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A model balancing cooperation and competition can explain our right-handed world and the dominance of left-handed athletes

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An overwhelming majority of humans are right-handed. Numerous explanations for individual handedness have been proposed, but this population-level handedness remains puzzling. Here, we present a novel mathematical model and use it to test the idea that population-level hand preference represents a balance between selective costs and benefits arising from cooperation and competition in human evolutionary history. We use the selection of elite athletes as a test-bed for our evolutionary model and find evidence for the validity of this idea. Our model gives the first quantitative explanation for the distribution of handedness both across and within many professional sports. It also predicts strong lateralization of hand use in social species with limited combative interaction, and elucidates the absence of consistent population-level ‘pawedness’ in some animal species.

Keywords: evolution; handedness; laterality; mathematical model

1. INTRODUCTION

Although the precise definition of handedness is often debated, it is widely accepted that roughly one in 10 humans are left-handed [1,2]. Since prehistoric times, some cultural and geographical variations in this percentage have been observed (3–26%), but every historical population has shown the same significant bias towards right-handedness [1–5]. Both genetic and environmental factors seem to contribute to handedness for individuals [5–10]; nonetheless, individual handedness does not necessarily lead to species-level handedness. It is well established that for an individual, lateralization can be advantageous [11,12]: for example, it allows for specialization of brain function [7,13], which may lead to enhanced cognition through parallel information processing [14,15]. This advantage relates only to the degree of lateralization, not the direction; so it cannot explain lateralization at the species level [16]. Negative frequency-dependent selection, in which the fitness of a trait is inversely related to its frequency, is a primary mechanism by which polymorphisms are maintained [17,18]. However, owing to the symmetric nature of handedness, this mechanism can only produce a balanced distribution of left- and right-handers in the absence of other selection pressures [4].

There have been various modelling approaches that explain this species-level asymmetry in terms of ‘fitness functions’ either as an evolutionary stable strategy

[11,15,19] or based on frequency-dependent selection [18] (for further discussion of these models, see electronic supplementary material, §S1). Nonetheless, empirical validation of these models has proved elusive [11]. We propose a different approach to the problem.

2. OUR MODEL

We define a function $P_{RL}(l)$ representing the mean probability that right-handed individuals are replaced with left-handed offspring over a given time period (typically after many generations). $P_{LR}(l)$ is analogously defined. These probabilistic transition rates account for frequency-dependent selection effects, and can be approximated given a biological model for inheritance (see electronic supplementary material, §S2 and figure S1). A minimal model for the evolution of the societal fraction left-handed l in terms of these arbitrary frequency-dependent transition rates is given by

$$\frac{dl}{dt} = (1 - l)P_{RL}(l) - lP_{LR}(l). \quad (2.1)$$

Similar to previous work by Ghirlanda *et al.* [11], we assume symmetry between right- and left-handers (see electronic supplementary material, §S3), so that we may write $P_{LR}(l) = P_{RL}(1 - l)$ to obtain

$$\frac{dl}{dt} = (1 - l)P_{RL}(l) - lP_{RL}(1 - l). \quad (2.2)$$

To better understand the function P_{RL} , we break it up into two component functions, one monotonically decreasing and the other monotonically increasing.

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We refer to the decreasing component function of P_{RL} as $P_{\text{RL}}^{\text{comp}}$, because it drives non-conformity and is expected to dominate in societies where physical competition is prevalent (e.g. societies with exceedingly high homicide rates). When left-handers are scarce, they have an advantage in physical confrontations owing to their greater experience against right-handers and the right-handers' lack of experience against them. As their numbers grow, that advantage weakens [1,4,18].

Similarly, we refer to the increasing component function of P_{RL} as $P_{\text{RL}}^{\text{coop}}$, because this term drives individuals towards conformity and is expected to dominate in cooperative societies where, for example, tool-sharing is common. In a hypothetical society that was exclusively 'cooperative' in this sense, all individuals would tend to the same handedness because individuals that did not conform would be more likely to suffer exclusion from lateralized group activity [4,11,15]. The modern presence of a higher accidental death rate for left-handers [20–22] supports the idea that conformity to the right-handed majority remains advantageous in human society (this differential death rate may also be partially attributed to brain lateralization). In both cooperative and physically competitive societies, we assume that disadvantaged individuals are more likely to die prematurely and thus produce fewer offspring on average.

For a system involving both cooperative and competitive interactions, we therefore write

$$P_{\text{RL}}(l) = c P_{\text{RL}}^{\text{coop}}(l) + (1 - c) P_{\text{RL}}^{\text{comp}}(l),$$

where $0 \leq c \leq 1$ represents the relative importance of cooperation in interactions and the monotonicity properties of each component function are as given earlier. For physically reasonable choices of these functions, there may exist one, three or five fixed points l^* in this system, depending on the value of c .

