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Original Article

Fitness costs and benefits associated with hand preference in humans: A large internet study in a Dutch sample

Nele Zickert^{a,*}, Reint H. Geuze^b, Fleur E. van der Feen^b, Ton G.G. Groothuis^a

^a University of Groningen, Faculty of Mathematics and Natural Sciences, GELIFES – Groningen Institute for Evolutionary Life Sciences, Groningen, The Netherlands

^b University of Groningen, Faculty of Behavioural and Social Sciences, Department Clinical & Developmental Neuropsychology, Groningen, The Netherlands

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1. Introduction

Human hand preference, the preferential use of one hand over the other to perform gross and fine movements, is a phenomenon reflecting lateralization of motor functions. The lateralization of motoric functions to one side of the body can be measured behaviourally by observations or questionnaires and has its origins at the level of lateralized neuronal activation in the brain (Corey, Hurley, & Foundas, 2001; Hervé, Zago, Petit, Mazoyer, & Tzourio-Mazoyer, 2013; McManus & Bryden, 1992). Such lateralization is widespread in the animal kingdom, but unlike most other animal species humans show a strong directional bias at the population level. A ratio of left- to right-handers around 1 to 9 is a consistent finding in different communities all over the world, indicating dominance for this function of the left hemisphere. Although there is some variation among societies, left-handers are always clearly in the minority (Coren & Porac, 1977; McManus & Bryden, 1992; Perelle & Ehrman, 1994). Due to their relative rarity, left-handers are often viewed as being special or divergent in ways that exceed their hand preference alone (Grimshaw & Wilson, 2013; Kushner, 2013; Llaurens, Raymond, & Faurie, 2009). One of the important questions in laterality research is not only why evolution seems to favor right-handedness over left handedness but also why left-handers, if being selected against, still exist in human populations. In the present study we explore

differences in fitness costs between groups with right and left hand preference.

Hand preference in humans can be traced back until the early Paleolithic (Steele, 2000; Uomini, 2009) and is at least partly a heritable trait and thus subject to Darwinian selection. Alongside parental, societal, and environmental influences, 24% of the variance in hand preference is estimated to be caused by additive genetic effects (Annett, 2004; Llaurens et al., 2009; McManus, Davison, & Armour, 2013; Medland et al., 2009; Ooki, 2014). The question addressed in this paper has been fuelled by research showing that left-handedness might be associated with fitness disadvantages, but that it stays in the population by frequency dependent benefits (Raymond, Pontier, Dufour, & Møller, 1996). As for the fitness costs, it has been suggested that left-handers have a somewhat lower immune function and are more susceptible to allergies and accidents. Furthermore, it has been shown that some mental and developmental disorders (e.g. schizophrenia, dyslexia) are more prevalent in left-handers (Coren & Halpern, 1991; Dragovic & Hammond, 2005; Graham & Cleveland, 1995; Llaurens et al., 2009; Morfit & Weekes, 2001; Tønnessen, Løkken, Høien, & Lundberg, 1993; Tyler, Diamond, & Lewis, 1995), although these data have been challenged (McManus & Wysocki, 2005). Accordingly, it can be expected that over the course of time, natural selection would act on these traits, causing a complete shift to right-handedness in the population. However, this is not the case, raising the question why left-handedness has persisted until today, if only in a small fraction.

Stable presence of a minority of left-handers in human populations over time despite the associated fitness-costs could be explained by negative frequency-dependent selection, a model of evolutionary dynamics that grant higher fitness benefits to individuals of a certain phenotype the rarer the phenotype is in the overall population (Billiard, Faurie, & Raymond, 2005; Goldstein & Young, 1996; Llaurens et al., 2009). This results in a fluctuation of this phenotype's prevalence

* Corresponding author at: University of Groningen, Faculty of Mathematics and Natural Sciences, GELIFES – Groningen Institute for Evolutionary Life Sciences, Nijenborgh 7, 9747 AG Groningen, The Netherlands.

E-mail address: n.zickert@rug.nl (N. Zickert).

around a certain equilibrium. If left-handedness does indeed have fitness costs this would mean that it could remain in the population if it also has frequency-dependent benefits. It has been suggested that one such benefit may be that left-handed people have an advantage in close-range combat and interactive sports – the so called ‘surprise-effect’. Evidence for this was claimed by Faurie and colleagues who found that left-handers are more frequent in pre-industrial societies that exhibit higher rates of homicide (Faurie et al., 2011; Llaurens et al., 2009). Winning combats enhances fitness as it can increase survival and grant access to sexual partners and other essential resources. The higher winning chances of left-handers relative to right-handers are consistent with the finding that left-handers are over represented in combat sports (Groothuis, McManus, Schaafsma, & Geuze, 2013; Loffing & Hagemann, 2012). Other authors have suggested, however, that the observed patterns could also be due to a stronger inclination of left-handers to engage in fights in the first place (Dinsdale, Reddon, & Hurd, 2011; Pollet, Stulp, & Groothuis, 2013) for which some evidence exists (Dane & Sekertekin, 2005), or that higher winning chances of left-handers in combat sports may be due to other correlated traits as extensively discussed in (Groothuis et al., 2013).

Another interesting trait to be considered within the framework of frequency-dependent selection is creativity since it has been suggested to be higher in left-handers. Creativity is potentially open for frequency dependent selection via mate preference for exceptional creative partners (Llaurens et al., 2009). Generally, two types of creativity are distinguished: artistic creativity and problem solving creativity. The latter may be split into divergent thinking and convergent thinking (Sawyer, 2012). While divergent thinking involves the creation of many ideas or solutions in a free-flowing way that is focused on broad and novel exploration of a problem, convergent thinking is applied in problem solving, i.e. sorting many options to find the best possible solution to a problem. Comprehensive scientific research on this topic in relation to hand preference is scarce, however, and the results from the existing body of literature are largely inconclusive and often only address one of the two aspects of creative thinking. One study found that male left-handers showed better divergent thinking performance than right-handed males (Coren, 1995). Götestam found that the prevalence of left-handers among students of music and architecture was higher compared to a control group (Cosenza & Mingoti, 1993; Götestam, 1990). Similarly, Nicholls found higher incidents of left-handedness in a group of professional artists compared to a non-artistic control group (Nicholls, Chapman, Loetscher, & Grimshaw, 2010). One additional interesting finding is that mixed-handers scored higher on a creativity test compared to participants with strong hand preference in a study with 62 students of which 30 were mixed handed (Shobe, Ross, & Fleck, 2009).

