in the three species, and this has been followed by a plateau. Based on a Gompertz model, the current best performances reach 97.4% of maximal velocity in greyhounds to 100.3 in humans. Further analysis based on a subset of individuals and using an 'animal model' shows that running speed is heritable in horses ($h^2 = 0.438$, $P = 0.01$) and almost so in dogs ($h^2 = 0.183$, $P = 0.08$), suggesting the involvement of genetic factors. Speed progression in humans is more likely due to an enlarged population of runners, associated with improved training practices. The analysis of a data subset (40 last years in 800 and 1500 m) further showed that East Africans have strikingly improved their speed, now reaching the upper part of the human distribution, whereas that of Nordic runners stagnated in the 800 m and even declined in the 1500 m. Although speed progression in dogs and horses on one side and humans on the other has not been affected by the same genetic/environmental balance of forces, it is likely that further progress will be extremely limited.

Introduction

Locomotor performance is a key trait in mobile species that is closely associated with fitness (Irschick & Losos, 1999). In particular, improving running speed might allow for reaching prey or avoiding predator more efficiently (Husak, 2006). It is therefore of importance to better evaluate those factors, whether genetic or environmental, affecting maximum speed. However, experimentally evaluating how far maximum speed can improve is difficult, because assessing it over meaningful time periods is not always feasible. We propose a way to alleviate this issue by using race records in species in which fastest speeds have been monitored over a long time span. Such data are available in horses, dogs (greyhounds) and humans.

Speed progression, that is, the increase in maximal speed over time, in these three species results from both genetic and environmental factors, although to various extents according to species (Nevill & Whyte, 2005; Niemi & Majamaa, 2005; Davids & Baker, 2007). Moreover, some variables acting on speed progression depend on training (relating to physiology, psychology, biomechanics, technology or tactics improvement), whereas others are outside the athletes' control (genetics, anthropometric characteristics, climatic conditions; Smith, 2003; Brutsaert & Parra, 2006). In domesticated animals, sustained selection by breeders has long been known to cause large and accelerated phenotypic changes contributing to short-term evolutionary processes (Darwin,

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1868; Falconer & Mackay, 1996). Racing horses have indeed been selected from the 16th century, based on closed populations and a very small number of founders (Willett, 1975). Beginning later, similar selection processes have been imposed on greyhounds for dog racing. This means that phenotypic expression (such as running speed) relies on a narrow genetic basis in comparison with the variation available in these species. However, genetic variance for performance has recently been detected in thoroughbred horses (Gu *et al.*, 2009; Hill *et al.*, 2010).

The improvement in fast-running performances in humans does not (of course) rely on selective breeding, but on the detection of fast-running athletes generally during adolescence or later through national systems that were optimized after World War II (Guillaume *et al.*, 2009). Importantly, the athlete population has increased in size proportionally to the development of modern sport throughout the last century. For example, 241 athletes from 14 national Olympic committees participated in the first modern Olympic games (Athens, 1896), whereas 10 942 athletes coming from 204 nations attended the 29th games in Beijing (2008). Thus, the best human runners are now selected from a much larger number of countries (Guillaume *et al.*, 2009), presumably over a larger genetic basis for performance (Yang *et al.*, 2003; Williams & Folland, 2008). This is to be opposed to the limited variation for running capacity observed in dogs and horses (Denny, 2008). A striking tendency in humans is also related to geographical origins of runners, with, for example, the massive rise of African runners among best performers (BPs) in middle to long distance over the recent decades (Onywera *et al.*, 2006).

Other factors relating to runner physiology (e.g. training, running style, nutrition and, sometimes, doping activities) or to environment *sensu lato* (e.g. climatic conditions, riding style, rules, betting activity, reward) have also played a significant role in improving running performance (Norton & Olds, 2001; Noakes, 2004; Pfau *et al.*, 2009; Toutain, 2010). The respective influence of genetic and nongenetic factors may therefore largely differ in domesticated animals and in humans (Brutsaert & Parra, 2006). Whatsoever, recent studies have demonstrated that the maximal running speed may soon reach its limits in dogs, horses and humans (Berthelot *et al.*, 2008, 2010; Denny, 2008).

