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1 Article

2 **Get a grip: Variation in human hand grip strength and implica-**  
3 **tions for human evolution**4 **Ameline Bardo** <sup>1,\*</sup>, **Tracy L. Kivell** <sup>1,2</sup>, **Katie Town** <sup>1</sup>, **Georgina Donati** <sup>3</sup>, **Haiko Ballieux** <sup>4</sup>, **Cosmin Stamate** <sup>5</sup>, **Trudi**  
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18 \* Correspondence: ameline.bardo@gmail.com19 **Abstract:** Although hand grip strength is critical to the daily lives of humans and our arboreal great  
20 ape relatives, the human hand has changed in form and function throughout our evolution due to  
21 terrestrial bipedalism, tool use, and directional asymmetry (DA) such as handedness. Here we in-  
22 vestigate how hand form and function interact in modern humans to gain insight into our evolu-  
23 tionary past. We measured grip strength in a heterogeneous, cross-sectional sample of human  
24 participants (n=662, 17 to 83 years old), to test the potential effects of age, sex, asymmetry (hand  
25 dominance and handedness), hand shape, occupation, and practice of sports and musical instru-  
26 ments that involve the hand(s). We found a significant effect of sex and hand dominance on grip  
27 strength, but not of handedness, while hand shape and age had a greater influence on female grip  
28 strength. Females were significantly weaker with age, but grip strength in females with large  
29 hands was less affected than those with long hands. Frequent engagement in hand sports signifi-  
30 cantly increased grip strength in the non-dominant hand in both sexes, while only males showed a  
31 significant effect of occupation, indicating different patterns of hand dominance asymmetries and  
32 hand function. These results improve our understanding of the link between form and function in  
33 both hands and offer insight into the evolution of human laterality and dexterity.34 **Citation:** Bardo, A.; Kivell, T.L.; Town, K.; Donati, G.; Ballieux, H.; Stamate, C.; Edginton, T.; Forrester, G.S., Get a grip: Variation in human hand grip strength and implications for human evolution. *Symmetry* **2021**, *13*, x. <https://doi.org/10.3390/xxxxx>

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41 Submitted for possible open access publication under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).42 **Keywords:** power grip strength; directional asymmetry; hand dominance; hand shape; manual activities; human evolution; functional morphology43 **1. Introduction**44 The hand is essential for how modern humans interact with their environment, as it  
45 was for our extinct relatives. The enhanced dexterity of the human hand is unique among  
46 living primates and is generally considered to have evolved through both (1) adaptation to bipedalism and a relaxation of locomotor selective pressures on the hands and (2) increasingly more complex tool production and use in hominins (i.e., group consisting of modern humans and our closely related extinct relatives) [1,2]. The use of stone tools would have allowed early hominins to access different and potentially higher-quality foods (e.g., marrow) [3,4]. The manufacture and use of even relatively simple stone tools, such as Oldowan technology (2.6-1.7 million years ago) [5,6] would have required both

47 increased cognitive function (e.g., learning, working memory/future thinking, planning  
48 and decision-making etc.) [7,8] and particular biomechanical demands on the anatomy of  
49 the hands [9-11]. Thus, it is likely that tool production and use played a critical role in  
50 shaping both cognitive development (e.g., with the crucial role of social learning) [12]  
51 and hand morphology. For example, a long, powerful thumb and relatively short fingers  
52 facilitate the forceful precision and power-squeeze gripping that are considered unique  
53 human abilities [1, 13]. Although modern humans are also adept as using their hands for  
54 locomotion [14, 15], the upper limbs are predominantly used for manipulation.

55 Humans are unique among primates in the strength of population-level hand di-  
56 rectional asymmetry (DA) or laterality (i.e., preference for one hand, called the dominant  
57 hand, over the other, non-dominant hand), with 85-90% of humans being right-handed  
58 regardless of geographical region and ethnicity [16-19]. Non-human primates also show  
59 population laterality for object manipulation, but not with the same strength as that  
60 found in humans [20-22, but see 23], and their laterality can also vary depending on the  
61 complexity of the manual task (e.g., bimanual manipulative action versus tool use) [24].  
62 Moreover, motor skill biases for tool use in chimpanzees may be supported by anatomi-  
63 cally asymmetric, left-biased brain regions analogous to Broca's and Wernicke's area in  
64 humans [25], both brain regions that are implicated in the perception and production of  
65 speech. Handedness (i.e., side preference for the right or the left hand) in humans is  
66 thought to have played an important role in lateralization of the human brain for lan-  
67 guage [26] and the emergence of other complex cognitive functions, including tool use  
68 [27, 28], manual gestures [29, 30], and throwing [31]. Greenfield [32] proposed that it was  
69 the motor sequencing for tool use – requiring dexterous hierarchical motor activities –  
70 that paved a way for the emergence of language that likely emerged first in the form of  
71 hand gesture [33, 34]. Thus, more dexterous hands may have increased object manipula-  
72 tion capabilities that, in turn, increased hemispheric specialisation and DA, suggesting  
73 the capacities for tool use and language evolved together [32]. However, when popula-  
74 tion-level handedness first evolved within the hominin clade remains unclear [35, 36].

75 Hand size, shape [37-40], and bone morphology are also highly variable among re-  
76 cent human populations [41, 42]. How this variability potentially affects hand function  
77 may provide insights into the evolution of the human hand. For example, ergonomic  
78 studies have shown that handle design is important for hand grip performance (e.g., time  
79 to complete the task and strength use) [43] and that hand size strongly affects perform-  
80 ance [44], indicating the importance of designing tools in accordance with current an-  
81 thropometric data. Moreover, individuals with relatively longer fingers and therefore  
82 larger joint surfaces require less force during stone tool production than those with  
83 shorter fingers [45]. Key and Lycett [46] found that through experimental stone tool use,  
84 grip strength was the primary contributing biometric factor for stone cutting efficiency.  
85 Therefore, both hand shape and hand strength were likely important factors in efficient  
86 stone tool production and use, and would have played an important role in the evolution  
87 of hominin cultural technology.