For all hypotheses mentioned above (left-handers having more health problems, winning fights more often or having a stronger inclination to join combat sports, and being more creative) we can find a small body of literature yet always with mixed results. Other issues with the existing literature is that often studies are conducted with small or very select sample populations and that there is a substantial risk of publication bias (for a critical review see Groothuis et al., 2013). Therefore, the evolutionary explanation of left-handers being always in the minority still remains an enigma. To bring more clarity into the discussion of the evolutionary explanations for the prevalence of left-handedness, we focused on the four traits associated with left-handedness mentioned above – higher susceptibility for health and developmental problems, higher aggressive tendencies and higher winning chances in fights, as well as higher creativity as a possible trait playing a role in the maintenance of left-handedness in human populations. In addition, we analyzed the number of offspring in relation to handedness as a direct measure of fitness.

Our study circumvented the problem of small, select sample populations by making use of a very large range and number of participants by means of a national online survey in the Netherlands. The cooperation

with a popular yearly event (“Weekend van de Wetenschap” – weekend of science) which is aimed at involving a broad audience in scientific research allowed us to reach out to a large and varied population. Data were collected from participants who were informed about the study via news websites, a popular scientific site with news and options to participate in research (quest.nl), newspaper articles, internet, and radio interviews. Since the respondents were distributed along the whole spectrum of hand-preference, this provides excellent power to examine the association of both direction and strength of hand preference with the traits mentioned above. Apart from the *direction* of hand preference (i.e. left or right) the strength or the degree of that preference could be of equally great importance for classifying handedness and evolutionary questions (Christman & Prichard, 2016; Corballis, Hattie, & Fletcher, 2008; Schaafsma, Geuze, Lust, Schiefenhövel, & Groothuis, 2013). Moreover, to our knowledge this study is the first one testing all four aspects (health, creativity, and aggression, as well as reproduction) together in one sample.

Thus, if left-handedness were associated with the above-mentioned costs and benefits, we expect to find the following outcomes:

Health problems are more prevalent in left-handers than right-handers. This was studied by asking how often and for how long the participant had been ill in the past year and whether he/she suffered from specific diseases reported to be associated with left-handedness in the literature.

Left-handers score higher on creativity than right-handers. Here we asked about the number of artistic hobbies and also included questions targeted at differentiating between two forms of problem solving creativity (convergent and divergent thinking).

Left-handers score higher on winning fights and/or measures of irritability and aggression. This was studied by asking the participants about their past experience with fights and by asking how they would react in several imaginary situations of conflict.

In addition to examining the connection of hand-preference with traits that selection could act upon in order to shape the characteristic right-shifted population bias, we also looked at a more direct measure of fitness: the number of offspring.

2. Methods

2.1. Questionnaire

Between October 2014 and May 2015 an internet survey was open to the Dutch speaking public through the website “helpeehandje.nl” where background information on the project and the link to the questionnaire was given (see Appendix A.3.). The questionnaire was designed and implemented on the platform Qualtrics (qualtrics.com). In cooperation with the “Weekend van de Wetenschap” and NEMO Science Museum Amsterdam the public was informed through press release, interviews in national papers and radio, press channels of NEMO Science Museum and the University of Groningen, and internet platforms such as twitter, and facebook.

2.1.1. General questions

In the questionnaire first a statement of informed consent was presented, followed by general questions on gender, year of birth, limitations in the upper limbs, number of children, and hand preference of each parent (appendix).

2.1.2. Self-assessment

In the second part participants were asked to rate themselves on a scale from 0 to 100 on their artistic creativity, problem solving skills, irritability and occurrence of health problems. The midpoint of each scale was described as ‘not more or less [trait] than others’. Additionally, participants estimated their own hand preference on a scale from –100 (complete left-handedness) to 100 (complete right-handedness). The exact wording and appearance of these questions can be found in the

appendix. This part was concluded by feedback in terms of the individual score as compared to the average score obtained from the subjects that had already participated in this questionnaire earlier.

2.1.3. Hand preference and hand skill

The following section of the questionnaire consisted of a standard measurement of hand preference and hand skill. For hand preference we used the ten questions of the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971), which were offered in a modified Dutch translation in which four of the original questions were replaced with similar ones that have been tested to be more reliable indicators of hand preference (see appendix) (van Strien, 2003, 1992). Participants were asked with which hand they use to perform a certain task (e.g. ball throwing) and were given the choice to answer ‘always left’, ‘mostly left’, ‘no preference’, ‘mostly right’ or ‘always right’, coded as -2 , -1 , 0 , 1 or 2 respectively. The sum of the coded answers represented the hand preference score (EHI score). The EHI score ranged from -20 , representing complete left-handedness, to $+20$ (complete right-handedness) with 0 as no preference for either hand.

Based on this scale we classified participants in one of five groups: strongly left-handed (-20 to -16), moderately left-handed (-15 to -5), no preference (-4 to 4), moderately right-handed (5 to 15), and strongly right-handed (16 to 20). These groups were used to visualize the results of the statistical models. This classification ensured sufficient number of subjects in each group for statistical analyses (for a review and discussion of cut-offs, see Edlin et al., 2015).

To measure difference in skill between the hands participants performed a tapping task on a computer keyboard. The results of this test and its relation with the fitness measures will be presented in a separate paper (van der Feen, Zickert, Groothuis, & Geuze, in preparation).

2.1.4. Creativity

In the third part we established the participant's artistic creativity by asking how often they performed a specific artistic activity. We provided six categories: creating images, music, writing and storytelling, design, plastic arts and performance arts. Participants were asked to indicate on a five point scale how often they performed these activities, ranging from ‘I do it a lot’ to ‘I never do it’. From the answers we calculated a sum score for artistic creativity – participants who never engage in any of these artistic activities received a score of 0 and the highest reachable score was 30 (see appendix).

2.1.5. Aggression

Irritability (as a proxy for aggression) was assessed in two different ways; in one part participants were asked how they would respond in situations that would typically elicit annoyance. Answer possibilities were given on a five- or six-point scale, ranging from staying completely passive in the situation (“do nothing”) over non-verbal and verbal reactions up to physical responses. In a second part of the assessment we asked about voluntary involvement in fights, including fights during childhood, within the past ten years, and verbal fights. Answers could be given on a five point scale ranging from “never” to “more than ten times” (for questions and answer options, see appendix). A composite irritability score was calculated (for details see Appendix A. 1.5. and Eq. A1.8.). All participants who answered “2 to 5 times or more” to the question about fighting within the last 10 years received an additional question where they could indicate how often they had won these fights. The answers they could choose from were “always”, “won more than lost”, “lost more than won”, “never”.