Best running performances in humans have been under scrutiny (Nevill & Whyte, 2005; Berthelot *et al.*, 2008), but a full analysis of speed progression in greyhounds and horses is not available. The comparison of speed progression in animals (horses and dogs) with that in humans requires long-term data over comparable periods and distances.

We collected data built up over more than a century (up to 118 years) for the 10 BPs in races (450–500 m in dogs, 2200–2800 m in horses and 200–1500 m in

humans) – the larger range in humans allowing direct comparison with the two other species over similar running times. We also tested the heritability of BPs using pedigrees of dogs and horses, whereas in humans, performance analysis from different geographical regions allowed us to test the progression of maximum running speed according to the geographical origin of runners. Our objectives here are (i) to compare the progression of speed performances in humans, horses and dogs and (ii) to evaluate the potential influence of genetic factors in horses and dogs, based on a so-called animal model approach (Kruuk, 2004), and of geographical origin in humans. Our approach is comparative (not experimental) in essence as it is based on observational data over the long term in three species, although it allows to dissect the respective influences of genetic and environmental factors on patterns of speed progression based on fairly large data sets.

Materials and methods

The performance progression of the 10 BPs was recorded yearly throughout the world in flat, thoroughbred horse races (years: 1898–2009; distances: 2200–2800 m; effort duration from 130 to 170 s) and greyhound races (years: 1929–2009; distances: 450–500 m; effort duration from 24 to 28 s). Men's track and field races (years: 1891–2009; distances: 200, 400, 800 and 1500 m; effort duration from 20 to 230 s) were used to express human 10 BPs. The means of 10 BPs from sprint (200 and 400 m) and short to middle distances (800 and 1500 m) were considered separately for a best correspondence to thoroughbred and greyhounds' BP times, respectively. For each species, only the best yearly performance of a single athlete or animal was kept, so that any given athlete appears only once per year in the data sets. The yearly BP records were obtained in thoroughbreds from 30 events at the highest competitive level over the world ('Group 1 and 2' in Europe, Oceania and Asia and 'Stakes' for North America). In greyhounds, we collected the yearly 10 best performances recorded in short race's rings (25 events in Great Britain, Ireland, Spain, United States, Australia and New Zealand). In humans, track and field outdoor best performances were collected. Speed data were collected with similar methodology as recently reported (Denny, 2008; Desgorces *et al.*, 2008) from various sources in humans (Associations of Track and Field Statisticians; Rabinovich, 2010), horses (Galop course, 2011; Galopp sieger, 2011) and greyhounds (Greyhounds-data, 2011). A total of 6620 performances were gathered (4720 in humans, 1120 in horses and 810 in dogs). The BPs in dogs and humans were male only, whereas the horse data set included some females as well. However, as the fraction of female BPs was limited, we did not account for a sex effect when analysing the data. Speed data were expressed in m s^{-1}

Progression pattern of maximal running speeds

Previous studies reported that best performances' progression over the last century was best described by logistics and/or multiexponential curves (Nevill & Whyte, 2005; Berthelot *et al.*, 2008; Denny, 2008). Blest (1996), analysing a set of world records in athletics, showed that Gompertz models provided lower standard errors of estimates compared with other models (i.e. antisymmetric exponential and logistic models). They also described well best performances in humans (Berthelot *et al.*, 2010). We therefore opted for such a model using the following function:

$$Y(t) = a.e^{be^{c.t}} + d$$

where a gives the upper asymptote of y, b sets the value of t displacement, c is the curve steepness and d accounts for the fact that the minimum y value is not 0. a and d takes here positive values, whereas b and c are negative. The model parameters were estimated using a nonlinear least-squares method on the uniformized [(0, 1) range] vector of recorded values. The physiological limit for each species was given by computing the year corresponding to 99.95% (1/2000th) of the estimated asymptotic value. Curve fitting was performed using MATLAB (version 7.11.0.584, MathWorks, Natick, MA, USA).

The yearly progression of human speed was compared with that of greyhounds (200–400 m in humans) and thoroughbreds (800–1500 m in humans) and expressed as the percentage of a human–animal ratio. The annual speed variation was also observed in each species through coefficient of variation (CV) changes.

