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Review

Why Are Most Humans Right-Handed? The Modified Fighting Hypothesis

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Abstract: Humans show a population-level preference for using the right hand. The fighting hypothesis is an influential theory that suggests that left-handedness persists because its rarity provides a surprise advantage in fighting interactions, and that left-handedness is less frequent because it has a health cost. However, evidence for the health cost of left-handedness is unsubstantiated, leaving the greater frequency of right-handers unexplained. Research indicates that homicide may have been common in early hominins. We propose that the hand used to hold a weapon by early hominins could have influenced the outcome of a fight, due to the location of the heart and aorta. A left-handed unilateral grip exposes the more vulnerable left hemithorax towards an opponent, whereas a right-hand unilateral grip exposes the less vulnerable right hemithorax. Consequently, right-handed early ancestors, with a preference for using the right forelimb in combat, may have had a lower risk of a mortal wound, and a fighting advantage. This would explain their greater frequency. In accordance with the original fighting hypothesis, we also suggest that left-handed fighters have a surprise advantage when they are rare, explaining their persistence. We discuss evidence for the modified fighting hypothesis, its predictions, and ways to test the theory.

Keywords: tools; warfare; ancestor; hand preference; lateralized function

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1. Explaining Handedness

Lateralization of the brain and of behaviour is so widespread that it is likely to have fitness advantages [1–4]. These advantages include avoiding the unnecessary duplication of functions in the brain [5,6] while facilitating parallel processing and perceptual and motor learning [3,7–9]. However, the advantage that lateralization conveys to an individual does not explain population-level lateralization, which can be expected to have costs as well as benefits [3], nor does it explain why approximately 90% of humans are right-handed and only 10% are left-handed [3,8,10,11].

Several theories have been proposed to account for population-level handedness in humans. Theorists have proposed that there is a genetic link between the evolution of speech and gesture, which causes both to be left-brain lateralized [12–16]. Other theorists suggest that left-handedness is a pathological state caused by birth trauma [17], or due to imbalances in testosterone that result in an auto-immune disorder [18]. Another important theory of the origins of human handedness is the fighting hypothesis, which suggests that left-handedness persists because it provides a fighting advantage [10,19–21]. We discuss the fighting hypothesis in this article. The aim is not to give a comprehensive review of the evidence for the fighting hypothesis, as several such reviews already exist [21,22]. Instead, we aim to examine its key assumptions and propose a modification to the hypothesis. A further aim is to explore the fighting hypothesis as a framework with which to predict laterality phenotypes and to examine the origins of population-level handedness in humans.

There are a number of core features of human handedness that a theory of its origins at the population level should be able to explain. First, there is a stronger maternal influence on the inheritance of left-handedness [23,24] and there are sex differences in rates of left-handedness [25–27], with males (10.6–11.62%) showing slightly higher rates than females (8.6–9.53%) [28,29]. This suggests that a form of sex difference might be related to the emergence of population-level laterality in humans. Second, handedness developed early in the evolution of humans [30,31], may have been present in the Pleistocene period [32], and in Neanderthals [33], and shows early ontogenetic development, with evidence of handedness preferences in the human foetus [34,35]. This suggests that the evolutionary selection of handedness occurred early in human history and that it has a genetic origin rather than an environmental cause [36]. Current research indicates that handedness is highly polygenetic, with many genes contributing small amounts to handedness [36–38]. Finally, lateralization in left-handers is not simply the reverse of right-handers, because, on many measures of brain function and behaviour, left-handers are less strongly or consistently lateralized compared to right-handers [39–46]. The likely reasons for reduced functional brain lateralization are genetic factors rather than experiential [42], but the presence of reduced lateralization in left-handers could indicate that reduced lateralization conveys important advantages, which caused its selection and maintenance. It is potentially important that male left-handers are less lateralized than female left-handers [47], as it might indicate that left-handed males benefit more from any advantages of reduced lateralization.

A plausible mechanism by which population-level lateralization emerges is via social interactions with other members of a species [3,4,10,48–55]. As Vallortigara and Rogers note, behavioural lateralization is not beneficial in every context and can be expected to have costs [3]. For example, it does not seem to be advantageous to have an attentional bias to one side compared to two sides, as it can make an animal more predictable and vulnerable to predation. However, such laterality phenotypes can occur at the population level because they convey advantages for the individual with respect to their interaction with conspecifics. For example, in the rusty grain beetle (*Cryptolestes ferrugineus*), rice weevil (*Sitophilus oryzae*), and flour beetle (*Tribolium confusum*), males with a bias to approach females from the left have greater copulatory success [56,57] (see [58] for side preferences in Poeciliid fish in copulatory attempts). In addition, male blowflies (*Calliphora vomitoria*) show a preference for using their right leg for boxing which conveys a fighting advantage [59]. In Australian cuttlefish, both fighting and mating success is influenced by lateralized eye preferences, with less frequent right-eye preferring males having a fighting advantage, and more frequent left-eye preferring males having a mating advantage [60]. Population-level behavioural lateralization also occurs in many mammalian species, with mothers having a preference for keeping infants on their left side. This preference appears to convey advantages in communication and social bonding between the infant and mother [61–63].