2.1.6. Health and developmental problems

A general measure of health status was obtained by asking participants how often they had been ill within the past 12 months using a six point scale ranging from ‘never’ to ‘more than five times’. All participants who indicated they had been ill at least once, were then asked how many days they had been ill within these past 12 months on a

seven point Likert-type scale ranging from “1–3 days” to “chronically ill”. Both questions had the option ‘I don’t want to answer’. These cases were excluded from this analysis. In addition to the general health status, we asked if the participant had any allergies, dyslexia, or if he/she was born prematurely (earlier than eight months). The answer possibilities to these questions were “yes”, “no”, or “I don’t know”. All participants who did not know were excluded from the statistical analysis of this part. When an allergy was indicated we asked the number of allergens the participant was sensitive to on a six-point scale ranging from “one” to “more than five”. From the number of times being ill and the number of days being ill a sum score (Health problems composite score) was calculated ranging from 0 (never ill) to 13 (very often and/or chronically ill). For the complete question text and answers, see appendix (A.1.6).

2.1.7. Intermittent feedback

Following the assessment of health problems and developmental aspects participants received an overview of their hand preference and hand performance scores as well as their sum scores on artistic creativity and irritability. Next, participants optionally could enter any comments. At this point participants could choose to submit their answers and exit/quit or to continue with further questions about problem solving creativity, more specifically, divergent and convergent thinking.

2.1.8. Creativity – divergent thinking

For divergent thinking we used the alternate uses task in which participants were asked to name as many usages for a common object within a limited time span (Fink, Benedek, Grabner, Staudt, & Neubauer, 2007; Piffer, 2012). Specifically, we asked “Within two minutes, enter as many uses for a book that you can think of.” Answers could be entered as free text, each in a separate field. The participant had the option to terminate this part if (s)he was exhausted of any further answers before the 2 min. Three divergent thinking measures were calculated: fluency, originality, and originality per fluency. The individual fluency score was the number of valid answers, and the originality score the sum of the creativity scores of the valid answers. Valid answers were defined as recognizable words. The creativity score of an answer was based on the frequency of an answer compared to all answers given by all participants. Answers with a high frequency (that is, answers mentioned by many participants) were assigned a low creativity score and answers with a low frequency (that is, answers that were rare or unique) were assigned a high score. Using a procedure described in detail in the appendix we determined 3527 unique answers. The answers were divided into 10 classes, i.e. the 10% most common answers were assigned a creativity score of 1 and the 10% least common words were assigned a creativity score of 10 . The answer ‘to read’ was assigned a score of 0 , and therefore excluded from the analysis because virtually all participants provided this answer. The measure originality per fluency was calculated by dividing the participant's originality score by the number of valid answers they gave to correct for the fact that the originality score is dependent on the number answers given.

2.1.9. Creativity – convergent thinking

Lastly, we estimated convergent thinking through twelve questions that required the participant to “think outside of the box”. Six questions addressed mathematical thinking and another set of six targeted verbal processing in the sense that close reading of the questions was essential (a complete list of all questions and answers can be found in the appendix). For each question five answers were given to choose from of which only one was correct. The remaining options consisted of two incorrect answers, a field for free text entry if the participant considered none of the other options correct, and an option to indicate that they were already familiar with this question. For example, in the mathematical part one question was “Water lilies double every 24 hours. There is 1 water lily in a lake at the start of each summer. It takes 60 days to fill the lake completely with water lilies. After how many days is the lake half

full?” In the section of verbal convergent thinking one of the six questions was the following: “In what year did Christmas and New Year’s Day fall in the same year?” The full set of questions and answers can be found in the appendix section. The convergent thinking score (convergent thinking total) was calculated as the number of correct answers divided by number of unfamiliar questions. Similarly, subscores were calculated for mathematical and verbal convergent thinking.

2.1.10. Number of offspring

Questions on the number of offspring were added one day later than the launch of the questionnaire accounting for approximately 10,500 people who have not seen these questions, resulting in a lower sample size ($n = 11,669$). The number of offspring was calculated by adding up the number of biological sons and daughters a participant indicated to have. Participants who indicated to have no biological children were coded with 0 children.

The research project was approved by the committee of human participant research of the Department of Psychology, University of Groningen (license number ppo-013-056).

2.2. Data analysis

All statistical models and graphs were produced using SPSS Statistics software version 22.

2.2.1. Exclusion criteria

Before starting the analysis, we applied a list of strict exclusion criteria on the complete dataset. We excluded cases that:

- had missing data on any of the questions that were used in the statistical analysis and were not optional (except for the number of children as this question was added to the questionnaire in a later stage of the project).
- did not specify their sex as male or female.
- were under the age of 15 years and over 100 years.
- indicated that they have a temporary or permanent limitation in one of their arms or hands.
- gave nonsensical answers (e.g. being 20 years old having three grandchildren).

2.2.2. Principal component analysis

Our three hypotheses relate to health problems, aggression and creativity. Each of these measures were assessed through a cluster of scores and self-assessments. To reduce the number of dependent variables within a cluster we performed a principal component analysis (PCA) for each cluster, using the following specifications: covariance matrix, factor Eigenvalue > 1 , and varimax rotation (component solution, Distefano, Zhu, & Míndrilă, 2009). The resulting components were used in the further statistical analysis and interpretation of the results. The factor loadings are listed in Table 1. For health problems the PCA revealed one principle component explaining 70.5% of the variance in the sample and the loadings of the separate variables on this component are listed in Table 1A. Three principal components were extracted for creativity, respectively explaining 31.6% (PC 1 creativity (convergent thinking)), 26.0% (PC 2 creativity (divergent thinking)), and 16.8% (PC 3 creativity (self-assessment and artistic creativity)) amounting to a total of 74.4%. The aggression principal component explains 51.1% of the variance in the sample. We consider the fact that only one component is extracted for health and aggression measures, respectively, and three components for creativity as support for the adequateness of our measurements.

2.2.3. General linear regression model (GLM)

To examine the influence of hand preference on scores of health, aggression, and creativity we applied a linear regression model with the extracted PCA components as dependent variables. Hand preference

Table 1

Loadings of separate measures of health problems, creativity, and aggression on components extracted by principal component analysis.