88 Hand grip strength is commonly measured in a clinical or sports medicine context  
89 as an indicator of overall muscle strength [47-51]. Grip strength reflects the gross power  
90 of the hand and has been found to be strongly associated with physical activity [52-55], as  
91 well as anthropometric traits, such as age and sex [56-58], hand length and shape [59, 60],  
92 handedness [61], and body mass index [62-64]. For example, males typically have a  
93 stronger average grip strength than females [56, 65]. In both sexes, hand asymmetry in  
94 grip strength was found, with the dominant hand (defined as the hand used most within  
95 the context of object manipulation) is approximatively 10% stronger than the  
96 non-dominant hand [61], although this difference is more pronounced, and so more a  
97 DA, for right-handed individuals than left-handed [66]. Furthermore, hand size has been  
98 shown to be positively correlated with grip strength for both sexes [67-70]. It was also  
99 found that hand shape influences grip strength [59, 71], such that, for both sexes, people

with bigger hands (i.e., large hand length and width) were significantly stronger than people with smaller hands. Moreover, Carlson [72] proposed that, although variation in hand grip strength primarily reflected differences in soft tissue and skeletal morphology, changes in grip strength across the lifespan were also significantly influenced by neural mechanisms (e.g., central nervous system recruiting motoneurons to mediate the control of coordinated movement). Thus, grip strength can be used as a marker of brain health [72]. Indeed, maximum grip strength provides a discriminating measure of cognitive function, such as how central nervous system disorders (e.g., vascular disorders, structural disorders or degeneration) affect the quality of motor coordination [72]. The rate of decline in cognitive function (e.g., motor and perceptual speed, memory, and spatial functioning) has also been shown to correlate with decline of grip strength, especially towards the end of life [73].

However, most previous studies of grip strength have focused on specific populations [57, 74–76], occupations and activities [51, 52, 54], or sex and age [77–79] with the aim to better understand health, but these same methods may also be useful for understanding the broader scope of form and function from an evolutionary perspective. Although informative, these studies do not fully capture the potential variability in the key factors that can affect grip strength, particularly hand size, shape, and daily use. To broaden our understanding of the link between hand form and function, this study aims to evaluate the variation of grip strength in a heterogeneous and international group of humans adults across the lifespan. We test the potential influence of age, sex, asymmetry in hand dominance and preference (i.e. right- vs. left-hand), hand shape, and lifestyle factors (i.e., occupation, practice of sport and music) on grip strength. In this context, we explore hand asymmetry in grip strength as an indicator of brain/manual lateralization, with hand dominance (i.e., significant difference between the dominant and the non-dominant hand, without taking into account the left-right direction) and DA (i.e., pattern of bilateral variation observed when one side, right or left, is significantly stronger than the other). Based on previous studies, we predict that 1) males will be significantly stronger than females; 2) younger participants will be stronger than the oldest participants; 3) hand asymmetry will be found, with the dominant hand significantly stronger than the non-dominant hand and that this effect will be stronger for right-handed than left-handed individuals indicating DA; 4) participants with wider hands (i.e., hand wider than it is long) will be significantly stronger than those with smaller or longer hands (hand longer than it is wide); and 5) participants that regularly practice sport, music or occupational activities that engage their hands will be stronger than those who do not.

## 2. Materials and Methods

### 2.1. Sample

The participants were visitors to an interactive, three-month public engagement and citizen science collaboration project called Me, Human ([www.mehuman.io/](http://www.mehuman.io/)) hosted by Live Science at the London Science Museum between 02/07/2019 and 31/09/2019. Me, Human consisted of a series of experiments exploring motor-sensory behavioural biases and cognitive ability. Experiments included measures of grip strength, dexterity, cognitive puzzles, and functional brain laterality, in which participants could engage in as many of the experiments as they wanted. Volunteer participants first completed a baseline demographic questionnaire, including date of birth, sex, and handedness for writing (our hand asymmetry indicator), before engaging in the experiment(s). More than 1600 individuals participated in the Me, Human experiments, of which  $n=1286$  took part in the ‘Get a grip’ experiment that measured grip strength and hand size, and collected further information about lifestyle and daily activities using the hands. Within this sample, 719 were classified as ‘adults’ between the ages 17–83 years old because the hand is fully developed (i.e., complete fusion of hand bones) by 17 years of age [80, 81]. The remainder of the sample ( $n=567$ ) were children and adolescents (6–16 year-olds), which were ex-

cluded from this study. Of the total adult sample, 57 participants were removed from the data set due to incomplete data or because they had a recorded hand and/or arm injury within one year of the testing date, making the final sample size  $n=662$ . Of the 662 participants, 89.6% ( $N = 593$ ) self-reported as right-handed, 9.0% ( $N = 60$ ) left-handed, and 1.4% ( $N = 9$ ) as ambidextrous. Participants self-reported as ambidextrous were excluded from subsequent analyses, with the remaining sample containing 653 participants (Table 1; Fig. S1). Our sample was divided into 10 age categories (Table 1) of five-year intervals, excluding the first (17-19 years) and last (60 years and older) age categories.

All participants gave their written informed consent before participating in the study. The study was conducted in accordance with the Declaration of Helsinki, and the protocol was approved by the Department of Psychological Sciences Ethics Committee at Birkbeck (ref: 181996), University of London.

**Table 1.** Sample used in the analyses with details on the number of participants for each sex by age range and self-reported handedness, type of job, and according to thus practicing a musical instrument and sport.

Age (years)	Dominance to write	Total participants		Forceful manual labour		Office job/work		Precision manual work		Playing a musical instrument		Practicing sport	
		M	F	M	F	M	F	M	F	M	F	M	F
17-19	R	25	42	-	-	25	42	-	-	12	19	20	29
	L	3	5	-	-	3	5	-	-	1	3	2	5
20-24	R	43	56	6	4	32	46	5	6	15	27	36	33
	L	3	2	-	1	3	1	-	-	2	1	2	1
25-29	R	21	33	6	5	17	22	1	6	7	9	20	16
	L	3	4	-	-	1	3	2	1	2	1	1	-
30-34	R	21	34	2	-	17	28	2	6	7	10	17	16
	L	3	4	1	1	2	3	-	-	1	-	2	2
35-39	R	22	33	5	5	17	24	-	4	8	8	18	17
	L	4	4	-	-	4	3	-	1	1	-	1	1
40-44	R	28	47	5	2	21	42	2	3	9	13	17	21
	L	3	4	1	1	2	2	-	1	1	2	2	1
45-49	R	30	51	5	3	22	42	4	6	4	12	20	24
	L	-	6	1	-	-	6	-	-	-	1	-	2
50-54	R	23	31	2	-	19	29	2	2	6	11	15	19
	L	4	4	1	-	3	4	-	-	2	1	-	2
55-59	R	2	12	-	-	2	11	-	1	2	3	2	8
	L	1	1	-	-	1	1	-	-	-	1	1	-
60 and +	R	16	23	1	-	14	20	1	3	4	4	6	10
	L	2	-	-	-	2	-	-	-	2	-	2	-
Total		257	396	36	22	207	334	19	40	86	126	184	207

-handed (R), left-handed (L).