There is now considerable evidence, from many different species, for the role of social interactions between individuals in producing population-level lateralization [1,11,50,51,62,64]. Evidence from this research suggests that population-level lateralization tends to emerge for quite specific behaviours, due to asymmetries in interaction for that behaviour, rather than more generalized behaviours [1]. Example behaviours include mating, schooling, turning, cradling, and aggressive interactions such as fighting.

As evidence from other species indicates that population-level lateralization occurs for specific interactions between conspecifics, it suggests that handedness in humans may also have developed from a specific behavioural interaction. In addition, however, as no other species shows population-level lateralization to the same degree as humans, including non-human primates [65–67], it is possible there is something unique about human interactions which caused this proportion to arise. Two attributes that no other species possesses to the same extent, and which could promote human levels of lateralization, are complex tool use (including the use of weapons) and the development of language.

2. The Fighting Hypothesis of Handedness

The fighting hypothesis of human handedness proposes that left-handedness persists due to a negative frequency-dependent fighting advantage in left-handed males [10]. It is suggested that the rarity of being left-handed gives them an advantage when fighting in a population of mostly right-handed males and increases a left-handed male's chances of surviving and reproducing [10,19].

The starting point of the fighting hypothesis was an aim to explain levels of left-handedness in human populations. As left-handedness is only exhibited by a minority of humans, it must have a fitness cost. This fitness cost was proposed to be a health cost, based on some evidence [10,20,21]. In addition, as left-handedness is maintained in a population it must also have an advantage, and a negative frequency-dependent fighting advantage was suggested. The left-handed health cost is a key pillar of the fighting hypothesis because without it the theory does not explain the greater prevalence of right-handers. It suggests that right-handers are more numerous, not because of some specific advantage intrinsic to being right-handed, but because there is a disadvantage to being left-handed. An alternative starting position might be to ask, why are most people right-handed and what adaptive advantages does it have?

The fighting hypothesis is compatible with a body of research indicating that it is highly adaptive for human males to be good at fighting and that the sexual selection of males has been strongly influenced by intra-sexual competition with other males [68–71]. Sexually dimorphic characteristics of humans, with males showing greater upper body strength and proportionately longer arms than females, are consistent with this view [69–71], as is the finding that arm length in males is positively associated with fighting success in mixed martial arts fighters [72].

The strongest direct evidence in support of the fighting hypothesis is the finding that left-handed males are over-represented in fighting sports [10,73–75] and one-on-one interactive sports such as fencing and table tennis [76,77], but not non-contact sports, such as darts, golf, and bowling [78]. Crucially, some studies have also found left-handers to be more successful fighters [71,75] (but see [73,79]).

In addition to being over-represented in interactive sports, left-handers have a sporting advantage [80], which is stronger for males than females [10,81,82]. Tennis players, of different levels of expertise, are better able to predict the direction of a tennis stroke from right-handed players than left-handed players [83]. Similarly, the actions of left-handed volleyball players are predicted worse than those of right-handed players [82], and left-handed fencers are less lateralized and show greater improvements from training than right-handed fencers [77] (see also [84]). It appears that reduced visual experience with left-handers in one-on-one interactive sports [76] gives left-handers an advantage and an equivalent advantage could be expected in fights between left-handed and right-handed men [3,10,75].

The fighting hypothesis appears able to explain several core features of population-level handedness in humans. Billiard et al. suggest that left-handedness is inherited via the mother, leading to a stable population of left-handed women, despite the fact that women may be less involved in fighting than men [48]. If fighting proficiency resides in males, it may explain the slight increase in male left-handers over female left-handers [28]. In addition, if being less lateralized gives left-handed fighters an advantage it might explain why left-handed males are less lateralized than left-handed females [47], and why left-handed males show a bigger sporting advantage than left-handed females [10,81].

Other evidence for the fighting hypothesis, such as the suggestion that there will be an increase in homicide with an increase in the frequency of left-handers in pre-industrial societies, or that left-handers are more aggressive, has not received clear support [22,85,86]. Moreover, as we discuss below, the suggested link between left-handedness and health problems is highly contentious [22,87]. Some evidence from other species is also not in favour of the fighting hypothesis, with Backwell et al. finding that left-clawed male fiddler crabs (*genus Uca*) do not show a frequency-dependent fighting advantage [88].

2.1. Does Left-Handedness Have Health Costs?

2.1.1. Neurodevelopmental, Cognitive, and Psychiatric Disorders

A central assertion of the fighting hypothesis is that left-handedness has health costs, as this is used to explain why left-handers are always in a minority in human populations. However, there are reasons to question this assertion. The best estimate of rates of left-handedness in adult populations is approximately 10% [28,29]. If the health cost applies to only a small proportion of left-handers, with large samples it should be possible to detect health problems in significant numbers of left-handed people, but several large studies have not detected this [86,89]. These findings are not compatible with mathematical models of the fighting hypothesis, which suggested that because left-handedness never approaches 50% in any human population, the fitness cost of left-handedness 'is relatively high' ([48] p. 92). In addition, being left-lateralized is a natural variant that is common throughout the animal kingdom [1,6]. There appears to be no association in other species between health costs and being left-lateralized, making it unclear why it should be specific to humans. It also remains unspecified why, when human ancestors moved from individual handed preferences without a health cost, to population-level handedness, the left-hand preference developed an associated health cost.