3. ANALYSIS OF MODEL

Figure 1 shows the typical positions of stable and unstable equilibria for equation (2.1), where $P_{\text{RL}}^{\text{coop}}$ and $P_{\text{RL}}^{\text{comp}}$ have been chosen to be generic sigmoid functions. The shapes of these equilibrium curves are consistent with those predicted by prior models [11], and are similar for a variety of transition rate functions $P_{\text{RL}}^{\text{coop}}$ and $P_{\text{RL}}^{\text{comp}}$ (see electronic supplementary material, §S1). When the degree of cooperation c is less than a critical threshold, the only stable equilibrium is $l^* = 0.5$: a 50/50 split between left-hand and right-hand-dominant individuals. This is consistent with studies showing individual but not population-level bias in various species [10,23].

When the degree of cooperation exceeds a critical threshold, two new stable equilibria appear as a result of either a subcritical or supercritical pitchfork bifurcation (depending on the exact form of the function P_{RL}). These equilibria indicate population-level lateralization as seen in human society. (We use the terms 'lateralization' and 'lateral bias' in reference to hand preference unless otherwise noted.) The fraction right- or left-handed will depend on the exact value of the cooperation parameter c .

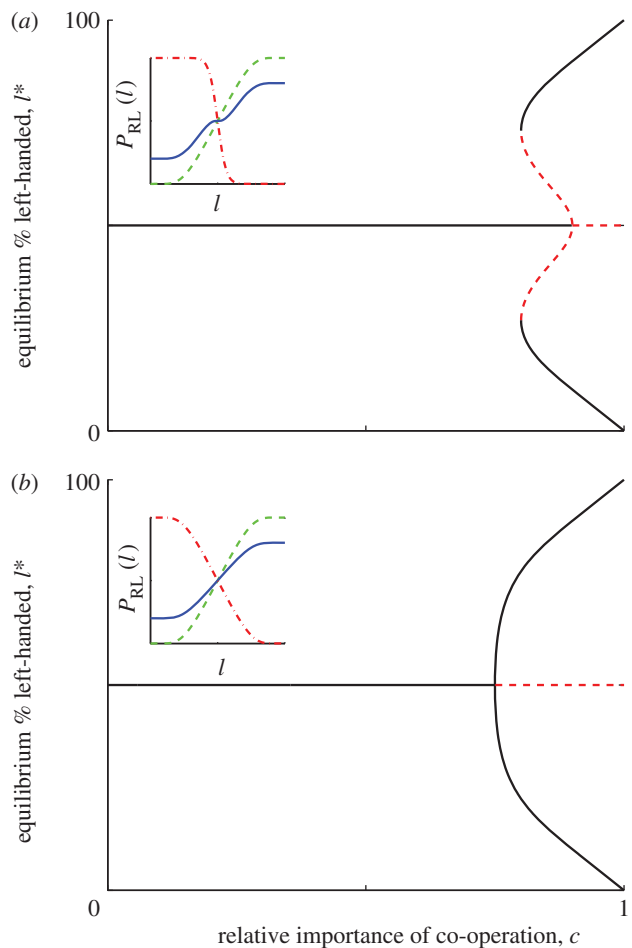


Figure 1. Equilibrium percentages left-handed as a function of societal cooperativity. Solid black lines indicate stable equilibria, dashed red unstable. (a) Monotonic dP_{RL}/dt on $(0, 1/2)$. (b) Non-monotonic dP_{RL}/dt on $(0, 1/2)$. Insets: P_{RL} and its component functions $P_{\text{RL}}^{\text{coop}}$, $P_{\text{RL}}^{\text{comp}}$. Dashed green line, cooperative; solid blue line, combined; dash-dot red line, competitive.

There is a qualitative difference between the two situations depicted in figure 1, a difference that holds for a broad class of sigmoid functions P_{RL} . In the case of the subcritical pitchfork (figure 1a), no weak population lateralization should ever be observed because equilibria near 50 per cent are unstable; however, in the case of the supercritical pitchfork (figure 1b), population lateralization near 50 per cent will be possible, though only stable for a small range of values of c . Both suggest that weak population lateralization (fractions approx. 50–70%) should be rare in the natural world, while indicating that a high degree of cooperation may be responsible for the strong lateralization (fractions approx. 70–100%) observed in some social animals (e.g. humans and parrots [24]).