## 2.2. Data collection procedure

### 2.2.1. Questionnaire

Participants were asked first if they had a hand or arm injury in the 12 months prior to the test date, and only those participants who answered “no” were allowed to continue the experiment. Participants were then asked several multiple-choice binary questions about their type of occupation, if they regularly played musical instruments (e.g., violin, guitar, piano, saxophone, flute, drums), or engaged in sport using their hands (e.g., rock climbing, bouldering, gymnastics, acrobatics, archery, racket sports, lifting, cricket, golf,

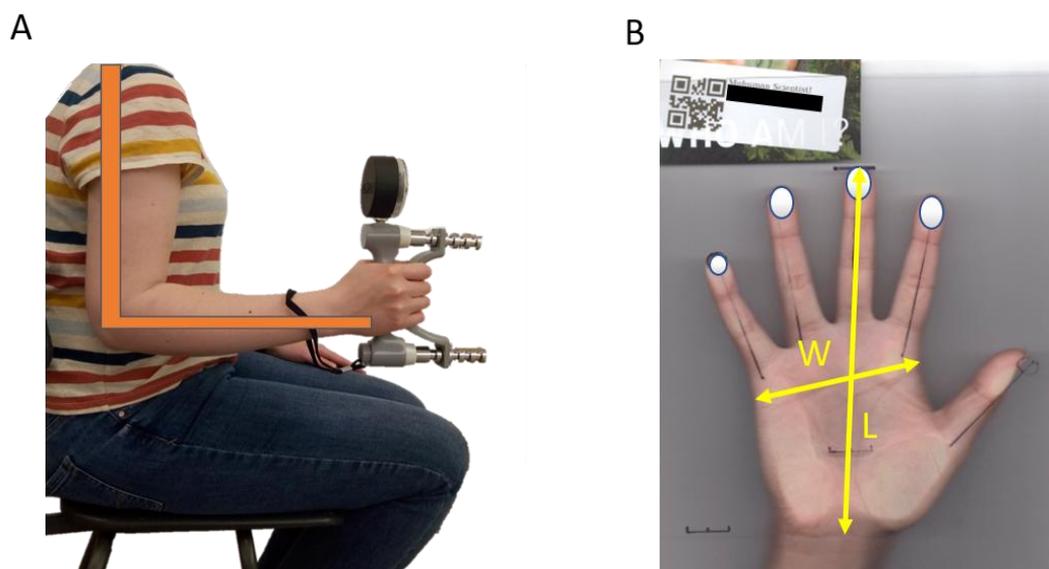
205 hand ball games and bike riding (including commuting to work)). Regarding occupation,  
206 participants could choose between (1) office job or work that requires limited manual  
207 strength (e.g., typing, shop teller); (2) precision manual work (e.g., jeweller, dressmaker,  
208 artist, lab technician); or (3) forceful manual labour (e.g., builder, carpenter, farmer). We  
209 considered as “office job/work” students and stay at home parents, who would use their  
210 hands for a variety of tasks, but not specialised enough to be considered “precision” or  
211 “forceful” manual labourer. From this questionnaire we created three measures: music  
212 with two levels (yes/no), sport with two levels (yes/no), and occupation with three levels  
213 (office/precision/forceful).

#### 214 2.2.2. Grip strength

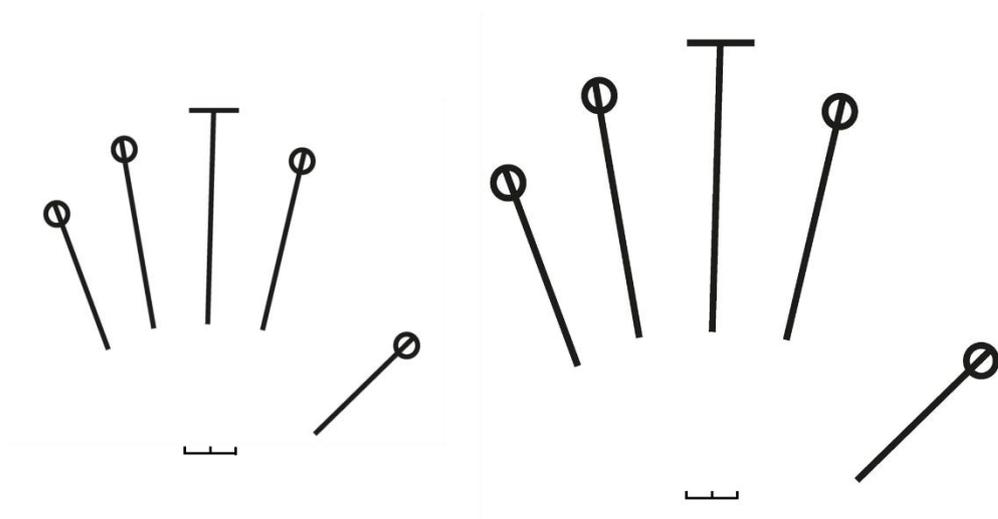
215 Grip strength was measured using a Jamar dynamometer (Sammons Preston, USA)  
216 while the participant was in a seated position. The size of the grip span was adjusted  
217 according to the hand size of the participant, visually evaluated by the experimenter, and  
218 tested by the participant before they did the grip test. The experimenter first demon-  
219 strated the appropriate sitting position and how to hold and use the dynamometer with  
220 the elbow bent at 90 degrees, as recommended by the American Society of Hand Therapy  
221 (ASHT) [82]. A poster demonstrating the appropriate posture and arm/hand position was  
222 also visible to the participant (Figure 1a). The participant was asked to squeeze the dy-  
223 namometer to their maximum ability for two seconds. Grip strength was measured (lbs)  
224 for the left and right hand and after a rest of approximately one minute, each hand was  
225 measured again. An average of both measures for each hand was used in the analysis. All  
226 staff and volunteers of the Me, Human project were trained to measure grip strength  
227 with the same protocol to limit measurement error.