Various types of health issues have been proposed to co-occur with left-handedness, including allergies, birth trauma, and stresses to the foetus in utero [10]. The suggestion that birth trauma causes left-handedness [17] is not supported by evidence [90]. A large cohort study by McManus using a dataset of 11 thousand births and handedness records at ages 7 and 11 suggested no relationship with birth trauma [91]. Similarly, Bailey and McKeever [92], after examining pregnancy and birth risk factors in over 2 thousand births, failed to find a relationship between birth stress and left-handedness (see also [93,94]). A review of the research evidence by Bishop suggested that if birth trauma did cause left-handedness, it was for a small minority of left-handers, and it could not explain left-handedness in the majority of left-handed individuals [95].

Differences in foetal testosterone levels have also been proposed as an underlying pathological cause of left-handedness [18], but results from several studies have not supported the theory. Richards et al. found that prenatal sex hormone exposure was not associated with the direction of hand preference in either males or females [96]. Other research has also failed to find a relationship between prenatal testosterone levels and the direction of lateralization in humans [97,98]. In a large study on human adults, there were also no differences in levels of testosterone and estradiol between left-, mixed-, and right-handers [99]. In addition, digit ratios, which have been viewed as a marker for foetal androgen levels, have not shown an association between prenatal androgens and handedness [96].

A body of research has, however, obtained associations between atypical handedness and different neurodevelopmental and psychiatric disorders, including schizophrenia, autism, and dyslexia [100,101]. Associations between atypical handedness and reductions in cognitive and motor ability have also been found [94,102–105]. These associations have often been weak and inconsistent, and difficulties exist in the literature with the different measures of handedness that have been used. The use term of the term 'atypical handedness' also varies but is often used as a proxy for a combination of both left-handed and mixed-handed individuals. Papadatou-Pastou's meta-analysis found no cognitive difference between left-handed and right-handed individuals when they were classified by hand preference and direction [106]. This is in line with other studies which found no differences in cognitive or motor ability between left- and right-handers but did find deficits in mixed-handers (e.g., [104,105]). Increased cognitive deficits (and health problems) in mixed-handers or ambidextrous individuals, including moderate right-handers [26,86,107] could be due to atypical functional organisation of the brain being related to poorer cognitive performance [103].

The reason for the association between atypical handedness and neurodevelopmental disorders is unclear but a plausible explanation is that a proportion of individuals are left-handed for pathological reasons. Satz proposed that if brain injury occurs randomly in either hemisphere and affects brain organization and lateralization, because right-handers are more numerous than left-handers, it will cause an increase in the number of people who are left-handed for pathological reasons [108]. By contrast, as left-handers are rarer, a brain injury that causes a switch in handedness will result in fewer pathological right-handers. This account remains valid, and it is accepted by many researchers that a small proportion of individuals who are left-handed (or mixed-handed) are so for pathological reasons. However, this does not apply to most individuals who are left-handed, because many studies show no differences between left- and right-handed individuals [106]. As neatly summarised by Porac (p. 149), "it is a *fact* that specific forms of atypical handedness, such as ambiguous handedness, are linked to various pathological conditions" and "it is *fiction* to argue that all left-handedness has a pathological origin" [87].

2.1.2. Is Left-Handedness Associated with Other General Health Problems?

Several researchers have concluded that the evidence that left-handedness is associated with health problems is unconvincing [22,87,109]. A number of findings that suggested a left-handed health cost, and were used as evidence for the fighting hypothesis, have also not been substantiated. The claim that left-handers die younger received a lot of publicity [110] but handedness does not appear to affect longevity [111,112]. Research has shown that being left-handed is not linked to an increased risk of earlier death [113–115]. As described by McManus, the UK biobank data, consisting of 500,000 people, shows that left- and right-handers have the same longevity [109].

Studies which have reported specific health costs in left-handers have sometimes used small samples or shown weak effects and mixed results. A reported increased risk of breast cancer in left-handed women [116], (1637 right-handed, 93 left-handed) was based on a very small number of seven left-handed women who developed cancer, making any conclusions unconvincing. Similarly, a reported increase in health conditions in left-handers (e.g., epilepsy, heart disease, and thyroid disorders) by Bryden et al. was based on very small numbers of individuals with these conditions (e.g., one or two people), questioning the reliability of any conclusions [107]. Moreover, left- and right-handers did not differ in terms of the total number of reported health problems, with only mixed-handers showing an increase, and only when defined by the throwing hand and not the writing hand. Porac and Searleman's study with a larger sample (N = 1277) found no differences in physical health, in terms of illness and injury, between left-hand and right-hand preferring participants [117]. Only a subset of left-handers, those who had unsuccessfully attempted to switch hand preference, showed lower levels of well-being, and there were no reductions in health or well-being in left-handed participants compared to right-handed participants.

Other recent studies, with large samples, have also failed to find a relationship between left-handedness and health costs. Zickert et al.'s study, with over 10,000 individuals, found that left-handers showed no evidence of more health problems [86]. They also showed similar levels of reproductive success to right-handers, were not more aggressive, and had no increase in allergies. This latter finding replicates other studies with large samples, by Peters et al. [26] (N > 250,000) and Wysocki and McManus [118] (N > 1 million), which both found no increase in allergies in left-handers. Peters et al. also did not obtain clear evidence of more health problems in left-handers, and Wysocki and McManus found moderately strong evidence that left-handedness was associated with lower rates of ulcers and arthritis.