Component matrix			
A) Health problems			
	Component 1		
Health problems self-assessment	,511		
Times being ill	,881		
Days being ill	,893		
Health problems composite score	,985		
B) Creativity (rotated)			
	Component 1	Component 2	Component 3
Artistic creativity self-assessment			,870
Problem solving creativity self-assessment			,529
Artistic creativity score		,146	,861
Divergent thinking fluency		,909	
Divergent thinking originality		,979	
Divergent thinking originality per fluency		,773	,158
Convergent thinking mathematical	,842		
Convergent thinking verbal	,848		
Convergent thinking total	,997		
C) Aggression			
	Component 1		
Aggression self-assessment	,658		
Aggression score	,857		
Frequency fights	,645		
Frequency fights childhood	,649		
Frequency verbal fights	,743		

was entered in the model as continuous EHI scores as well as its squared value (EHI^2) in order to capture both linear and quadratic effects of hand preference to model the effect of strength of hand preference. This is relevant as for example extreme handedness independent of direction may have similar scores that differ from ambidextrous handedness. Sex, age, and the quadratic values of age (to account for an increase over young ages and a decrease in older age) were entered in the model as fixed factor (sex) and covariate (age and age^2) in order to control for their confounding effects on the scores. No interactions were entered in the model since we did not have a priori hypotheses concerning these. In order to determine the relevance of the effect of hand preference, we assessed the effect size of all predictors in the model (partial eta squared). The only topics analyzed without the help of a principal component are the number of allergens and estimated winning of fights, since these questions were optional and their inclusion would have limited the population to participants with allergies or fight-prone individuals.

2.2.4. Generalized linear regression model (GLZM)

For the analysis of questions that only required a “yes” or “no” answer, we applied a generalized linear model with a binomial logit function: these concern questions about allergies, dyslexia and premature birth. We used a negative binomial log link function for testing the effect of the number of children (Schaafsma et al., 2012). Since Schaafsma and colleagues found a stronger effect of hand preference on the number of offspring in males we repeated this analysis with male participants only. For all models sex, age, and the quadratic values of age were entered in the model as fixed factor (sex) and covariate (age and age^2) and no interactions were entered in the model. In order to determine the effect size of all predictors in the model we used the slope (B-value) of the respective factor in the model as estimate.

2.2.5. Calculation of residual scores and graphs

In order to better interpret the results of the G(Z)LM analyses we chose to visualize the data as the mean score for each of the five hand-preference groups defined above. To depict the effect of hand

Fig. 1. Number of participants per attainable EHI score. Negative numbers indicate left side preference, positive numbers right preference. Dark gray indicates strong preference, light gray moderate preference, and white no preference for either side.

preference per se, we eliminated the effects of sex, age and age² in those graphs, by plotting the residuals of the dependent variables from a model that contained only sex, age, and age².

2.2.6. Calculation of relative maximal change

In order to get a better grasp on the actual impact of the different degrees of hand preference on the measured traits in a biological sense rather than a statistical one, we compared the maximal distance between two hand preference groups (highest and lowest group mean) to the mean of all five groups together: Relative maximal change (rmc) = maximum distance / total mean. This allows us to evaluate the maximum percentage of change over the different groups, facilitating a better estimation for the biological relevance of the effect of hand preference on the traits.

3. Results

The distribution of EHI scores and the five groups for hand preference ($n = 22,590$) are presented in Fig. 1. Surprisingly, we had a much higher percentage of strongly left-handed participants compared to the general population, even surpassing the number of strong right-handers. Similarly, women outnumbered men slightly by about 5%. Detailed information about group sizes, mean age and sex composition can be found in Table 1 in the appendix.

3.1. Health and developmental problems

The results of the GLM are depicted in Table 2 and revealed a significant linear and quadratic effect of hand preference as well as significant

Table 2

Effects of hand preference (EHI) on measures of health problems. Abbreviations: SL = strong left, ML = moderate left, A = ambidextrous, MR = moderate right, SR = strong right, * = optional question (see also Fig. 2).

Health problems measure		EHI	EHI ²	Sex	Age	Age ²	n	Shape of residual plot
PC health problems	P	<0.001	0,013	<0.001	<0.001	<0.001	13,718	MR score highest by far, SL score lowest. ML, A, and SR fall in-between. Fig. 2a
	η_p^2	0,001	0,000	0,013	0,005	0,006		
Separate components								
Health problems self-assessment	p	<0.001	n.s. 0,000	<0.001	n.s. 0,000	0,030	22,590	SL and ML score lowest, MR and SR score highest. A falls in-between. Fig. 2b
	η_p^2	0,007		0,005		0,000		
Times being ill	p	<0.001	0,020	<0.001	<0.001	<0.001	22,439	Similar to PC health problems
	η_p^2	0,003	0,000	0,014	0,008	0,003		
Days being ill	p	0,015	0,002	<0.001	<0.001	<0.001	13,718	Similar to PC health problems
	η_p^2	0,000	0,001	0,009	0,002	0,003		
Health problems composite score	p	<0.001	0,003	<0.001	<0.001	<0.001	22,382	Similar to PC health problems
	η_p^2	0,003	0,000	0,014	0,004	0,002		
Number of allergens*	p	n.s. 0,000	0,001	<0.001	0,001	0,007	8030	Inverted U-shape. SR score lowest, MR score highest. ML, A, SL fall in-between.
	η_p^2		0,001	0,017	0,001	0,001

Fig. 2. Mean residual scores of health problems ($\pm$ SEM), per hand preference group, corrected for effects of sex, age, and age². PC health problems (A), Health problems self-assessment (B).

effects of confounding factors (sex, age, age²) on the health principal component. Fig. 2A shows that the scores increase from low in strong left-handers to highest in the group of moderate right-handers and show again a low score in strong right-handers; in contrast to expectation the strong left-handers score the lowest. The effect size of each factor (partial eta squared, η_p^2), however, is small for all predictors, with sex having the strongest influence (Tables 2 and 6).

Analysis of the separate components revealed a very similar pattern to that of the principal component with the exception of the self-assessment of the occurrence of health problems for which no quadratic effects of hand preference and age were found. Fig. 2B shows a clear increasing linear effect from strong left-handers scoring to moderate right-handers. However, unlike for PC health problems, in the self-assessment strong right-handers have a similarly high score as moderate right-handers.