#### 228 2.2.3. Hand size and shape

229 We measured hand size and shape from scans using a flatbed scanner (Epson Per-  
230 fection V39). Participants were asked to place each hand palm side down, lining up their  
231 fingers to fit within an outline drawn on a transparent plastic sheet and keeping the fin-  
232 gers and palm flat (Figure 1b). Two differently sized outline transparencies for interme-  
233 diate and large hands were available to allow a participant to best align their hand in a  
234 standardized manner (Figure 2). A 2 cm scale was included in each transparent plastic  
235 sheet to facilitate accurate measures of hand size from the scans. Hand size and shape  
236 were measured from each scan using freeware tpsDig2 software version 2.31  
237 (<http://www.sbmorphometrics.org/soft-dataacq.html>) [83]. The hand width (W) was  
238 measured from the radial side of the second metacarpal joint to the ulnar side of the fifth  
239 metacarpal joint and hand length (L) from midline of the distal wrist crease to the tip of  
240 the middle finger (Figure 2b), following [59]. A ratio of hand width to length (W/L) was  
241 used as an indicator of hand shape such as in [59] We hands with a ratio > 0.5 as ‘wide’  
242 hands and hands with a ratio < 0.5 as ‘long’ hands. To correct the potential effect of hand  
243 size on grip strength,  $W \cdot L$  was used as an estimate of hand area to quantify relative grip  
244 strength (i.e., grip strength/hand area). All measurements were taken by one researcher  
245 (KT) and to test interobserver error, 20% of both right and left hands ( $n=266$ ) were  
246 measured by a second researcher (AB). An intraclass correlation coefficient (ICC) was  
247 used to test for interobserver reliability in R (R Core Team, 2020) with the “irr” package  
248 [84]. Both measurements of right and left hands were consistent between the two ob-  
249 servers (ICC = 0.981,  $p < 0.0001$ ), indicating an excellent reproducibility and repeatability  
250 of the measurements. Therefore, we only used the measurements of the first researcher  
251 for all subsequent analyses.



**Figure 1.** Appropriate posture and arm/hand position for the grip strength on the poster showed to participant (A) and the measurements taken on hand scans (B). W = hand width, L = hand length.



**Figure 2.** The two different size of outline transparencies (intermediate to the left and for large hands to the right) used on the flatbed scanner to allow participant to best align their hand in a standardized manner. The scale of 2 cm was placed in the middle of the palm.

### 2.3. Statistical analyses

Shapiro-Wilk Normality tests ( $p > 0.05$ ) revealed all data were normally distributed. We used an ANOVA to test our predictions that males would be stronger than females and the dominant hand (defined here as the hand used to write) would be significantly stronger than the non-dominant hand (dominant hand asymmetry) using, first, absolute grip strength and, second, relative grip strength (i.e., grip strength/hand area). A Levene's test was performed to test the homogeneity of variance between males and females and for both hands. An ANOVA was also used to assess the difference in absolute grip strength between both hands across age categories within (1) males, (2) females, and (3) right and left-handers (sexes pooled) (DA).

Next, we fitted four linear multiple regressions to predict the four outcome measures of: 1) male dominant hand, 2) male non-dominant hand, 3) female dominant hand,

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4) female non-dominant hand. Our predictor variables were age, occupation, hand shape, hand preference, playing music, and playing sport. These six predictor variables were considered as fixed effects and grip strength was considered a random effect. The function “predictorEffects” from the package “effect” [85] was used to graphically represent the model effects. An ANOVA was performed for each model to statistically test the effect of the predictor variables on grip strength. Tukey corrections were used for post-hoc analyses. All tests were performed with R 3.6.3 [86] with level of significance set at  $p \leq 0.05$ .

### 3. Results

First, we tested whether there were differences in grip strength between males and females and, for each sex, between both hands to test the effect of hand dominance asymmetry using ANOVAs. We investigated potential differences in both absolute grip strength and relative grip strength, in which hand area was used as proxy for size. Results of the ANOVA showed that males were significantly stronger than females for both absolute grip strength ( $F(1, 1303) = 1782.72, p < 0.0001, \eta^2 = 0.58$ ) (Table 2 and Figure 3) and relative grip strength ( $F(1, 1303) = 820.36, p < 0.0001, \eta^2 = 0.39$ ), and both males and females were significantly stronger with their dominant hand than their non-dominant hand (grip strength,  $F(1, 1303) = 16.16, p < 0.0001, \eta^2 = 0.005$ ; relative grip strength,  $F(1, 1303) = 16.88, p < 0.0001, \eta^2 = 0.007$ ), indicating dominant hand asymmetry. When looking at the strength of this asymmetry, we found a mean difference in grip strength between the two hands of 5.5% for males, ranging between 1.9% (35-39 years old) and 11.4% (55-59 years old), and 4.2% for females, ranging between 0.4% (40-44 years old) and 8.8% (60 years and older) (Table S1). As a result, we searched for possible differences in the strength of hand dominance asymmetry across ages, and we found no significant interaction between age category and grip strength difference between dominant and non-dominant hands for either males ( $F(9, 494) = 0.134, p > 0.05$ ) or females ( $F(9, 772) = 0.207, p > 0.05$ ) (Table S1). We tested for the homogeneity of variance between males and females, and for both hands, males showed significantly more variation than females across all age categories ( $F(3, 1302) = 41.822, p < 0.0001, \eta^2 = 0.09$ ).

