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The fighting hypothesis as an evolutionary explanation for the handedness polymorphism in humans: where are we?

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The ubiquitous and persistent handedness polymorphism in humans requires an evolutionary explanation. It has been suggested that left-handers have a frequency-dependent advantage during a fight, such that this advantage decreases when their frequency increases. Many independent studies are providing data from interactive sports (a specific class of fights), and are very supportive of the fighting hypothesis. The only intercultural study on traditional societies is also consistent with the fighting hypothesis, although it has not yet been replicated. The frequencies of left-handers in the few remaining violent societies are likely to be rapidly decreasing, due to Western colonization (long-range weapons, religion, and money market) dramatically affecting the frequency-dependent selection associated with handedness. Clearly, more data are urgently needed outside the Western influence.

Keywords: handedness; human; evolution

Introduction

There is significant heritability for hand preference in humans, suggesting that natural selection could contribute to the evolution of handedness (see Ref. 1 for a review). Right- and left-handed individuals have apparently coexisted since at least the Paleolithic period, and are present in all know human societies. If this trait was neutral, the frequency of right-handers (RHs) should change in each generation by drift alone, and the frequency of left-handers (LHs), at a given time, could take any value. In all known societies, LHs have always been a minority compared to RHs, suggesting that the neutral model does not adequately describe the evolution of handedness polymorphism. Some sort of selection must be present. Which one?

Conditions for a stable polymorphism

There are only a few possibilities to explain the maintenance of a polymorphism over a long time frame. Negative frequency dependence has been proposed as a possible mechanism acting on the polymorphism of handedness, according to the fighting hypothesis.[2,3] In short, the relative rarity of LHs compared to RHs results in LHs being unfamiliar to RHs. This unfamiliarity provides two types of advantages for LHs: they naturally perform actions that are unexpected and whose outcomes are more difficult to predict.[4–6] When the frequency of LHs increases, they become more familiar to RHs, and their advantage in fights decreases. Such negative frequency-dependent advantage for an inheritable trait is a sufficient condition to maintain a stable polymorphism. As the expected equilibrium value is 50%, well above the observed value, another type of selection must exist, such as an intrinsic cost associated with being a LH (see Ref. 1 for a review).

The fighting hypothesis does not exclude other explanations. Other types of frequency-dependent selection are still possible, particularly in modern societies, where fighting may be reduced compared to traditional societies (see below).

Testing the fighting hypothesis

Handedness assessment

For a given manual action, each individual shows a preference for the use of one hand, and it is not always the same hand for two different actions.[7] This suggests that right- and left-handedness are not

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general categories, but rather are defined as functions of specific tasks. When the tasks considered are highly skilled and complex, and the individuals tested are specialized in these tasks, there is a very strong correlation between the different tasks.[1] To study handedness variations in humans, it is important to choose tasks that are typical among human populations from different cultures. Thus, some tasks commonly used in studies in Western societies to measure handedness, such as writing or teeth brushing, are meaningless in other cultures. The tasks chosen to measure handedness should be logically related to the biological hypothesis tested. For example, if one wants to assess handedness in the context of the hypothesis of a frequency-dependent advantage of LHs in fights, tasks should be related (as much as possible) to fighting actions, such as hand preference for throwing or holding a knife. As a consequence, all studies on the fighting hypothesis should provide evidence (or counter evidence) based on functional handedness related to fighting. Thus, data where the writing hand is used to define handedness are irrelevant, as well as data using the Edinburgh inventory that creates an arbitrary index mixing handedness for using, for example, a toothbrush, a broom, a comb, and scissors. Studies using these irrelevant measurements are omitted below.

Sport data

Many studies have been published to assess the relevance of the fighting hypothesis using sport data. The first prediction is a higher LH frequency in interactive sports (where individuals are interacting to win, thus reflecting some fighting abilities), compared to noninteractive sports. The second prediction is that LH frequencies are limited by the 50% threshold, above which RHs have an advantage because they start to become uncommon. Overall, there is very strong support for these two predictions from various research teams and for many interactive sports.[2,4,8–11] Additionally, consistent with the fighting hypothesis, several experiments with videos have shown that it is more difficult to predict the outcome of an action performed by a LH than by a RH, and that this difference is attenuated, or even reversed, by specific training.[4–6,12]