For both allergies and dyslexia there is a linear and a quadratic effect of hand preference whereas there is none for premature birth (Table 3). Against our hypothesis allergies and dyslexia show a similar linear increase from strong left to moderate right, but with the lowest scores in strong right-handers for dyslexia overall (Fig. 3, Tables 3 and 6). When estimating the severity of allergies by testing how many substances the participants were sensitive to we find a significant but small quadratic effect of hand preference which indicates that weak

hand preference is associated with a higher number of allergens (Fig. 3C, Tables 3 and 6).

In summary, and in contrast to expectation, incidences of health problems are highest in moderate right-handers and relatively low in strong right and strong left-handers.

3.2. Creativity

The GLM analysis of convergent thinking (PC 1 creativity) shows a clear linear effect with a small effect size and a quadratic but small effect of hand preference with strong right-handers having by far the highest score, in contrast to expectation (Fig. 4a, Table 4). Sex, age, and age² have also a significant effect on PC 1 creativity with small or marginal effect sizes (Tables 4 and 6). For artistic creativity (PC 2 creativity) there is only a linear effect of hand preference with a small effect size and a quadratic but very small effect of age (Fig. 4b, Tables 4 and 6). Moderate, and to a lesser extent strong right-handers have again the highest scores, indicating better performance of right-handers with respect to divergent thinking. Artistic creativity and problem solving (PC 3 creativity) show only a quadratic effect of handedness with small effect size and significant but very small effects of all three confounders (Fig. 2c, Tables 4 and 6). The results deviate from the other components in that strong right-handers have the lowest scores (Tables 4 and 6). This pattern is also found for artistic creativity only (Fig. 4d, Table 4), showing that strong right-handers are least involved in artistic creativities.

In summary, we find that measures of creativity are significantly influenced by hand preference. PC 1 creativity, which combines the three convergent thinking scores, shows low scores in strong left-handers and high scores in strong right-handers. PC 2 creativity, which mainly consists of divergent thinking scores shows lowest scores in strong left-handers and highest scores in moderate and strong right-handers. PC 3 creativity, combining mainly the self-assessment scores of artistic and the artistic creativity score, is lowest in strong right-handers and highest in moderate right-handers. None of these findings are consistent with the expectations.

3.3. Aggression

Analysis of the principal component for aggression reveals a quadratic effect of hand preference with small effect size (Tables 5 and 6).

Table 3

Effects of hand preference (EHI) on binary measures of health problems (does occur/does not occur) corrected for effects of sex, age, and age². Abbreviations: SL = strong left, ML = moderate left, A = ambidextrous, MR = moderate right, SR = strong right (see also Fig. 3).

Health problems measure	EHI (p-value)	EHI ² (p-value)	n	Shape of residual plot	Prevalence in sample
Occurrence of allergy	0,038	<0.001	22,439	Inverted U-shape. SR score lowest, MR score highest. ML, A, SL fall in-between. Fig. 3a	36,1%
Premature birth	n.s.	n.s.	21,885	n.a.	4,4%
Occurrence of dyslexia	<0.001	<0.001	22,382	Similar to occurrence of allergy. Fig. 3b	6,6%

Fig. 3. Mean residual scores ($\pm$ SEM) of allergy occurrence (A), occurrence of dyslexia (B), and number of allergens (C), per hand preference group, corrected for effects of sex, age, and age².

Confounding factors also have a significant effect on PC aggression of which sex has the largest, but still with a small effect size (Table 5). Graph 5A clearly shows that the group with no or moderate right hand preference score highest on aggression whereas the strong preference groups score lowest. The separate indices for aggression show a similar result (Table 5). In Fig. 5B, showing the estimated winning probability of fights over the last 10 years, we can see a somewhat similar effect of hand preference. Moderate left-handers and the group without preference score highest, which can be interpreted as that they win fights more often than the other groups.

In conclusion, weakly lateralized groups show the highest score on aggression and winning fights, which is again against the expectation.

3.4. Number of children

We find a significant quadratic effect of hand preference on the number of children participants have ($p = .002$; $B < 0.001$) as well as a significant linear ($p < .001$; $B = 0.262$) and quadratic ($p < .001$; $B = -0.002$) effect of age. Fig. 6 shows that moderate right-handers have

the smallest number of children although all three moderate and low preference groups score low. Of all five hand preference groups strong right-handers have the highest number of children. In a secondary analysis we selected male participants only and repeated the same analysis, resulting in the same significant factors: quadratic effect of hand preference ($p = .007$) as well as a significant linear ($p < .001$) and quadratic ($p < .001$) effect of age.

3.5. Relative maximum change

By comparing the maximal distance between the two hand preference groups with the highest and lowest mean to the mean of all five groups together we calculate the relative maximal change (rmc) of a trait (Table 6). The effect size for the difference between the highest and the lowest group is given in Table 6 as well. Particularly the factors health problems self-assessment, health problems composite score, occurrence of allergy, premature birth, occurrence of dyslexia, artistic creativity, fluency and originality of divergent thinking, and the number of children are affected by hand preference.

Fig. 4. Mean creativity residual scores ($\pm$ SEM), per hand preference group, corrected for effects of sex, age, and age². PC 1 creativity (A), PC 2 creativity (B), C – PC 3 creativity (C), artistic creativity (D).

4. Discussion

The evolution of the asymmetric distribution of human hand preference is topic of a long standing debate and as yet unresolved. A widely cited hypothesis assumes that left handedness bears health costs but nevertheless stays in the population because of negative frequency dependent benefits. These benefits would concern winning in fights and a higher level of creativity (see [Introduction](#)). We collected data in a very large diverse sample of subjects to test these ideas. To the best of our knowledge this is the first study based on such a large sample size in which not only the direction but also the strength of hand preference was taken into account as well as the combination of several fitness traits in the same study, including number of children. Moreover, we assessed hand preference for a variety of tasks using the EHI rather than for a single task. The associations we found for the direction of hand preference were weak, however, we found many associations with the strength of hand preference.

4.1. Health and developmental problems

Left-handed participants did not indicate more health problems as is often suggested by literature (see [Introduction](#)). In contrast, for self-assessment of health problems, i.e. perceived health compared to others, the two right-handed groups reported more health problems than both left-handed groups. Prevalence of allergies which we specifically included because left-handedness has been suggested to be associated with lower immune function (see review [Llaurens et al., 2009](#)), was not higher in left-handers. This is in concordance with the large internet studies of [Peters, Reimers, and Manning \(2006\)](#) and [McManus and Wysocki \(2005\)](#), who also did not find a connection between hand preference and allergies, nor a lower prevalence of ulcers and arthritis in left-handers. However, the prevalence of allergies might not necessarily be closely related to immune deficiencies, as the latter renders an individual more vulnerable to infections but does not promote the development of allergies. We also did not find a higher prevalence among left-handers of dyslexia and premature birth, both of which have been

Table 4

Effects of hand preference (EHI) on creativity measures (abbreviations: SL = strong left, ML = moderate left, A = ambidextrous, MR = moderate right, SR = strong right) (see also Fig. 4).