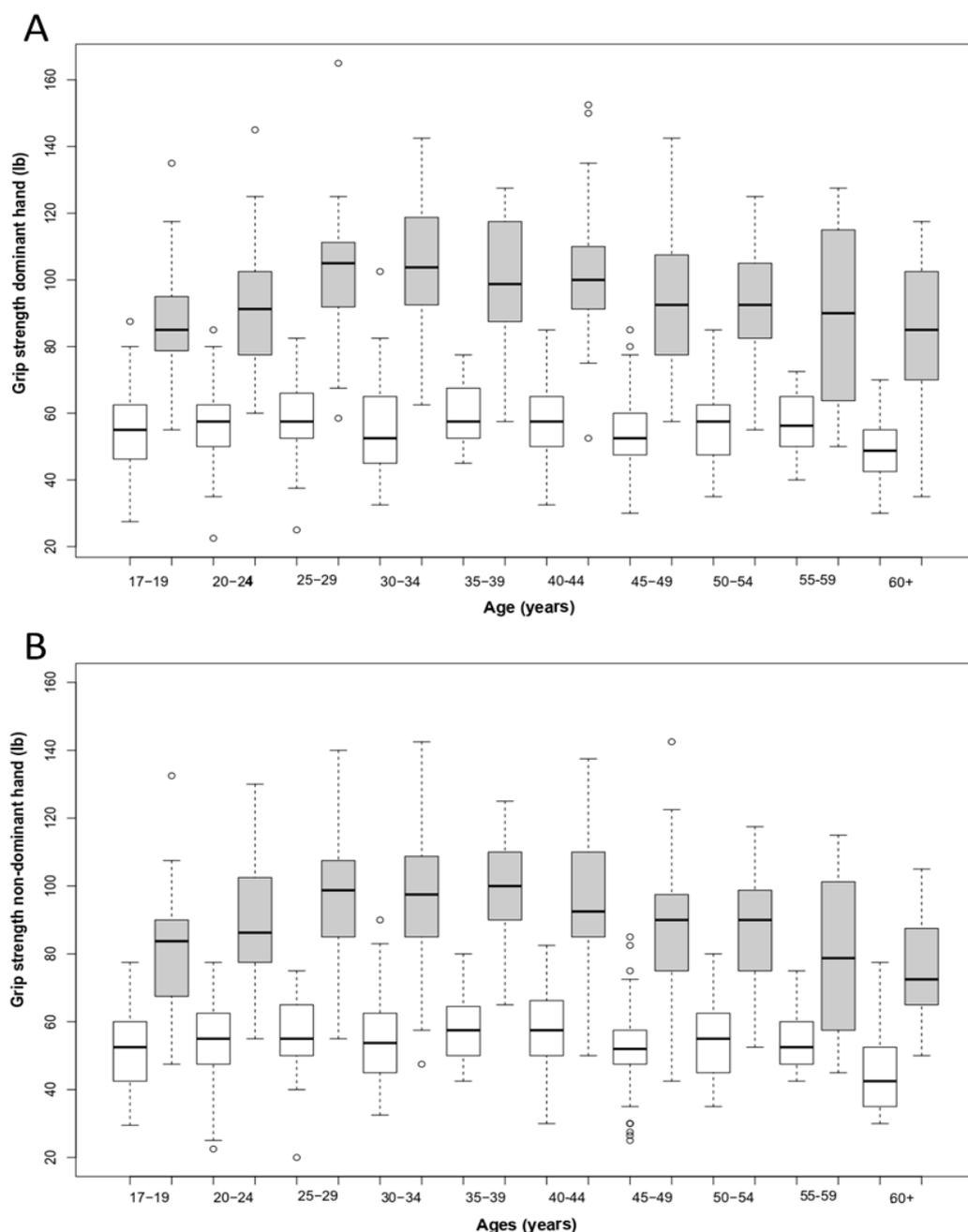
We then tested differences in handedness, as an indicator of DA, in absolute grip strength (sexes pooled). There were no significant differences in grip strength between right- and left-handed participants for either hand ( $F(1, 1302) = 0.180, p > 0.05$ ), although left-handed individuals had, on average, a higher hand dominance asymmetry with a stronger difference in grip strength between their dominant and non-dominant hand (males = 8.2%, females = 6.4%) compared to right-handed individuals (males = 5.2%, females = 4.0%). No significant interaction was found between age category, handedness and grip strength difference between dominant and non-dominant hands ( $F(9, 1266) = 0.028, p > 0.05$ ) (Table S1).

**Table 2.** Summary statistics for grip strength (lbs) of the dominant and non-dominant hand according to the sex and the age categories.

Age (years)	Sex	Dominant hand		Non-dominant hand	
		Mean	SD	Mean	SD
17-19	M	87.9	17.7	81.1	17.8
	F	55.5	13	51.8	12.5
20-24	M	93.1	18.9	88.9	18.1
	F	56.3	11.7	54.2	11.7
25-29	M	101	22.3	96	19.2
	F	59.4	11.6	55.6	11.6
30-34	M	106	19	96.7	20.5

	F	56.8	15.3	54.2	13.6
35-39	M	99.8	18.1	97.9	17.9
	F	59.8	9.36	57.7	10.3
40-44	M	102	21.1	96.7	19.1
	F	57.7	11.5	57.5	12.1
45-49	M	93.1	21	87.9	21.1
	F	54.7	12.1	52.3	12.4
50-54	M	92.3	17.7	87.8	17
	F	55.4	12.3	54.2	11.2
55-59	M	102	25	90.8	22.7
	F	56.9	10.6	54.5	8.95
60 and +	M	81.4	22.2	75.1	17.1
	F	48.4	9.31	44.1	11

Males (M), Females (F), Standard deviation of the mean (SD)