Traditional societies

Only one cross-cultural study has been published in traditional societies;[2] clearly more data points are needed particularly for violent societies. There are, however, some difficulties in gathering such additional data. For example, violent societies are becoming scarce, at least for the type of violence generating a strong differential selection on survival between LHs and RHs. The generalization of firearms and weapons of high energy interferes with the link between homicide and frequencies of LHs. Data collected in the Eipo population are a good illustration of such recent change. A far lower percentage of LHs has recently been recorded, compared to what we observed in photographs taken during field studies in the 1970s.[3,13] It has been proposed that the discrepancy between measurements taken 40 years apart is incompatible with a large change in LH frequency, suggesting that our measurement is incorrect.[14] This is perhaps true. However, during these 40 years, colonization and Westernization occurred. For example, "Since the Eipo accepted Christianity as their primary religion around 1980 . . . , tribal wars came to an end, and thus homicide rate diminished dramatically."[13] Clearly, the traditional Eipo society has dramatically changed during that time; wars stopped and interpersonal violence decreased. Incidentally, the frequency of LHs in the Eipo is now not lower in older individuals (and is even higher, although not significantly: +3.1% for knife use for individuals over 41, compared with 15- to 40-year-old individuals); thus in contrast with what is observed in Western countries, this suggests that the selection for LHs has indeed recently decreased. As differential fecundity, mortality, and emigration were not measured, it is difficult to estimate the fitness costs of being a LH, potentially explaining the change in 40 years.[13] Such costs would be higher than any estimate from Western countries, but there are no theoretical reasons to expect that the fitness cost of being a LH does not vary across cultures. Handedness measures from another ethnic group, during a similar drastic cultural change associated with a large decrease in homicide rate, are required to better understand the Eipo data.

The Spearman correlation between LH frequency and homicide rate is 0.83, with $P = 0.008$, two-sided.[3] When considering sampling errors (binomial for LH frequencies; Gaussian for population size, with variance = mean/3, thus a conservative high value; Poisson for the annual number of homicides), and 100,000 resampling within the distribution for each point, the 95% confidence interval of the Spearman correlation is 0.39–0.96

(unpublished data; R code and graphs available upon request). If the Eipo is removed (thus only seven points are remaining), this Spearman correlation becomes 0.82 and is still significant (two-sided, $P = 0.034$). Incidentally, a one-sided test is also appropriate ($P = 0.017$), as there is a clear theoretical prediction of a positive correlation between LH frequency and violence.[15]

Alternative hypotheses

Several possible innate characteristics of LHs that induce a fighting superiority have been proposed; for example, higher aggressiveness. The only published evidence concerns 52 soccer players, whose handedness was assessed using an arbitrary index.[16] On a large cohort ($n = 1161$), no effect of hand preference on the probability of fighting in a lifetime was detected, suggesting that the innate propensity to fight does not differ between LHs and RHs.[17] Other authors proposed that LHs have more efficient motor skills, such as improved eye–hand coordination or better visual ability. Such innate superiority should operate specifically in interactive sports, in order to be consistent with the robust finding of overrepresentation of LHs in interactive sports. They are, however, noninteractive sports (e.g., darts, snooker) where precise visuomotor control is required, and where LHs are not overrepresented.[11,18] Sometimes this advantage is measured using a task unrelated to the fighting hypothesis, and thus could not be considered here (e.g., Ref. 19 refers to writing handedness).

Additionally, any absolute advantage of LHs in a given sport should lead to a large overrepresentation of left-handers, not necessarily bounded by the 50% threshold predicted by the frequency dependence of the fighting hypothesis. This is particularly true when competition is intense, such as the champion categories at national or international levels. However, this situation has not been reported so far, suggesting that any possible innate advantage is currently not supported.

Conclusion

The fighting hypothesis is well supported by sport data, thus suggesting that handedness is far from a neutral trait, and that fights have probably been pivotal to maintain the handedness polymorphism during recent human history. There is however one aspect that deserves further understanding: the link between fights and fitness advantages. It is possible that most fitness effects of the frequency-dependent advantage of LHs are not survival-mediated (through an advantage in lethal fights). Indeed such fights are probably relatively rare, even in violent cultures, compared to all other types of general fights (data are needed on this point). Ritualized fights, fake fights as part of playing behavior, interactive sports, and other behavior reflecting the ability to win a fight are frequently practiced by most men in most societies. Their outcomes certainly affect men's attractiveness to potential mates, either directly or indirectly through an impact on social status, which is known to strongly influence reproductive success in any culture.[1,20] A man's fighting ability is indeed a proxy for a man's capability to protect his mate and his offspring, and to produce sons with similar ability. This link is probably distorted when ethnic groups with different economic power are in contact, as socioeconomic factors become a stronger proxy for reproduction. It is possible that the fighting hypothesis explaining the persistence of LHs applies only to situations where fighting abilities are directly linked to success (as in sports) or to Darwinian fitness, as in most past societies, or in the few remaining groups not yet affected by Western colonization and a market economy.

Conflicts of interest

The authors declare no conflicts of interest.

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