Creativity measure		EHI	EHI ²	Sex	Age	Age ²	n	Shape of residual plot
PC 1 creativity (convergent thinking)	p	<0.001	0,005	<0.001	<0.001	<0.001	7936	SL score lowest, SR by far the highest. ML, MR, and A fall in-between.
	η_p^2	0,012	0,001	0,052	0,009	0,016		
PC 2 creativity (divergent thinking)	p	<0.001	n.s.	n.s.	n.s.	<0.001	7936	SL score lowest, followed by ML, A, and SR scores. MR score highest.
	η_p^2	0,006	0,001	0,001	0,000	0,002		
PC 3 creativity (self-assessment and artistic creativity score)	p	n.s.	<0.001	<0.001	0,002	0,011	7936	Inverted U-shape. SR have lowest scores, MR by far the highest. A, ML, and SL fall in-between.
	η_p^2	0,000	0,003	0,007	0,001	0,001		
Separate factors								
Artistic creativity self-assessment	p	0,002	<0.001	<0.001	0,005	n.s.	22,590	Inverted U-shape. SR lowest, MR highest scores. ML, A, SL fall in-between.
	η_p^2	0,000	0,002	0,025	0,000	0,000		
Problem solving creativity self-assessment	p	0,005	0,001	<0.001	<0.001	<0.001	22,590	Inverted U-shape. SL lowest, MR highest scores. ML, A, SR fall in-between
	η_p^2	0,000	0,000	0,019	0,013	0,011		
Artistic creativity score	p	n.s.	<0.001	<0.001	n.s.	n.s.	22,590	Inverted U-shape. SR score lowest, MR score highest. ML, A, SL fall in-between.
	η_p^2	0,000	0,007	0,015	0,000	0,000		
Divergent thinking fluency	p	<0.001	0,012	n.s.	<0.001	<0.001	9089	Similar to PC 2 creativity
	η_p^2	0,006	0,001	0,000	0,007	0,015		
Divergent thinking originality	p	<0.001	0,012	n.s.	<0.001	<0.001	9089	Similar to PC 2 creativity
	η_p^2	0,007	0,001	0,000	0,001	0,005		
Divergent thinking originality per fluency	p	<0.001	n.s.	0,002	n.s.	n.s.	9089	Similar to PC 2 creativity
	η_p^2	0,003	0,000	0,001	0,000	0,000		
Convergent thinking mathematical	p	<0.001	n.s.	<0.001	<0.001	<0.001	9563	Similar to PC 1 creativity
	η_p^2	0,007	0,001	0,031	0,004	0,008		
Convergent thinking verbal	p	<0.001	n.s.	<0.001	<0.001	<0.001	9561	Similar to PC 1 creativity
	η_p^2	0,007	0,000	0,031	0,010	0,017		
Convergent thinking total	p	<0.001	n.s.	<0.001	<0.001	<0.001	9556	Similar to PC 1 creativity
	η_p^2	0,010	0,000	0,044	0,009	0,017		

claimed to be associated with handedness (Tønnessen et al., 1993). Interestingly, and against the hypothesis, we found a higher prevalence of health problems and dyslexia in the group of moderate right-handers and to some extent ambidextrous subjects.

Even though it might be more accurate to determine health problems based on medical dossiers, our approach can still be considered valuable. Less severe health problems for which the general practitioner is usually not consulted are taken into account by our questionnaire. In addition, the way we formulated the question explicitly addresses the effect an illness or injury had on the person's well-being and participation in work or school life. Furthermore, we aimed at a general estimate of health status as opposed to the specifically-targeted health aspects of previous studies. Clearly, the hypothesis that impaired health is a cost to left-handers could not be supported.

4.2. Creativity

For all three components of creativity (convergent thinking, divergent thinking, and artistic creativity), we find a significant effect of hand preference, but for none of these left-handers scored better. For

convergent thinking the effect of hand preference was even opposite to the prediction of the hypothesis – strong right-handers perform best while strong left-handers perform worst. This is consistent with literature indicating that right-handers have somewhat better cognitive abilities (reviewed in Nettle, 2003). However, this author argues that direction of hand preference is often confounded with its strength, and that improved analyses point to higher cognitive abilities in strongly lateralized persons rather than in right-handers. This is in line with Crow, Crow, Done, & Leask, 1998. This is clearly not something we find in our large dataset. While our results for convergent thinking were in line with existing literature this was not so for divergent thinking. In his study with large groups of students (ca. 500–1000) Coren assessed divergent thinking with several tests and found either no difference between groups of strongly and mixed left/right-handers or a significantly better performance of consistent left-handers (Coren, 1995). In our dataset left-handers showed the weakest performance of divergent thinking (as measured with principal component 2).

An effect of strength of hand preference is found to some extent on the other components of creativity. For PC 2 creativity (divergent thinking), which is explicitly targeted at the de-novo generation of answers,

Table 5

Effects of hand preference (EHI) on measures of aggression (abbreviations: SL = strong left, ML = moderate left, A = ambidextrous, MR = moderate right, SR = strong right)* = optional question (see also Fig. 5).

Aggression measure		EHI	EHI ²	Sex	Age	Age ²	n	Shape of residual plot
PC aggression	p	n.s.	<0.001	<0.001	0,027	<0.001	22,590	Inverted U-shape. A and MR score highest, SL and SR score lowest. ML fall in-between.
	η_p^2	0,000	0,002	0,022	0,000	0,001		
Separate factors								
Aggression self-assessment	p	n.s.	n.s.	<0.001	<0.001	<0.001	22,590	A score highest; SL, ML, MR, and SR score lower and similar to each other.
	η_p^2	0,000	0,000	0,003	0,005	0,005		
Aggression score	p	n.s.	<0.001	<0.001	<0.001	<0.001	22,590	Inverted U-shape. A scores highest, SL and SR score lowest. ML and MR fall in-between.
	η_p^2	0,000	0,001	0,036	0,006	0,007		
Frequency fights	p	n.s.	<0.001	<0.001	<0.001	<0.001	22,590	Similar to PC aggression
	η_p^2	0,000	0,002	0,012	0,029	0,015		
Frequency fights childhood	p	n.s.	<0.001	<0.001	<0.001	<0.001	22,590	Similar to PC aggression
	η_p^2	0,000	0,002	0,037	0,001	0,001		
Frequency verbal fights	p	n.s.	<0.001	<0.001	0,012	<0.001	22,590	Similar to PC aggression
	η_p^2	0,000	0,001	0,006	0,000	0,002		
Fights won*	p	n.s.	0,026	<0.001	0,017	0,002	1765	ML and A score highest, SR score lowest. SL and MR fall in-between.
	η_p^2	0,000	0,003	0,057	0,003	0,006		

Table 6

Effect sizes based on group means, distance of highest- and lowest-scoring group, relative maximal change (rmc), and highest- and lowest-scoring group (abbreviations: SL = strong left, ML = moderate left, A = ambidextrous, MR = moderate right, SR = strong right, * = optional question).