The majority of Zickert et al.'s findings were replicated by a further large internet study (N > 20,000) which examined measures of health and handedness, including a measure of hand skill preferences [89]. Again, there was no relationship between handedness and health problems (combined score), allergies, and days ill. They noted that " … the more left-skilled individuals have fewer health problems than the more right-skilled individuals, which is completely contradictory to our hypothesis" ([89] p. 75). For dyslexia and prematurity, the findings were again opposite to predictions, with self-reported prematurity and dyslexia more common for right-skilled compared to left-skilled participants. Like Zickert et al., they found no differences in reproductive success between left- and right-handers, with no differences in the numbers of offspring. There was, however, evidence of slightly increased aggression in left-skilled participants, but not for self-assessed aggression or the number of childhood fights and verbal fights. In addition, a meta-analysis of handedness and depression, which analysed data from 87 studies and over 35,000 participants, found no link between handedness and levels of depression [119].

It could be argued that advances in modern health care in Western societies have eliminated health costs associated with left-handedness, which is why recent studies fail to find effects [89]. However, health costs associated with left-handedness have also not been found in some nonindustrial societies [120], suggesting that there are no differences in health between left- and right-handers.

Overall, the findings from studies with large samples, which have the most power to detect a relationship, do not support the view that left-handedness is associated with health costs, such as a reduction in longevity, reduced fertility, or more allergies and autoimmune disorders [22,86,89]. Increases in cognitive deficits and health problems have been associated with mixed-handers or ambidextrous individuals, including moderate right-handers [86,103]. This could be due to a proportion of these individuals having atypical handedness for pathological reasons. Despite this, several large studies have shown that consistent left-handers are as healthy as right-handers. There is, therefore, sufficient evidence to question the health cost component of the fighting hypothesis and we suggest that it may be an unnecessary addition to the theory.

3. The Modified Fighting Hypothesis

Modifying the fighting hypothesis, by removing the health cost and retaining the negative frequency-dependent selection of left-handedness, has some important consequences. The modified fighting hypothesis proposes that, as fighting ability is adaptive, it operates for right-handed males and left-handed males. If fighting ability determined the proportion of left-handers (without intervening factors, such as health costs) then it is logically consistent for fighting ability to have also determined the proportion of right-handers. Frequency-dependent selection can operate on majority and minority forms of lateralization and become an evolutionarily stable strategy [50]. In the modified fighting hypothesis, we propose that, in general, right-handed early hominins had a fighting advantage when sharp weapons were used for fighting, which is why they became more numerous. When left-handers became rarer, they gained a surprise advantage and the proportions of left- and right-handers in a population stabilized.

3.1. Why Should Right-Handers Have a Fighting Advantage?

On theoretical grounds, if a fighting explanation of handedness is adopted, it is more consistent to argue that the adaptive value of fighting ability applied to both right- and left-handed males, and the greater frequency of right-handers in a population suggests they had a fighting advantage. There are also important physiological reasons why there might be a right-handed fighting advantage. The heart and the aorta are two essential and vulnerable organs that are situated mainly within the left thorax in all types of mammals. In humans, on average, 73% of the heart is situated in the left thorax ([121] see Figure 1), making the left thorax particularly vulnerable to attack from sharp weapons. The hypothesis presented here is that in early human history when weapons were used during fighting [122], the position of the heart and aorta resulted in a survival advantage for right-handed males [121].

The suggestion that the position of the heart, in combination with hand preference, influences the odds of survival in combat, was originally proposed in the 19th century. According to Harris, the medical scientist Pye-Smith first suggested that holding a shield in the left hand and a weapon in the right hand was more advantageous than the alternative arrangement for avoiding mortal wounds [123]. Similarly, the fencing master Roland (1824), cited in Harris ([124] pp. 37–38), noted that "In actual combat the left-handed person labours under a serious disadvantage", and Thomas Carlyle, the Scottish philosopher proposed that right-hand dominance "probably arose in fighting; most important to protect your heart and its adjacencies . . . " ([125] p. 278).