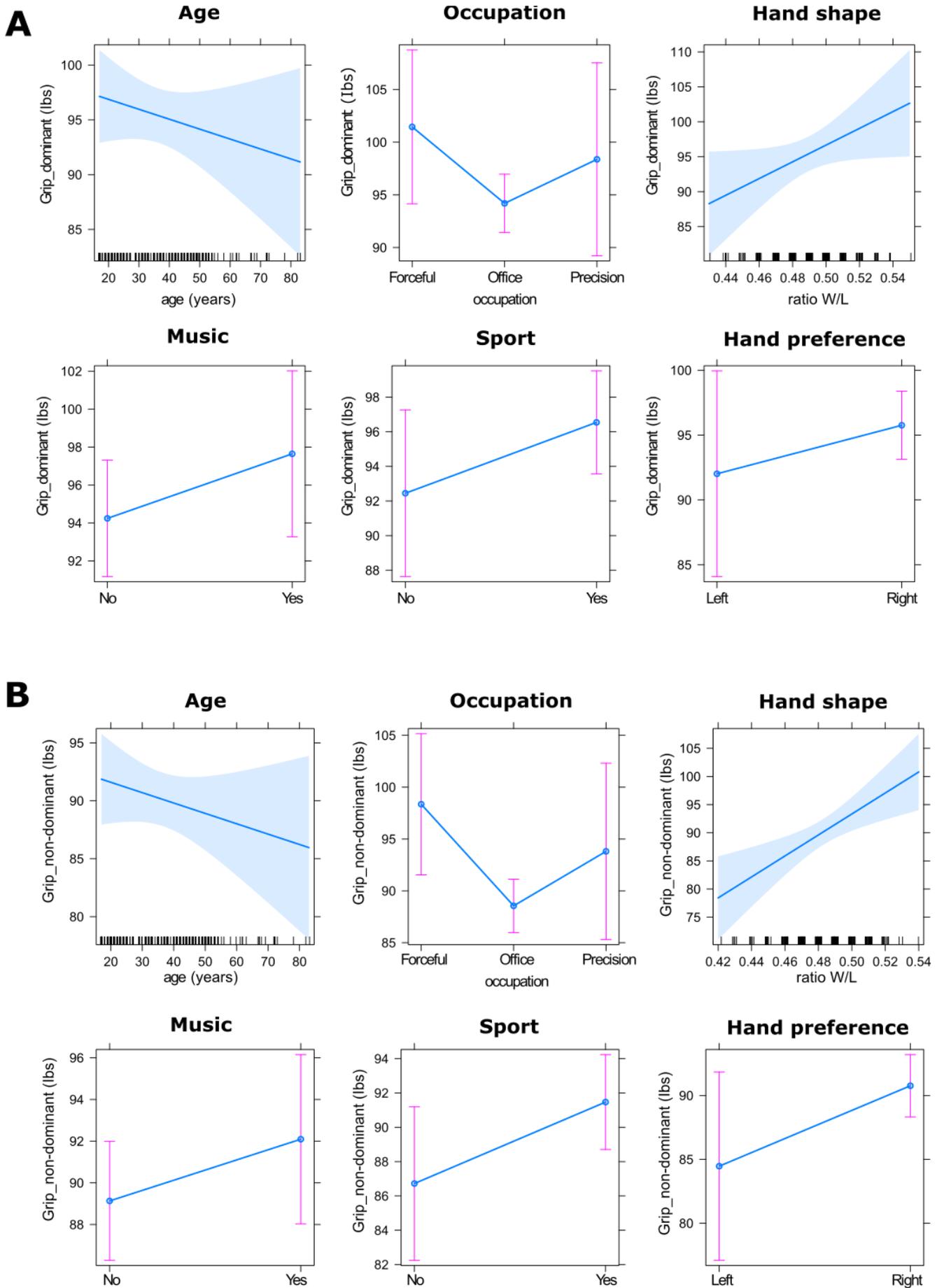
**Figure 3.** Grip strength (lbs) performance in males (grey) and females (white) for the dominant hand (A) and the non-dominant hand (B). The boxplots show medians (solid line) and interquartile ranges of grip strength according to age groups. The dotted lines indicate variability outside the upper and lower quartiles, except for "outliers" (dots).

We tested for effect of the predictor variables (age, occupation, hand shape, hand preference, playing music, and playing sport) on grip strength using Fitting linear models. Results revealed that male grip strength of the dominant hand showed a trend towards being affected by hand shape (Figure 4) but not significantly so ( $F(1, 249)= 3.562$ ,  $p = 0.06$ ). However, for the non-dominant hand, male grip strength was significantly affected by hand shape ( $F(1,249)= 9.489$ ,  $p < 0.01$ ,  $\eta^2= 0.034$ ), such that males with wider hands were stronger than males with longer hands (Figure 4). Grip strength for the non-dominant hand was also significantly affected by occupation ( $F(2, 249)= 5.278$ ,  $p < 0.01$ ,  $\eta^2= 0.038$ ), such that males doing forceful manual labour were significantly stronger

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than males doing an office job (post-hoc analyses,  $p < 0.05$ ), and males who practiced sports ( $F(1, 249) = 4.125$ ,  $p < 0.05$ ,  $\eta^2 = 0.015$ ), were stronger than males who did not (Figure 4).



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**Figure 4.** Predictor effect plots for the fitting linear models in males for the dominant hand (A) and non-dominant hand (B). On the age and hand shape graphics, the blue shaded area is a pointwise confidence band for the fitted values at a level of confidence of 95%. The rug plots at the bottom of the graphs shows the location of the age values and the ratio W/L values. On the other graphics, the pink bars represent the confidence intervals at a level of 95%.