4. COMPARISON OF MODEL PREDICTIONS WITH DATA

One challenge to modelling population-level handedness is a lack of data for empirical validation. To quote Ghirlanda *et al.* '...we need data from populations that differ in the balance between antagonistic and synergistic interactions but are otherwise as similar as possible'

[11]. Ideally, we would compare predicted equilibria of equation (2.2) to data from animal populations exhibiting varying degrees of cooperation. Unfortunately, for most species, quantifying the degree of cooperation is difficult, and the available data on the degree and direction of population-level lateralization vary from experiment to experiment depending on the task considered. This lack of consistent, conclusive data on handedness in the natural world leads us to examine the proxy situation of athletics (as done in Raymond *et al.* [1]), where data on handedness and cooperation are more easily accessible.

To explain the observed fraction of left-handed athletes, it is important to model the selection process because athletics, unlike evolution, should not cause changes in the population's background rate of laterality. We treat athletic skill s as a normally distributed random variable, and assume that minority handedness creates a frequency-dependent shift Δs that modifies the randomly distributed skill. We then model an ideal selection process as choosing the n most skilled players from a population of N interested individuals. Such a model (derived in detail in electronic supplementary material, §S4) predicts that the professional fraction left-handed l_{pro} will depend on the fraction selected $\psi = n/N$, and is determined implicitly by the equation

$$l_{\text{pro}} = \frac{1}{2} \frac{l_{\text{bg}} \text{erfc}(\hat{s}_c - \Delta \hat{s})}{\psi}, \quad (4.1)$$

where $l_{\text{bg}} \approx 10\%$ is the background rate of left-handedness, erfc is the complementary error function, \hat{s}_c is the normalized cut-off in skill level for selection and $\Delta \hat{s} \propto l^* - l_{\text{pro}}$ is the normalized skill advantage for left-handers. Here, l^* represents the fraction of the population that would be left-handed in a world consisting only of interactions through the sport under consideration. Its value is determined from equation (2.2), with a choice of parameter c appropriate for the sport under consideration (P_{RL} is reinterpreted as the mean probability that a right-handed player is replaced by a left-hander in a given time period). Note that l_{pro} must lie between l_{bg} and l^* : with very high selectivity ($\psi \rightarrow 0$), equation (4.1) implies that $l_{\text{pro}} \rightarrow l^*$, and with very low selectivity ($\psi \rightarrow 1$) $l_{\text{pro}} \rightarrow l_{\text{bg}}$.

Figure 2 shows our application of equation (4.1) to various professional sports. To reduce arbitrary free parameters, we assume that the cooperativity c is close to zero for physically competitive sports and one for sports (e.g. golf) that require lateralized equipment or strategy. Figure 1 then implies that the ideal equilibrium fraction left-handed l^* will be 50 per cent when c is close to zero, and will be either 0 or 100 per cent when $c = 1$.

The predictions for figure 2 were made by varying a single free parameter k , the constant of proportionality for the frequency-dependent skill advantage $\Delta \hat{s} = k(l^* - l_{\text{pro}})$. To avoid over-fitting, we took k to be a constant across all sports; given sufficient data, different values of k could be estimated independently for each sport. The fraction-selected ψ was estimated from the ratio of professional athletes to the number of frequent participants for each sport (see electronic supplementary material, §S5 for details).

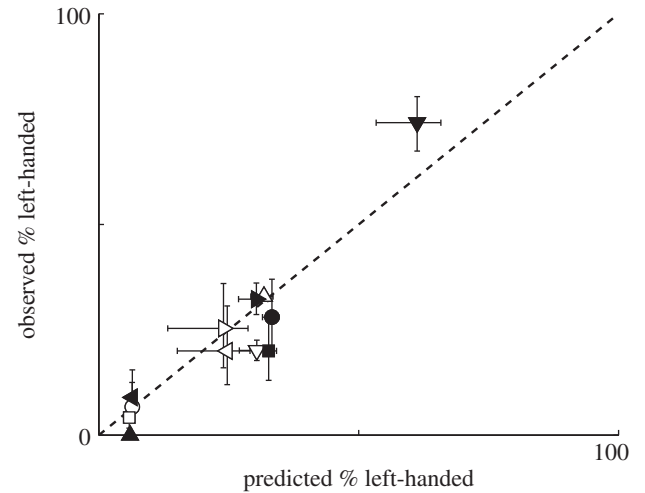


Figure 2. Observed percentage left-handed versus predicted for professional athletes of various sports. Open triangle, baseball; open inverted triangle, men's boxing; open left-facing triangle, men's fencing; open right-facing triangle, women's fencing; open circle, American football quarterbacks; open square, men's golf; filled triangle, women's golf; filled inverted triangle, hockey right wings; filled left-facing triangle, hockey left wings; filled right-facing triangle, hockey other positions; filled circle, men's table tennis; filled square, women's table tennis. Dashed line represents perfect agreement between predicted and observed values. Vertical error bars correspond to 95% CIs ($p = 0.05$); horizontal error bars correspond to predictions using plus or minus one order of magnitude in N , the primary source of uncertainty. Left-handed advantage $\Delta \hat{s} = k(l^* - l_{\text{pro}})$, where $k = 1.6108$ and both l^* and l_{pro} vary from sport to sport (see electronic supplementary material, table S1 and §S5).