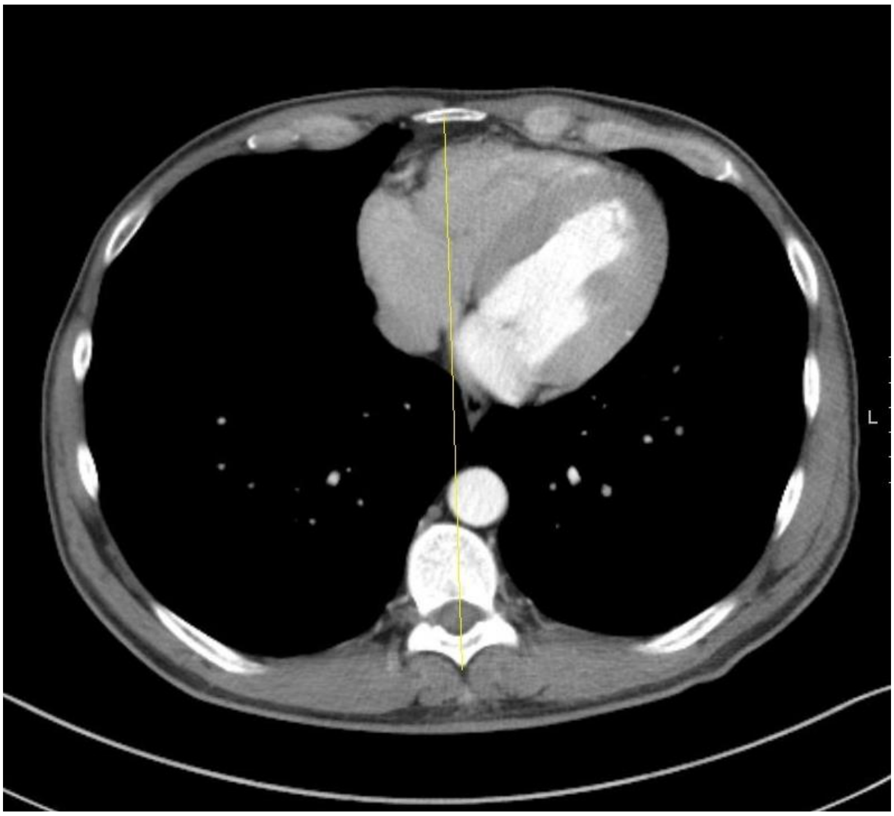

Figure 1. CT scan showing a typical configuration of the heart, with roughly three-quarters of the heart in the left hemithorax. The heart is shown in a cross-section, inferior view.

This explanation of the origins of handedness became known as the sword and shield hypothesis and has been dismissed on several occasions [125,126], primarily because human handedness developed long before the development of shields. However, the central idea of the theory, that right-handedness developed because it reduced fatal wounds when fighting with weapons, due to the position of the heart, does not depend on the presence or use of a shield. As described in detail by Larsson, when fighting with sharp weapons, the hand used to hold the weapon influences the area of the thorax that is most exposed to the opponent's weapon [121]. A left-hand unilateral grip will rotate the left hemithorax towards an opponent. Conversely, a right-hand unilateral grip exposes the right hemithorax, and therefore the heart will be more protected compared to a left-hand grip. In addition, an unoccupied left arm, especially when bent, may be used as a natural shield for the more vulnerable left thorax (see Figures 2 and 3). Consequently, right-handed early ancestors, with a preference for using the right forelimb in combat, may have reduced their risk of a mortal wound [121].

As can be predicted from right-handers being in the majority, several studies have found that stab wounds to a person's left side are more frequent [127,128], with left-sided stab wounds two and a half times more frequent than right-sided ones [129]. When Larsson asked 19 physicians to estimate the clinical outcome of weapons penetrating the thorax and abdomen at random points on the right or left sides, he found there was a significant increase in predicted mortality for left-side wounds [121]. This suggests a greater vulnerability of the left side of the body and of left-handed combatants, and the adaptive value of being a right-handed fighter. Note that, in agreement with the original fighting hypothesis, we suggest that, as left-handers became rarer in a population, they gained a surprise advantage in fighting, causing them to persist in human populations.

Figure 2. A right-hand grip exposes the right hemithorax whereas a left-hand grip exposes the left hemithorax. This will occur for long and short weapons. When holding the weapon in the right hand, the left arm, by partially covering the left thorax, may also provide some protection for the heart.

Figure 3. Right-handed fencers illustrating that the right hemithorax is more exposed when lunging with a weapon (Photo: Johan Harmenberg).

3.2. Could Weapon Use Have Caused Population-Level Handedness?

The modified fighting hypothesis proposes that the use of sharp weapons in early humans caused the emergence of population-level handedness. Several lines of evidence suggest that tool use may have had a special significance in the development of handedness. Chimpanzees (*Pan troglodytes*) are more lateralized when using tools than they are for any other no-tool-use tasks, such as manipulating objects [130]. They also use different objects as weapons and can throw them, like missiles, at conspecifics [131]. In human cultures without a written language, there appears to be little evidence of strong right-handedness for an extensive range of tasks, apart from the case of tool use, whereas precision-gripping tool use was exclusively right-handed [132]. Forrester et al. even propose that right-handedness developed through tool use and was inherited from an ancestor common to humans and the great apes [133].

While it is plausible that tool use has been important in the development of handedness, a common ancestor may not explain why humans are right-handed rather than left-handed unless being left-handed had some form of cost. Moreover, a comprehensive review of hand preferences in non-human primates found that levels of manual lateralization at the species level were largely uniform [134]. Lateralization levels did not correlate with phylogeny or with other biological predictors, with the findings suggesting that human hand preferences originated from a selection pressure that was unique to humans. Therefore, if tool use was critical for the development of handedness [133], evidence from non-human primates [134] indicates that this may have been a unique form of tool use that exerted a powerful selection pressure. The extensive use of tools such as sharp weapons could have been one such unique selection pressure.

Although it is unclear when tool use and manufacture began among hominins, cut marks on animal bones prior to 3.39 million years ago are the earliest indication of stone tool use [135]. Rolian and Carvalho suggest that the last common ancestor (LCA) of chimpanzees and humans is likely to have made and used tools [136]. The earliest direct fossil evidence of weapon manufacture is the discovery in South Africa of stone spear-points dating to ~500 thousand years ago [137], but weapons could certainly have existed before this.