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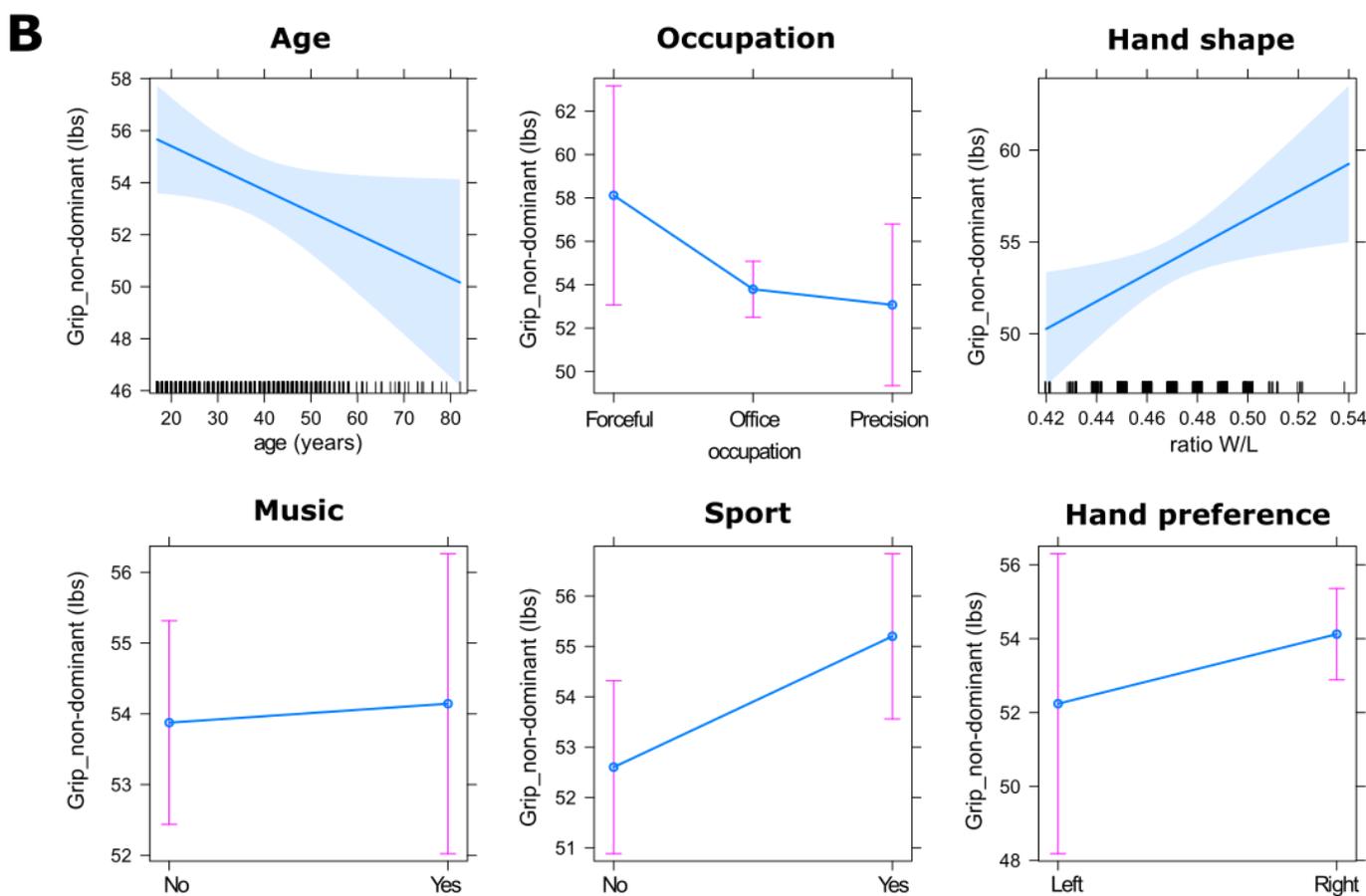
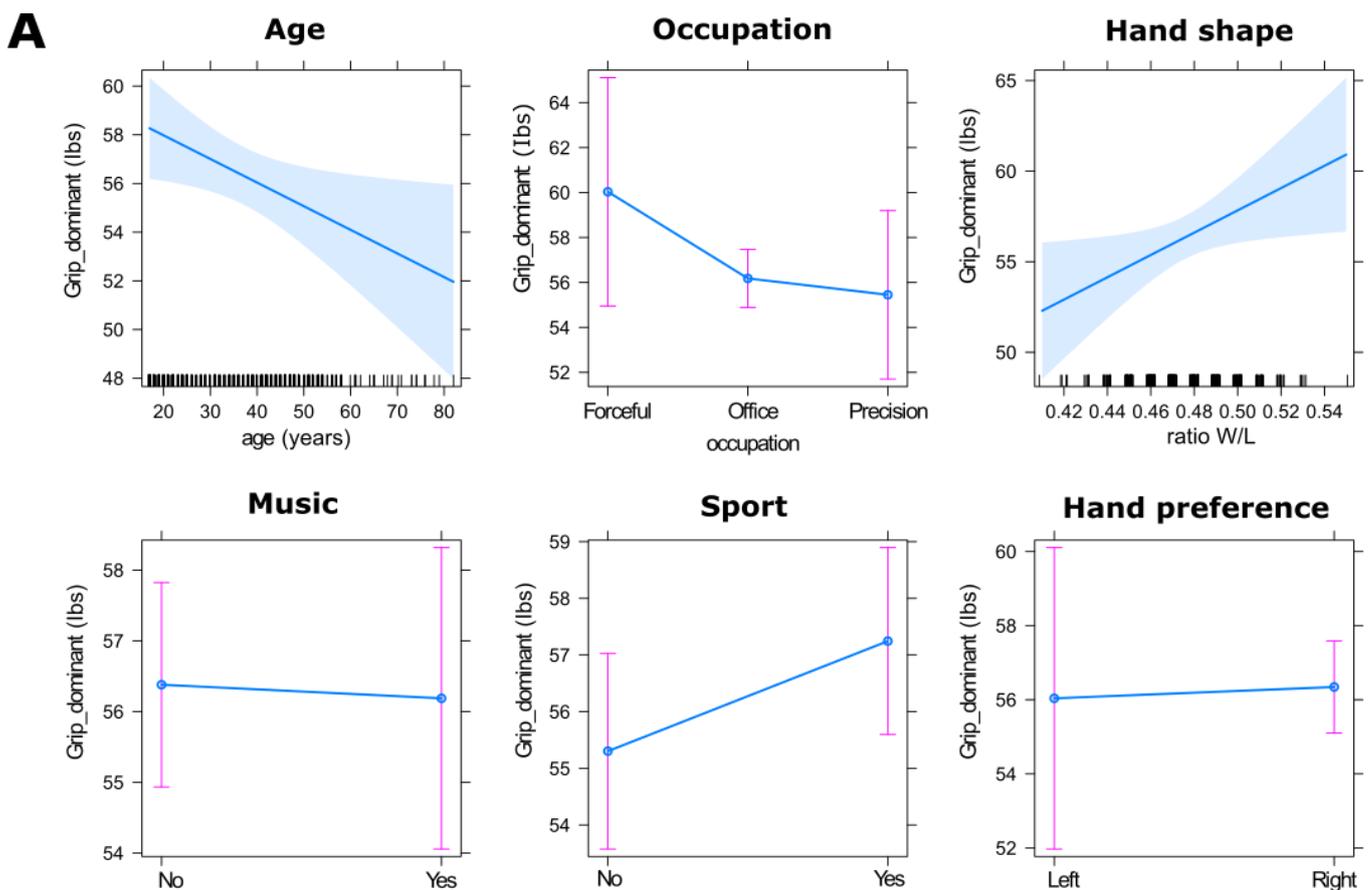
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For females, linear modelling revealed that grip strength of the dominant hand was significantly affected by hand shape ( $F(1, 388) = 4.733$ ,  $p < 0.05$ ,  $\eta^2 = 0.017$ ), with females having wider hands being stronger than females with longer hands, and by age ( $F(1, 388) = 5.369$ ,  $p < 0.05$ ,  $\eta^2 = 0.013$ ), such that younger females ( $\sim < 30$  age) were significantly stronger than older females ( $\sim > 50$  age; Figure 5). For the non-dominant hand, female grip strength was also significantly affected by hand shape ( $F(1, 388) = 5.891$ ,  $p < 0.02$ ,  $\eta^2 = 0.014$ ) and by age ( $F(1, 388) = 4.463$ ,  $p < 0.05$ ,  $\eta^2 = 0.011$ ), following the same pattern as the dominant hand. However, females practicing hand sports also had a significantly stronger non-dominant hand ( $F(1, 388) = 4.858$ ,  $p < 0.05$ ,  $\eta^2 = 0.012$ ) than females who did not (Figure 5). Given the effect of age on female grip strength, we tested which factors potentially interacted with age. Linear modelling revealed that for both hands, a significant interaction was found for grip strength between age (continuous) and hand shape (dominant hand,  $F(1, 388) = 4.123$ ,  $p < 0.05$ ,  $\eta^2 = 0.010$ ; non-dominant hand,  $F(1, 388) = 6.092$ ,  $p < 0.05$ ,  $\eta^2 = 0.015$ ). Moreover, while younger females ( $\sim < 30$  age) showed similar grip strength regardless of differences in hand shape, older females ( $\sim > 50$  age) with wider hands had stronger than older females with longer hands (Fig. S2).