Variable	Cohen's d	Maximal distance	rmc %	Max/min group
PC health problems	0,159	0,158	–	MR/SL
Health problems self-assessment	0,182	4,756	13,9	SR/SL
Times being ill	0,160	0,203	9,6	MR/SL
Days being ill	0,143	0,190	9,4	MR/SL
Health problems composite score	0,179	0,454	19,3	MR/SL
Number of allergens*	0,124	0,203	8,4	MR/SR
Occurrence of allergy	0,147	0,071	18,2	MR/SL
Premature birth	0,033	0,007	14,0	–
Occurrence of dyslexia	0,149	0,036	51,4	MR/SR
PC 1 creativity (convergent thinking)	0,280	0,267	–	SR/SL
PC 2 creativity (divergent thinking)	0,244	0,237	–	MR/SL
PC 3 creativity (self-assessment and artistic creativity score)	0,237	0,234	–	SL/SR
Artistic creativity self-assessment	0,174	4,712	8,4	MR/SR
Problem solving creativity self-assessment	0,109	1,664	2,2	MR/SL
Artistic creativity score	0,298	1,244	15,6	MR/SR
Divergent thinking fluency	0,233	1,085	11,2	MR/SL
Divergent thinking originality	0,266	5,380	16,5	MR/SL
Divergent thinking originality per fluency	0,169	0,160	5,1	MR/SL
Convergent thinking mathematical	0,202	0,047	8,6	SR/SL
Convergent thinking verbal	0,196	0,047	7,7	SR/SL
Convergent thinking total	0,259	0,052	8,9	SR/SL
PC aggression	0,168	0,165	–	A/SR
Aggression self-assessment	0,070	1,703	3,8	A/SL
Aggression score	0,113	0,531	3,2	A/SR
Frequency fights	0,152	0,099	7,6	A/SR
Frequency fights childhood	0,155	0,134	6,4	A/SR
Frequency verbal fights	0,114	0,143	5,9	MR/SR
Fights won*	0,165	0,125	4,1	A/SR
Number of children	0,137	0,143	13,5	SR/MR

left-handers are again the lowest-scoring group and moderate right-handers the highest, followed by ambidextrous subjects. This pattern is equal for PC 3 creativity (artistic creativity measured by the degree of involvement in artistic activities and self-assessment). Because the principal component analysis yielded the three main components of creativity, namely artistic creativity, divergent and convergent thinking (Sawyer & Robert, 2012), we are confident that we have covered the scope of creativity reasonably well.

The results clearly indicate that even with the multi-factored assessment of creativity, the popular myth that left-handers are more creative or artistic can be dispelled. Handedness and cerebral

asymmetry are not only variable but also imperfectly related, and a complementary model of left-brain specialization (right-handers) for language and logic and a right-brain specialization (left-handers) for creativity and intuition is too simple (Corballis, 2014). Recent research supports more the existence of multiple lateralized networks independent of handedness (Häberling, Corballis, & Corballis, 2016). We found in right-handers higher scores of convergent thinking that may represent the logic component of creativity, and higher scores for artistic ability among weakly lateralized subjects that may have been classified as left-handers in several studies (see Section 4.6. The effects on strength).

Fig. 5. Mean residual scores of aggression ($\pm$ SEM), per hand preference group, corrected for effects of sex, age, and age². PC aggression (A), Number of fights won within the past 10 years (B).

Fig. 6. Mean residual scores ($\pm$ SEM) of number of children, per hand preference group, corrected for effects of sex, age, and age².

In summary, we found no evidence for left-handers being better at divergent or convergent thinking than right-handers, two important components of problem solving creativity, and no evidence for left-handers being more artistically creative. Again, weakly lateralized (right-)handers have somewhat higher scores for artistic creativity.

4.3. Aggression

Strong hand preference in either direction predicted low scores of PC aggression while no or moderate right preference were associated with the highest scores. This refutes the hypothesis that left-handers are overrepresented in martial arts and contact sports due to a more aggressive nature rather than an advantage due to their left-handed fighting technique (Groothuis et al., 2013). In addition, the well cited fighting hypothesis (Faurie & Raymond, 2013) stating that left-handers have a frequency dependent surprise benefit in fights is also not supported by the self-reported number of physical fights won by the participants. Even in the subset of the sample of subjects who had voluntarily participated in physical fights in the past, strong left-handers did not win more fights. Rather, the significant quadratic term for hand preference shows that participants with no or moderate left-hand-preference won most fights relative to the other handedness categories.

4.4. Number of children

We tested the hypotheses that left-handers could remain in the population despite potential (health-related or other) fitness costs because of a higher reproductive success than right-handers, given the heritability of handedness (Medland et al., 2009).

We did not find this in our sample but there was a significant quadratic effect of hand preference on the number of children: groups with a strong hand preference have the most children and groups with no or moderate right preference have the least. This implies that not the direction but the strength of hand preference is related to reproductive success. This is consistent with a study of a Danish cohort where it was shown that mixed handedness is connected to lower fecundity (as measured in 'time to pregnancy') (Zhu et al., 2009). These interpretations/hypotheses, however, need thorough testing in future research. The results may explain why moderately strong or ambidextrous hand preference has such a low frequency in the population.

One could argue that due to the widespread use of contraceptives our data do not represent the original evolutionary selective pressures. However, in a pre-industrial society lacking almost completely health care some evidence was found too that strongly lateralized men, as measured with the pegboard task, had more offspring (Schaafsma et al., 2013). Nonetheless, it is also important to notice that current fitness measures cannot reveal if a relationship between hand preference and offspring has existed in the past.