Speed heritability in dogs and horses

For the recent period, genealogical data were available in both dogs and horses, allowing for a quantitative genetics approach. The speeds of current 10 BPs (2007–2009) were collected and compared with those of their ancestors (individual best performance; Galop course 2011, Galopp sieger 2011, Greyhounds-data 2011). These ancestor data sets bear on 67 dogs (1964–2009) and 64 horses (1960–2009) including six females in the current 10 BPs (2007–2009). All dogs and horses are part of a pedigree (seven generations in dogs and six in horses) with only male links known.

To decompose the phenotypic variance expressed in speed of greyhounds and horses lineages and to estimate the heritability (h^2) of this character, we used two methods: (i) a classic father–midsons regression and (ii) a restricted estimate maximum likelihood procedure to run a mixed model with the software ASReml (Gilmour *et al.*, 2006). An 'animal model' (Kruuk, 2004) was used in which the year was considered as a fixed effect and the total phenotypic variance (V_P) was broken into two components of variance as follows:

$V_P = V_A + V_R$, where V_A is the additive genetic variance and V_R is the residual variance, consisting of environmental effects, nonadditive genetic effects and error variance. A single speed record was available in 10 years in dog races and 20 years in horses; hence, a year could not be entered as a random effect in the model. The full model outlined above was compared with a simpler model where V_A was removed using a chi-squared test, to determine whether speed displayed significant additive genetic variance.

Geographical origin of human best runners

The full human data set (200–1500 m) was split according to the geographical origin (Africa, America, Asia, Europe and Oceania) of runners. Africa, Asia and Oceania are poorly represented in the 10 BPs over the period considered (1891–2009; Fig. S1). The analysis was further refined for short to middle distance (800–1500 m; year range: 1970–2009) by comparing the five BPs from North European countries (Nordic: Denmark, Norway, Sweden, Finland) and from East Africa (EAf; Djibouti, Eritrea, Ethiopia, Somalia, Tanzania, Kenya, Uganda, Burundi), for which large data sets are available, with runners from rest of world (ROW). An analysis of variance was used to determine the regional (Nordic, EAf, ROW) and time (data arranged per decade; 1970–1979; 1980–1989; 1990–1999; 2000–2009) influence on speed progression. When speed differences were detected, Tukey's *post hoc* tests were used to identify significant differences according to region and decade. The software package STATISTICA (version 6.1; Statsoft, Maisons-Alfort, France) was used for statistical analyses. The level of significance for all analyses was set at $P < 0.05$. Data are expressed as mean ± SD.