Chimpanzees (*Pan troglodytes*) are capable of using tools as weapons against conspecifics [131,138], and bonobos (*Pan Paniscus*) are able to make stick spears and use them as weapons [139]. This strongly indicates that early hominins, with a cortex of similar size, had the cognitive capacity to produce and use sharp weapons. Since primates are disposed to mimic the behaviour of others [114], the use of weapons in early hominins may have spread quickly within and among groups. Thus, it is possible that weapons may have been used by hominins in duels for millions of years. It has also been suggested that the reduction in canine tooth size in hominins [140] was due to their reduced use as a weapon [141–143], indicating that tools may have replaced big teeth as a weapon for protection, hunting, and in fights against conspecifics.

It is believed that during the Pleistocene, diverse primate species occupied nearby and overlying areas in Africa [144], possibly resulting in abundant conflict situations. An increase in hominin carnivory appeared around 2.5 million years ago with Homo habilis and peaked with Homo erectus as the apex predator [145]. Alexander [146] suggested that humans came to dominate their environment early in their evolution, and according to Flinn et al. [147] their competition and interactions would largely have been with other hominids (see [148] for a discussion of cannibalism). There is, therefore, considerable evidence of intraspecies aggression among hominins in their early [147] and more recent history [68,149], making the proficient use of weapons extremely important. This would be consistent with other species, where fighting skill and weapon use are important factors that can determine the outcome of fights between conspecifics [150,151].

4. The Cause of Population-Level Lateralization May Facilitate the Co-Ordination of Other Laterality Phenotypes in Individuals

The strongest evidence for the fighting hypothesis is the greater frequency and success of left-handers in interactive sports [73], particularly fighting sports [71,75]. Whether the left-hander's advantage is due to right-handers having less experience when opposing them, or because left-handers have the greater innate skill, is an ongoing debate [76]. While it has been suggested that it is due primarily, though not exclusively, to left-hander's scarcity [152], it is possible that both factors cause the overrepresentation of left-handers, and that there was a selection of laterality phenotypes that optimized fighting skill in left-handers.

Brain imaging studies provide a possible explanation of the motor advantage of left-handers. fMRI research has shown that movements with the dominant hand increase deactivation of the ipsilateral primary motor cortex, with the deactivation being a marker for manual preference [153,154]. Differences in patterns of ipsilateral deactivation exist between left- and right-handers. When moving their dominant hand right-handers show significantly greater deactivation of the ipsilateral primary motor cortex, compared to when moving their non-dominant hand. By contrast, left-handers show similar levels of deactivation of the ipsilateral primary motor cortex when moving either their dominant or non-dominant hand [154]. Tzourio-Mazoyer et al. also found that right-handers had significantly larger differences in manual skill between their right and left hands, compared to left-handers, due to the right-handers being relatively worse with their non-dominant left hand. They conclude that these and other findings suggest that left-handers "have two dominant motor cortices, which leads to lower asymmetry than right-handers, leading to a decreased manual lateralization" ([154] p. 11). This could explain the left-handers' superior performance with their non-dominant hand, compared to right-handers, suggesting that they might possess an innate superiority for some types of motor tasks.

Vallortigara and Rogers suggest that population-level lateralization of a particular function may cause brain changes to align the lateralization of other behaviours related to that function [3]. Similarly, we propose that if population-level lateralization of handedness was primarily determined by fighting proficiency, then other laterality phenotypes should also have been selected to be coordinated for proficient fighting. It is probable that proficient fighting requires several lateralised functions to be coordinated in an individual, the most obvious being attention and motor control of the hand, arm, and foot. For example, preferences for the throwing arm and kicking foot are closely related in both right- and left-handers [155]. Of those left-handers with a left-arm preference for throwing, 82% also prefer to use their left foot for kicking, and 78% of those who prefer to use their right arm for throwing also prefer to use their right foot for kicking. As Peters notes, for effective ballistic movements, it makes functional sense for the throwing arm and kicking foot to strongly correlate [156].

A further consideration is that right-handed and left-handed fighters may have developed different fighting strategies because they had different costs when fighting with their dominant hand, with greater exposure of the more vulnerable left thorax in left-handed fighters. Importantly, a difference in fighting strategy may be reflected in the particular selection of coordinated laterality phenotypes for fighting, that are present in left- and right-handed individuals.

If the selection pressure for right-handedness was to enable them to fight effectively against other right-handers who are in the majority, then laterality phenotypes for an attentional bias to the left [157], particularly in near visual space [158], where an opponent's weapon is likely to be, coordinated control of the right forearm [41], and coordinated footedness [44,155], may all have been important. Further adaptations could involve the left hand and arm. For example, the left hand of right-handers is able to react more quickly than the right hand [159,160], and right-handers are also surprisingly adept at catching a ball with their left hand, which contrasts with their limited ability at using their left hand for throwing [125]. Having a fast and accurate left hand that responds to approaching objects would be useful in deflecting possible attacks from other right-handed fighters. Overall, right-handers have several lateralized functions that appear to be beneficial for fighting other right-handed individuals.