For the sport of baseball, the great abundance of historical statistical information allows us to validate our proposed selection mechanism. To do so, we use our model to predict the cumulative fraction left-handed l_r as a function of rank r , then compare this to data.

In sports where highly rated players interact with other highly rated players preferentially (e.g. boxing), we expect the left-handed advantage $\Delta \hat{s}_r \propto l^* - l_r$ to be rank-dependent (i.e. depending on the fraction left-handed at rank r). However, within professional baseball leagues, all players interact with all other players at nearly the same rate; so the left-handed advantage $\Delta \hat{s}_r = \Delta \hat{s}$ should be independent of rank, i.e. a constant. This leads us (see electronic supplementary material, §S4 for derivation) to the equation

$$l_r = \frac{1}{2} \frac{l_{\text{bg}} N \text{erfc}(\hat{s}_r - \Delta \hat{s})}{r}. \quad (4.2)$$

Figure 3 shows the predictions of equation (4.2) as applied to the top-ranked baseball players from 1871 to 2009. Only one free parameter was varied: the left-handed advantage $\Delta \hat{s}$. All other parameters were constrained by known data [25]. The surprisingly good fit to this non-trivial curve can be seen as supporting evidence for the selection model. Together with the accuracy of predictions in figure 2, this supports

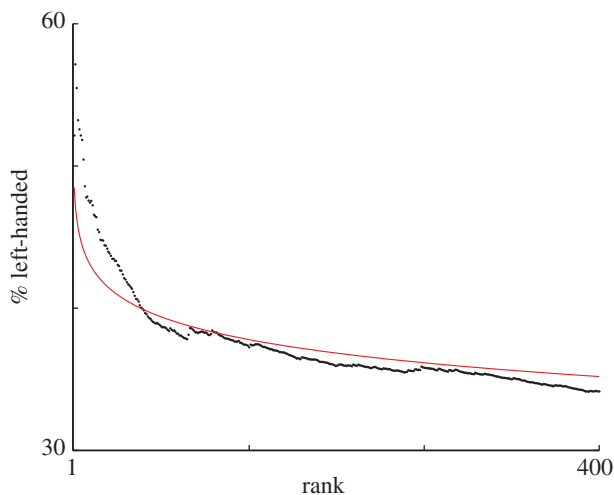


Figure 3. Cumulative fraction left-handed versus rank for seasonal top hitters in baseball, 1871–2009. Thin red line represents theoretical prediction from equation (4.2). Each black data point at rank r represents the left-handed fraction of all US born players that finished a season ranked in the top r by total hits. The left-handed advantage $\Delta s = 0.3003$ was computed by finding the least-squares best fit. This value differs slightly from the value used for baseball in figure 2 ($\Delta s = 0.2755$), suggesting that, in practice, the proportionality constant k may vary from sport to sport.

the conclusion that the equilibria of equation (2.2) are indeed relevant to real-world lateralized systems.

5. DISCUSSION

Despite the good agreement of our predictions with real-world data, we acknowledge that there are limitations in reducing a complex adaptive system to a simple mathematical model. Our model includes undetermined functions that would be difficult to measure precisely (although we found that qualitative predictions are robust—see electronic supplementary material, §S6). However, they can be roughly approximated from available data and may be easier to estimate than fitness functions proposed in other models. Sports data may not be completely analogous to data from the natural world; hence, further quantitative analysis of lateralization in social animal groups may be a fruitful line of future research.

Given the limited data on population-level lateral bias in the natural world, we feel that analysis of athletics provides new insights into the evolutionary origins of handedness. Our model predictions match the observed distribution of handedness in baseball with just a single free parameter. When applied to 12 groups of elite athletes, the same model does a good job of estimating the fraction left-handed in each, suggesting that the proposed balance between cooperation and competition accurately predicts the ideal equilibrium distribution of handedness. Our model is general enough to be applied to any species of animal, and may also have use in understanding population-level lateralized adaptations other than handedness, both physical and behavioural.

6. CONCLUSIONS

The model we have presented is the first to take a dynamical systems approach to the problem of laterality. It allows for the prediction of conditions under which population-level lateral bias can be expected to emerge in the animal world and its evolution over time. We exploit the connection between natural selection and selection in professional sports by introducing a novel dataset on handedness among athletes, demonstrating a clear relationship between cooperative social behaviour and population-level lateral bias.

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