Results

The Gompertz model fits speed progression with good accuracy in animals (horses: $R^2 = 0.56$, MSE = 0.169; greyhounds: $R^2 = 0.81$, MSE = 0.55; Fig. 1a,b) and in humans (800–1500 m 10 BPs: $R^2 = 0.97$, MSE = 0.006, Fig. 1c; 200–400 m 10 BPs: $R^2 = 0.94$, MSE = 0.008, Fig. 1d). The asymptotic limit in horses and dogs was 16.59 and 17.76 m s^{-1}, respectively, that is, 99.0% and 97.4% of the respective Gompertz asymptotes. In humans, the speeds of sprint and middle distances have already reached their estimated maximum based on the Gompertz curves (sprint: 9.54 m s^{-1} in 1996, 100.3% of asymptotic speed; middle distance: 7.45 m s^{-1} in 2001, 100.1% of asymptotic speed). Speed progression was evaluated by comparing the first 10 BPs recorded with the 10 BPs ever observed, and it appears similar in the three species (11.1% of initial value in horses, 9.4% in greyhounds, 11.1% in 200–400 m and 14.2% in 800–1500 m in humans; Fig. 1). Even less difference in speed progression was observed in the two animal species when
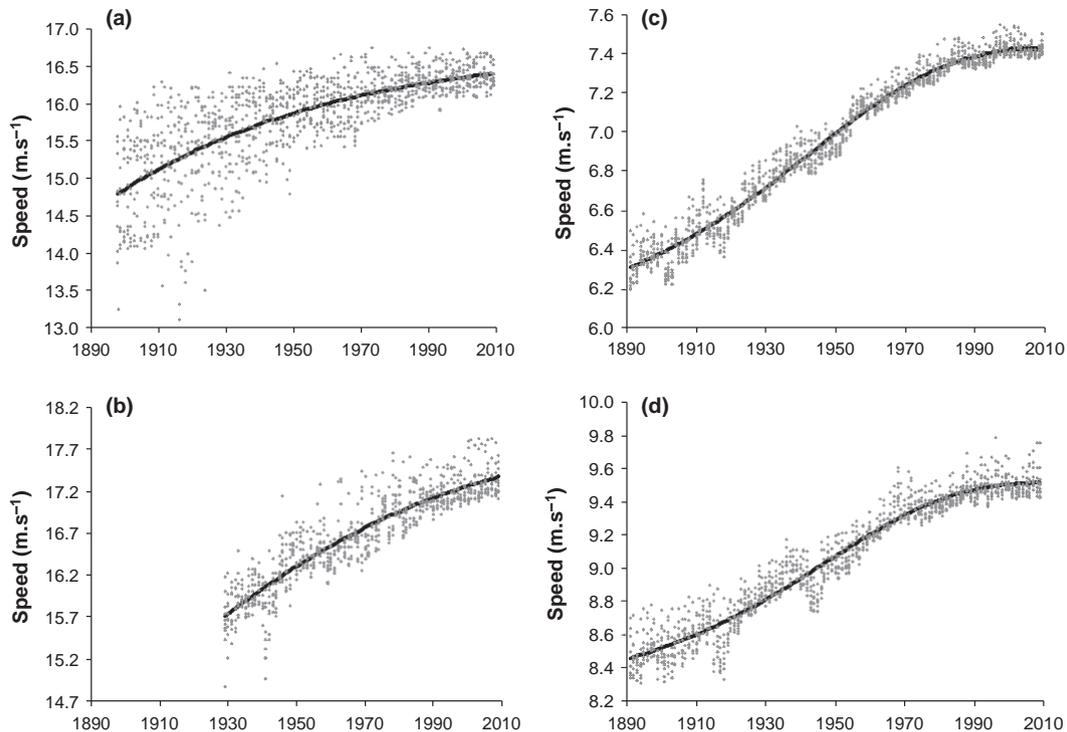
Fig. 1 Models fitting for speed progression (m s^{-1}) between 1891 and 2009, in (a) 10 best thoroughbred performers ($R^2 = 0.56$); (b) 10 best greyhound performers on short ring races ($R^2 = 0.81$); (c) Mean speed of the 10 best human performers on 800- to 1500-m track races ($R^2 = 0.97$); (d) Mean speed of the 10 best human performers on 200- to 400-m track races ($R^2 = 0.94$). The calculated *a, b, c, d* parameters of the Gompertz function were for thoroughbred (respectively, 77.8, 3.77, 0.46, 16.59), greyhound (respectively, 14.99, 1.99, 0.60, 17.7), 800- to 1500-m human races (respectively, 1.45, 0.26, 3.06, 7.44) and for 200- to 400-m human races (respectively, 1.29, 0.20, 3.31, 9.52).

using the asymptotic speed limit of the Gompertz curves rather than the 10 BPs ever observed (12.4% in horses, 11.9% in greyhounds, and 11.1% and 14.2% in humans).

Although the overall progression was similar, the curves differed in shape among species (*b* and *c* coefficients). The *b / c* ratios revealed a monoexponential shape (*b / c* > 3) in both horses and greyhounds, whereas performances of humans follow an S-shaped development (*b/c* < 0.1; Fig. 1). The CVs of dog and human speed were of the order of 0.02 (or less) over the period considered (Fig. 2). In horses, the CV was also 0.02 for the 1940–2009 period, but the 1898–1939 period had larger variance with CV up to 0.05. Humans have increased their mean speed compared with dogs over a comparable distance with a current human–dog ratio downward plateauing towards 53.2% (Fig. 3). The comparison with horses shows a current human–horse ratio of 45.2%. Both ratios have been stable for 18 years (dogs) and 42 years (horses).