If the selection pressure for left-handedness was to produce a more versatile fighter, with a fighting strategy that relied on their scarcity and versatility to implement a surprise advantage, then the selection of coordinated laterality phenotypes may have differed. In this case, reduced lateralization, particularly of the motor control of the hand, arm, and foot, and attention, may have given left-handed men greater flexibility and proficiency when fighting predominantly right-handed males. A surprisingly high proportion of left-handers (28–35%) prefer to use their right arm to throw and are more skilled when doing so [41,155,161]. By contrast, it is very rare (e.g., 1.6%) for right-handers to prefer to use their left arm to throw [41]. If the throwing arm is likely to be the stabbing or thrusting arm, then a large proportion of left-handed men will be able to stab with their right forearm, like a right-hander, and protect the more vulnerable left thorax. Therefore, left-handed early hominins with a preference for using their right forearm for throwing/thrusting when fighting with weapons may have had a fitness advantage. Reduced lateralization in male left-handers compared to female left-handers [47] is consistent with the view that being less lateralized may convey a fighting advantage, which developed more strongly in left-handed men.

Other laterality phenotypes displayed by left-handers also suggest more versatile fighting ability. Left-handers who are right-eye dominant appear to have a motor advantage in baseball [162], and left-handers have been found to have better intermanual coordination [163] and better manual dexterity when required to coordinate both hands [164]. Reduced hemispheric specialization in left-handers may enhance the performance of tasks requiring bihemispheric control and intermanual coordination [45], making them less predictable and facilitating the implementation of a surprise fighting advantage.

5. Novel Predictions

Several theories have attempted to explain the relationship in the brain between different lateralized functions, such as the complementary specialization theory and the statistical independence theory [165–170]. The fighting hypothesis, from an evolutionary perspective, leads to the proposal that lateralized functions may be more strongly correlated if the same evolutionary pressure is a causative factor in the lateralization of those functions. If the selection for fighting proficiency operated on other lateralized functions, in addition to handedness, this leads to a number of predictions. First, stronger correlations between lateralized functions related to fighting proficiency can be expected, such as handedness, footedness, and attention, but not between functions unrelated to fighting, such as language and handedness. These stronger correlations would be expected to occur in both left- and right-handers. Second, if different fighting strategies developed in left- and right-handers, then lateralized functions related to fighting proficiency will show greater differences between left- and right-handers, whereas those unrelated to fighting, such as language, will show smaller differences. Therefore, when comparisons are made between left- and right-handers they will show greater similarities in language lateralization and bigger differences in the lateralization of motor control (e.g., handedness, footedness) and attention.

Existing evidence could be interpreted to be in line with these predictions. Research has shown that handedness does not predict language lateralization and that to a large extent left- and right-handers are similarly lateralized for language [43]. Correlations between handedness and language lateralization are low [171] and most left-handers (73%) and right-handers (95%) are left-lateralized for language [172] (see also [173]). Those differences that do exist appear to be due to a small number of left-handed people who are right-hemisphere lateralized for language [174], and apart from this small subset of people, there appears to be little relationship between the lateralization of language and handedness [46].

In contrast to similarities in language lateralization, left- and right-handers have some prominent dissimilarities in motor control [155,156,175]. In the case of attention, there are also important differences between left- and right-handers. Many studies have shown that attention is drawn to the spatial position around the hand [176] and tools [177] but attentional biases to peri-hand space are not equivalent in left- and right-handers [178,179]. In Shiori et al.'s study, left-handers, as a group, did not show a significant effect of hand proximity on attention, with the effect of hand position on attentional allocation attenuated in left-handers (see also [180]). It can be speculated that if left-handers are more versatile fighters, it may be advantageous for attention to be less attracted to one hand and to have attention dispersed over both hands (see [181] for related evidence).

The pattern of relationships between lateralized functions may be mirrored in the genetic determinants of lateralization. We predict that, in both right- and left-handed individuals, the genes that contribute to the lateralization of handedness, footedness, and attention will overlap more than those for language and motor control. In addition, it is predicted that when left- and right-handers are compared, they will show greater differences in the genes for the lateralization of attention, handedness, and footedness, but smaller differences in the genes for language lateralization. We are not aware of a genetic study that has measured the lateralization of handedness, footedness, attention, and language in the same individuals, but research on genetic influences is progressing rapidly [36]. The genetic relationship of these different lateralized functions is likely to be measured in the near future, enabling the testing of the predictions derived from the modified fighting hypothesis.

Differences between the Original Fighting Hypothesis and Modified Fighting Hypotheses: Contrasting Predictions

The modified fighting hypothesis leads to different predictions from Raymond et al.'s [10] original fighting hypothesis (see Table 1). Faurie and Raymond [21] suggest that if fighting is no longer relevant in society, with the advantage of left-handedness removed, then left-handedness could reduce in incidence over future evolutionary cycles due to the associated health costs. By contrast, the modified fighting hypothesis proposes that, as there are no health costs associated with left-handedness, and fighting ability in right- and left-handers is no longer relevant, the population-level disadvantage of being a left-handed fighter is removed. Therefore, either there should be an increase in left-handedness across generations, or it should remain stable (in the absence of evolutionary influences), but there should not be a reduction.

Table 1. A comparison of the original fighting hypothesis (Raymond et al. [10]) and the modified fighting hypothesis.