The number of children is the most direct measure of Darwinian fitness, which is why we considered the effect size in this case to have more biological impact than for example artistic creativity as the latter does not necessarily translate into higher fitness in an individual. All factors besides the number of children are likely correlated with fitness, however, in a much more indirect way. The difference in fitness (as assessed by the number of children, see Table 6) between the handedness groups is 13.5%, which we think is a strong enough effect for selection to work upon.

We did not measure survival, nor life time reproductive success or inclusive fitness. Nevertheless, as far as the data go, we did not find

evidence that left-handers could persist in the population due to higher reproductive success.

4.5. Hand preference and personality

Aggression and creativity, and potentially also differences in health and reproductive aspects can be considered personality traits. Previous research has been undertaken to connect hand preference to personality traits in both human and non-human animals (Cameron & Rogers, 1999; Hardie & Wright, 2014; Hopkins & Bennett, 1994; Lyle, Chapman, & Hatton, 2013). The basis of these studies often assumes that the dominant hand reflects the dominant hemisphere (on the contralateral side) not just for motor output, but also for other functions such as certain dispositions or cognitive processing styles (Morton, 2013). This is most likely a too simple approach as recent evidence clearly shows that there is a lot of within-individual difference in how different functions are distributed over the two hemispheres, even within right or left-handers (Lust, Geuze, Groothuis, & Bouma, 2011). Nevertheless, some animal studies do find clear relationships between lateralization of some functions and traits such as aggression and foraging efficiency (Bisazza, Rogers, & Vallortigara, 1998; Rogers, 2000). Such studies may inspire the field to analyze these relationships in humans in a more precise and biological meaningful way.

4.6. Effect size, sample distribution

Many effect sizes of the significant factors are small, at times even smaller than 0,01 when estimated by partial eta squared. An exception is the number of children; here the effect size is biological meaningful and warrants further study because it represents the most direct measure of Darwinian fitness (Table 6).

One possible explanation for the small effect sizes could be the higher variability in the sample from the general population as opposed to more homogeneous samples from student or clinical populations often used in hand preference studies. The wider coverages in our study provides a better generalization of the results to the human species.

The small effect sizes do not per se mean that the differences associated with hand preference are too small for selection to act upon. By calculating the relative maximal change we evaluated the difference between the highest- and the lowest-scoring hand preference group (Table 6). This revealed that most measures of health problems, artistic creativity and divergent thinking as well as the number of children are sufficiently associated with hand preference to be subject to selection. Measures of aggression and convergent thinking were not.

4.7. The effects of strength

In many studies in the past, for reasons of convenience, handedness has been assessed by recording the writing hand. This seems sensible since for people with strong preference there is a very high congruency between writing hand and the laterality index (EHI). However, for groups with weak or no preference asking the writing hand may lead to a false classification and as a consequence also a false conclusions about left-handers. In addition this will miss the distinction between strong and weak hand preference. Moreover, if the direction of hand preference is determined by the writing hand only, the fact that in the past many left-handers were forced to write with their right hand is unaccounted for, which makes this classification unreliable for older subjects. Interestingly, in our own dataset, we find that only 8,6% of moderate left-handers write with their right-hand but 24,6% of moderate right-handers write with their left hand (of strong left-handers 3,3% write right-handed, of ambidexters 71,2% write left-handed and 15,4% right-handed, strong right-handers write with their left hand 1,0%). This suggests that when handedness is determined from observation of an artistic process like drawing, which is highly correlated with

writing in terms of hand use, a quarter of moderate right-handers could have been mistaken for left-handers and thereby have contributed to the myth of higher creativity in left-handers. Weak or no hand preference followed the predictions of hypotheses and myths in a manner that was predicted for left-handers. Specifically moderate right-handers showed more health-related concerns while at the same time scoring higher on creativity and aggression. This is consistent with several studies reporting that weak hand preference or mixed handedness is associated with somewhat lower performance, psychological disorders and cognitive ability, although these findings are not completely consistent throughout (Corballis et al., 2008; Crow et al., 1998; Nettle, 2003; Nicholls et al., 2010; Papadatou-Pastou & Tomprou, 2015; Rodriguez et al., 2010; Shobe & Desimone, 2016).

4.8. Study limitations

The use of an online questionnaire brings several limitations. The study sample is not representative with respect to hand preference in the population due to the great interest raised among lefthanders. However, this was also not the aim of the study. The study resulted in near equal numbers of left- and right-handed participants, which is actually an advantage for testing differences between these groups, which was the main purpose of our study. Furthermore, we cannot fully exclude the possibility that subjects answered questions about their characteristics with a positive bias; however, there is no reason to assume that such a bias would have been different among the different handedness groups. A strong argument to refute the influence of the overrepresentation of left-handers and/or biased recruitment of subjects is that none of our results went in the direction of the hypotheses (which were based on the confirmation of the generally-held beliefs). In most cases the results showed a relationship with handedness not related to common beliefs in the population.

4.9. Conclusion

We could not confirm hypotheses and popular myths about left-handedness. Left-handers showed no higher proneness to health problems nor greater creativity, and they were not more aggressive than right-handers and equal in reproductive success. A remarkable finding, however, was that often the group with weak or no hand preference stood out from the strongly lateralized groups. Weak hand preference was associated with more health problems, higher artistic creativity, higher aggression and lower reproductive success. The latter may account for the low relative frequency of that group. The main effects of the confounding factors (sex and age) included in the statistical analysis replicated results from previous studies (Papadatou-Pastou, Martin, Munafò, & Jones, 2008; Peters et al., 2006) confirming the robustness of our data. A potential worry is the fact that our sample consisted of many more left-handers than is reflected in the normal population. Clearly, left-handers perceive themselves as being different and are very interested in what this actually encompasses. Nevertheless we see no reason why this would have biased the results and in any case it cannot confound the results for ambidextrous and moderate right-handers.

It has been argued that evolutionary pressures are not relevant anymore in modern industrialized societies and that the current distribution of hand preference is just a relic from the past. However, there is increasing evidence that also in modern societies evolution still acts on human traits (e.g. Byars, Ewbank, Govindaraju, & Stearns, 2010; Tropic et al., 2015). Nevertheless, the original health costs for left-handers may now have been reduced by health care and the benefits by the declining importance of winning fight. Why then is the ratio of left to right not more equal than the current 1 to 9 ratio in modern societies? One possibility is that this is due to the fact that in modern societies effective population sizes are very large so that genetic drift would be very slow.

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Conflict of interest

The authors have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.evolhumbehav.2018.01.001>.

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