Heritability estimates based on father–midsons comparisons were significant neither in greyhounds (30 pairs; $h^2 = 0.042$, SE = 0.34, $P = 0.90$) nor in horses (34 pairs; $h^2 = 0.272$, SE = 0.23, $P = 0.25$). The 'animal model' confirmed this trend in greyhounds ($N = 67$ data points):

the additive variance was low (0.028, SE = 0.039), and model comparison (with and without V_A) showed that the heritability ($h^2 = 0.183$, SE = 0.240) did not differ from 0 (chi-square = 3.08, $P = 0.080$). In horses, though ($N = 64$ data points), more additive variance was detected (0.085, SE = 0.059), and the heritability differed from 0 ($h^2 = 0.438$, SE = 0.267; chi-square = 6.14, $P = 0.013$). We note here that our approach, based on BPs, underestimates the available phenotypic variance in both greyhounds ($V_P = 0.156$, SE = 0.003) and horses ($V_P = 0.193$, SE = 0.037).

Human speeds achieved in the 800- and 1500-m races by the five BPs over the 1970–2009 period differ according to performance years and geographical origin of runners (800-m races, $F_{1,39} = 5.89$, $P < 0.001$ and 1500-m races $F_{1,39} = 6.66$; Fig. 4). EAf and ROW runners clearly increased their speed in both distances, compared with Nordic runners. The Nordic-versus-EAf difference was not significant over the 1970–1989 decade, and both groups performed less well than the ROW group (all $P < 0.001$). Pairwise comparisons also showed a Nordic/EAf/ROW increasing hierarchy for 800-m races. In the most recent decade (2000–2009), speeds on the 800- and 1500-m races are lower in Nordic than in EAf runners (both $P < 0.001$), but there was no difference
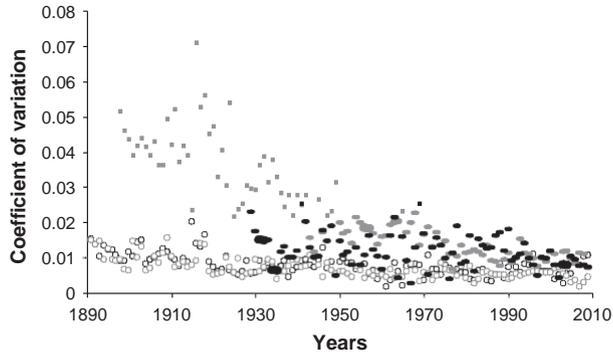
Fig. 2 Coefficient of variations of 10 best performers in thoroughbred (1899–2009; grey squares), greyhounds (1929–2009; black squares), human 200- to 400-m races (1891–2009; grey open circles) and humans 800- to 1500-m races (1891–2009; black open circles).
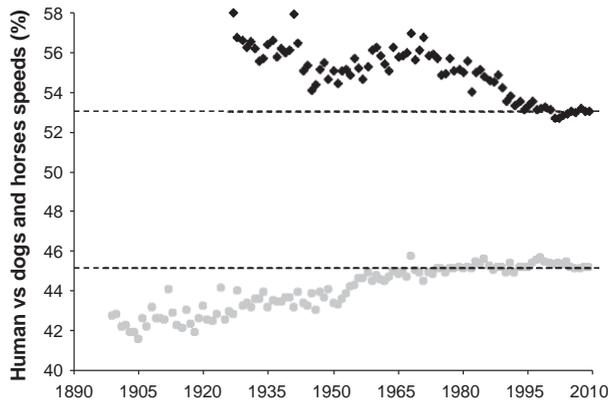

Fig. 3 Ratios of human vs. greyhound (black squares, comparison with human 200–400 m mean speed) and human vs. thoroughbred (grey circles, comparison with human 800–1500 m mean speed). Dashed lines for mean speed gap between humans and animals when stabilized.
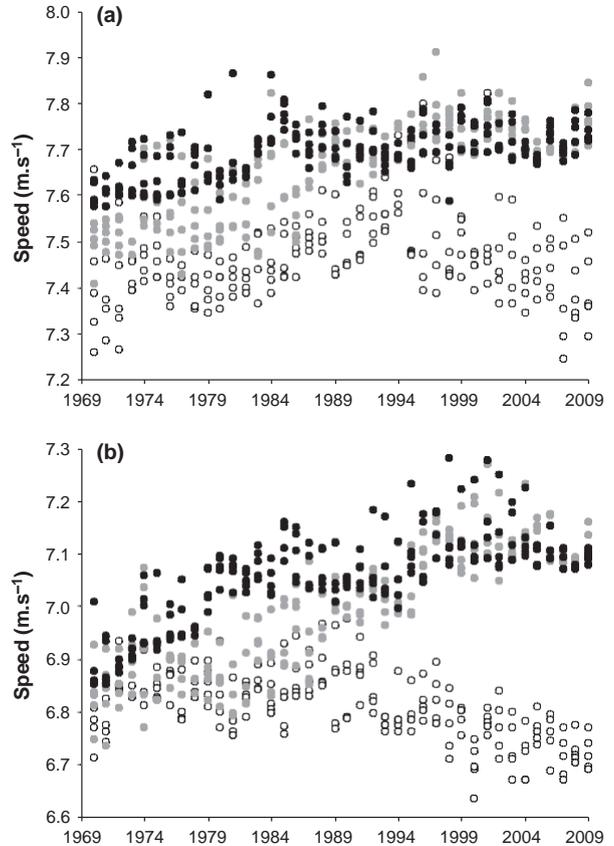