	Original Fighting Hypothesis (Raymond et al. [10])	**Modified Fighting Hypothesis**
Primary explicandum	Why are some people left-handed?	Why are most people right-handed?
Assumption	Right-handedness is the default; left-handedness needs an explanation.	Right-handedness and left-handedness both need explanations.
Hypothesis	Left-handers persist because they have a negative frequency-dependent fighting advantage. They are in the minority because they have a health cost. Right-handers are in the majority because they do not have a health cost.	Early male hominins fought with sharp weapons. Right-handers are in the majority because they had a fighting advantage due to the position of the heart when fighting with sharp weapons. Left-handers persist because they have a negative frequency-dependent fighting advantage.
Prediction: Left-handers over time	Left-handedness has a health cost. Frequency of left-handers will decline over time due to this health cost (as the fighting advantage no longer applies).	Left-handedness has no health cost. Frequency of left-handedness will remain stable or increase over time (as fighting with sharp weapons no longer applies).
Prediction: Relationships between the lateralization of different functions	Specific predictions not originally made.	The lateralization of different functions, that are related to fighting (e.g., handedness, footedness, and attention) will correlate more strongly with each other than with functions unrelated to fighting (e.g., language).
Predictions: Genetic factors	All lateralization is polygenetic, but theory makes no specific predictions about genetic clustering for different functions.	Greater genetic overlap for fighting-related functions than for other functions. Greater genetic differences between left- and right-handers for fighting-related functions. Greater genetic similarities for functions unrelated to fighting (e.g., language).
Prediction: Aggression	Left-handed males are more aggressive than right-handed males.	Left-handed males and right-handed males do not show different levels of aggression.
Prediction: Behaviours related to fighting (e.g., positioning and turning biases)	Predictions not originally specified. Would predict stronger behavioural biases in males than females. Could predict stronger biases in left-handed males than right-handed males.	Predicts stronger biases in males than females. Predicts that the biases will be equally strong in male right-handers and male left-handers.
Prediction: Fighting advantage	Left-handers have a fighting advantage in hand-to-hand combat and when using weapons	Right-handers have a fighting advantage when using sharp weapons. Left-handers could have an advantage in hand-to-hand combat.

Rates of handedness appear to have remained relatively stable over the last 5000 years [182]. Over recent centuries, there is some evidence of fluctuating levels of left-handedness. McManus et al. analysed the data from several large samples, taking into account possible response bias, and concluded that the frequency of left-handedness fell in the 19th century and increased in the 20th century [183]. An examination of the research literature also found that rates of left-handedness have risen in more recent publications [29], a finding which aligns with reports of an increase in left-handedness in young people [28]. Other research has also reported an increasing incidence of left-handedness in the 20th century [161], which could be due to a reduction in forcing people to be right-handed and a reduction in social pressures against left-handedness [28]. However, as Papadatou-Pastou et al. [29] note, there also appears to have been an increase in left-arm waving [184], which is not subject to cultural or social pressures. It is also possible that rates of left-handedness appear to have increased because left-handers are more likely to fill in handedness questionnaires [183], because of their greater interest in the topic. It is therefore unclear whether there is a genuine increase in left-handedness, or a change in social pressure causing increased reporting, but rates of left-handedness do not seem to be declining. If rates remain stable or are increasing, it is not compatible with the view that there is a health cost associated with left-handedness.

The modified fighting hypothesis also would not predict greater aggression in left-handed males, as suggested in the original fighting hypothesis [10]. Left-handers may have a greater chance of winning a fight when they are rare, but their scarcity may fluctuate in a population, making fighting a dangerous option, and it does not necessarily follow that they would have higher levels of aggression. If they have a higher chance of mortal injury, it may be a maladaptive strategy to be more aggressive and evidence supports the view that left- and right-handers do not show differences in aggression [86].

The original fighting hypothesis predicts a left-handed fighting advantage with or without weapons [48] whereas the modified fighting hypothesis suggests a right-handed fighting advantage when sharp weapons are used, due to the different vulnerabilities of the heart. In other types of fights, such as hand-to-hand combat (including fighting sports), where the vulnerability of the heart is not an issue, it is possible that the greater versatility and rarity of left-handed fighters gives them an advantage compared to right-handed fighters.

The original fighting hypothesis [10] and the modified fighting hypothesis suggest that in early hominins fights occurred between male conspecifics rather than females. Both variants of the hypothesis therefore apply to males rather than females. Indirect evidence that will be consistent with both fighting hypotheses may come from sex differences in threat and aggression detection, and positioning and turning behaviour of male–female dyads [53,185]. Expression of these behaviours could be expected to differ between the sexes, with males showing them more readily [185,186]. Importantly, however, the original fighting hypothesis suggests that left-handers have a fighting advantage over right-handers. Conversely, under the modified fighting hypothesis, both right-handed and left-handed males are proficient fighters. The original fighting hypothesis might therefore predict that threat detection and positioning behaviours will be stronger in left-handed than right-handed males, whereas the modified fighting hypothesis would predict that right-handed and left-handed males will exhibit these behaviours equally strongly. In Rodway and Schepman's study of male–female dyads, left-handed and right-handed males showed positioning behaviours to a similar extent, though in opposite directions, with the findings more compatible with the modified fighting hypothesis [185].

6. Conclusions

The defining difference between right-handed and left-handed individuals is the lateralization of motor control. Other differences, such as language lateralization, appear to be less marked. If population handedness emerged due to a specific interaction between conspecifics [1,3], a reasonable suggestion would be that the interaction involved an important motor behaviour. Fighting between males who held sharp weapons is a candidate behaviour. The modified fighting hypothesis proposes that handedness developed, and other laterality processes were shaped, because of different vulnerabilities in left-handed and right-handed human males who fought with sharp weapons.

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