Fig. 4 Five best human performances in 800-m (a) and 1500-m (b) races in runners from Nordic countries (open circles), East African countries (grey circles) and rest of World (black circles).

between EAf and ROW ($P = 0.48$ in 800-m and $P = 0.59$ in 1500-m races). Whereas the speed of ROW and EAf runners increased over both distances since 1970, that of Nordic runners actually stagnated (1500 m: 6.83 ± 0.05 in 1970–1979 vs. 6.73 ± 0.04 m s^{-1} in 2000–2009; 800 m: 7.42 ± 0.08 m s^{-1} in 1970–1979 vs. 7.44 ± 0.09 m s^{-1} in 2000–2009).

Discussion

Our study shows that the maximum running speed over short to middle distances increased over the last century in dogs, horses and humans, but is currently reaching its asymptotic value. This is a striking result because of the difference in genetic and environmental conditions leading to speed improvement in the three species. The fitted Gompertz curves do not exhibit the same shape

(see values of b/c for the three curves in Results section) – the initial plateau in humans is not detected in horses and greyhounds – but this might simply be due to the larger variance in dogs and horses in the first decades of records or the facts that data were collected earlier in the speed progression in humans than in dogs and horses. Human speed has indeed already reached its asymptote, whereas horses and greyhounds speeds are 1.0% and 2.6% down from their respective values. These results are in agreement with recent studies hypothesizing that current speeds are reaching the species' locomotory limits and explain their conclusions (Berthelot *et al.*, 2008; Denny, 2008).

However, the similarities do not appear only in the progression patterns over the last century, but also in the progression ranges that were very close, especially when using the asymptotic speed limits to estimate the maximal speed progression per species. Over the last decades, we also noted that the speed gap between species pairs remained remarkably stable (Fig. 3). The speed CVs among the ten BPs are low as well (Fig. 2) and very similar across species. The large CV recorded in the

earlier decades for horses and dogs might be accounted for by the fact that rank, rather than speed, was often recorded in races at the end of the 19th century and beginning of the 20th century. It is also likely that the homogenization in training methods and the selection of similar genetic backgrounds also lead to reduced CVs.

The similarity in speed patterns (progression, asymptotes, CV) across species is somewhat unexpected because the balance between genetic and environmental forces acting on this pattern is different. Dogs for about 20 generations and horses for 25 generations have been submitted to intense artificial selection over the period considered (artificial selection was indeed initiated much earlier in both species; Willett, 1975). Quite clearly, artificial selection has reached a phenotypic limit with regard to the maximal speed and minimal variance across the 10 BPs, at least under the environmental conditions imposed by humans on dog and horse champions. Interestingly, the quantitative genetic analysis indicated some genetic variance and heritability in horses. These genetic effects are larger than those reported recently for lifetime earnings in a larger thoroughbred population (Wilson & Rambaut, 2008). This marked genetic influence on speed appears surprising when considering the reduced speed progression over the last 40 years. However, the animal model was run on a much more reduced data set than that used for getting the general trend, and the ancestors of the current 10 BPs did not belong to the 10 BPs in their generation. It might also be that training and raising environments for best horse racing should have been homogenized over time, enhancing in return h^2 estimates. The heritability in dogs was on the verge of statistical significance ($P = 0.08$). Previous studies reported that selective breeding may have led to high homogeneity of predispositions for running (Gu et al., 2009; Hill et al., 2010), suggesting reduced chance for the occurrence of genetically gifted individuals. Our results highlight that genetic predispositions for running fast in these particular populations are still good indicators of individual speed.

The optimization of running speed in humans probably essentially relies on training and national detection systems, but these might also allow identifying favourable polygenic profiles for elite runners (Yang et al., 2003; Williams & Folland, 2008; Bejan et al., 2010). It remains therefore possible that part of speed progression in humans is due to genetic (evolutionary) processes because there might be some selection to run fast under some conditions. However, this effect might only be minor given the very short time period considered. Our data also suggest that estimated speed limits of the 10 BPs have already been achieved in 200–400 and 800–1500 m, although exceptional athletes may sometimes set atypical performances (Berthelot et al., 2010). Over the century, the number of individuals engaged in athletic competitions evolved with societies' development and their emphasis on sport (Guillaume et al.,

2009). America and Europe largely contributed to the 10 BPs with differences according to distance, whereas Asia and Oceania did not. The contribution of Africa to the 10 BPs in middle distance over the most recent decades is noticeable. Initially less engaged, East Africans achieved speed records comparable to those of Nordic athletes on the 1500 m in the 1970s. The striking speed improvement over the last 40 years now placed them in the first ranks, comparable to the other world regions. It is no less striking that running speeds of natives from Nordic countries stagnated over the same period in 800-m races and even declined in 1500-m race. Trainers and scientists from Northern Europe were indeed largely involved in the development of modern training methods and scientific results (Astrand, 1991), questioning their real impact on current best performances. On the other hand, Nordic athletes are still successful in other sports (i.e. jumps and throws in athletics, speed skating, cross-country skiing, rowing), suggesting that their genetic potential may be more favoured under the environmental constraints of other sports.

Over the last decades, the maximal human speed has progressed with the involvement of runners from new geographical origins, leading to optimized phenotypes (Guillaume et al., 2009). The enlargement of the runner population in humans certainly enlarged the genetic pools upon which elite athletes were detected (Williams & Folland, 2008). Furthermore, some studies suggested that successful runners from East Africa originated from distinct ethnic and environmental backgrounds compared with the general population of these countries (Onywera et al., 2006; Scott et al., 2009). Quite clearly, improving speed through artificial selection in dogs and horses or detecting better athletes through an increasing population can only be actually efficient under appropriate environmental conditions, including training and competing conditions (Davids & Baker, 2007; Desgorces et al., 2008). The decrease in the 10 BPs during the two World Wars (Guillaume et al., 2009) is an indication of the role of environmental conditions. Speed increase requires prosperous societies with a flourishing economy as described for improved health and body size over the 19th and 20th centuries (Fogel, 2003).

Our analysis is based on patterns exhibited in long-term data sets collected in arguably artificial environments. It would certainly be interesting to use more experimental approaches to test whether other species are not far away from their limit and whether this limit can be experimentally manipulated and increased. Speed increase has indeed been described in nature when environmental conditions allow for the improvement in maximal capacities (Miles, 2004; Husak, 2006) and recently suggested as describing phenotypic expansion in humans (Berthelot et al., 2011). For example, dietary and thermal conditions experienced both during embryogenesis and early in life may favour the expression of genetic predisposition for running (Elphick &

Shine, 1998; Le Galliard *et al.*, 2004). Trade-offs are of course expected between running performances and appropriate behaviour or the ability to migrate towards more favourable environmental conditions (Irschick & Losos, 1999; Husak & Fox, 2006). In natural conditions, such adaptations in animals have been associated with survivorship and reproductive success (Miles, 2004). It is ironical that behaviour training and migration to more favourable environments also occur in competitive sports.

Conclusion

The parallel progression of maximal running speeds in these three species over the last decades suggests that performances will no longer progress despite genetic selection in animals and best population detection in humans. Regardless of differences between species (biological, environmental and competition history), human pressure, which has accelerated the biological adaptations allowing to run faster, is a process with limited potential and reduced benefits in the near future.

Acknowledgments

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Humans 10 best performances in sprint, up figures: 200 m (grey circles), 400 m (black circles); and middle distance, down figures: 800 m (grey circles) and 1500 m (black circles) according to the geographic origin of runners.

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