**Figure 5.** Predictor effect plots for the fitting linear models in females for the dominant hand (A) and non-dominant hand (B). On the age and hand shape graphics, the blue shaded area is a pointwise confidence band for the fitted values at a level of confidence of 95%. The rug plots at the bottom of the graphs shows the location of the age values and the ratio W/L values. On the other graphics, the pink bars represent the confidence intervals at a level of 95%.

#### 4. Discussion

This study investigated different factors that predict hand grip strength in a large, heterogenous adult human sample. While some of the results support findings of previous studies, our study sheds new light on the variability in grip strength relative to sex, age, hand shape, hand dominance asymmetry (i.e., laterality) and daily hand use. We discuss these results below and their implications for understanding the evolution of the human hand.

Consistent with findings from previous studies [78, 79] and our predictions, we found that males were stronger than females. However, our study also investigated relative grip strength and found that males remained significantly stronger than females even when accounting for variation in hand size. This result is consistent with Leyk et al. [62], who showed that untrained males were, on average, stronger than highly trained female athletes. We also found a significant effect of hand dominance asymmetry, in which the dominant hand was significantly stronger than the non-dominant hand in both sexes, with an average difference being slightly higher for males (5.5%) than for females (4.2%) across all age categories. These mean differences were lower than the reported average of 10% higher grip strength for the dominant hand compared with the non-dominant hand for both sexes reported in previous studies [61, 74, 87]. Interestingly, we found that the difference in hand strength between the hands seemed to vary with age in both sexes (Table S1), but the differences were not significant. This result could be due to the uneven distributions of the sample across the age categories (e.g., more participants in the 20-24 age category than the 60 years and older), but also requires further investigation through a larger study to examine this general premise of 10% difference in grip strength between the dominant and nondominant hand by examining different age categories.

We also found that grip strength of both hands decreased significantly with age in females but not in males, which partially supported our expectations. Previous studies have shown an effect of age on grip strength for both sexes [77-79]. The non-significant effect of age for both hands in males in our study may reflect the greater variability in grip strength (Figure 3). Middle-aged participants (ages 35-39 for males and 40-44 for females) showed more hand symmetry with limited differences in grip strength between both hands, while younger and older individuals showed greater asymmetry in hand dominance. Although previous studies have shown that laterality decreased with age [88], this was not the case for grip strength in our male sample. The dominant hand was always significantly stronger than the non-dominant hand for both sexes, even for participants in older age categories (Table S1). One reason why this might be the case is that previous studies have typically only assessed differences in the average grip strength across all ages [61, 89, 90], and thus we demonstrate for the first time, to our knowledge, important grip strength variation at specific life stages for both sexes.

Our results showed that grip strength in our sample was not an indicator of handedness. We did not find a significant effect of self-reported hand preference, although left-handed participants tended to show a larger difference of grip strength between the dominant and non-dominant hand (males = 8.2%, females = 6.4%) compared with right-handed participants (males = 5.2%, females = 4.0%; Table S1). This result did not support our expectation or previous research showing more symmetry in grip strength between the hands in left-handed compared to right-handed people showing more DA [66, 75, 91]. However, previous work has yielded mixed results, with some studies finding left-handed individuals had a relatively stronger non-dominant hand [92, 93]. The

408 results of our study (and previous research) may be biased by differences in sample size  
409 (n=60 left-handed vs. n=594 right-handed participants), given the much lower proportion  
410 of left-handed individuals across human populations [16-19]. Left-handed individuals  
411 may also be expected to show more symmetry in grip strength between both hands (i.e., a  
412 relatively stronger right hand), because the world is more adapted for right-handed in-  
413 dividuals. Thus, our results are somewhat unexpected and require further investigation  
414 through a larger study of left-handed people across their lifespan to better understand  
415 the potential differences in grip strength between right- and left-handed individuals.

416 We found that grip strength of the non-dominant hand was also significantly in-  
417 fluenced by hand shape in both males and females, and in both hands for females only.  
418 Participants with wider hands were stronger than participants with longer hands, which  
419 is consistent with previous studies that reported that people with wider hands tend to  
420 have greater muscular strength (when controlling for height) [67-69]. The fact that hand  
421 shape did not significantly influence grip strength of the dominant hand in males may  
422 also reflect the greater variability in grip strength for males compared with females. In-  
423 terestingly, we found that the effect of hand shape is stronger for older females (~ > 50  
424 age) than younger females (~ < 30 age), with older females with wider hands being  
425 stronger than older females with longer hands. This variation by age may reflect younger  
426 females being, on average, more active than older females and potentially using both  
427 hands more frequently and/or with more muscular force during a variety of daily activi-  
428 ties. In contrast, older females are more likely to develop osteoarthritis within the hand  
429 [94, 95], and patients with this disease show weaker grip strength in the affected hand  
430 than healthy individuals [96]. As humans with longer digits appear to have relatively  
431 larger articular areas [45], females with longer digits could be less susceptible to os-  
432 teoarthritis, and thus could show less reduction of hand strength than females with  
433 shorter fingers. Additional research is needed to investigate the potential effect of hand  
434 shape on grip strength in older females and the potential clinical implications.

435 Variation in hand dominance asymmetry and hand function was observed accord-  
436 ing to the lifestyle factors (i.e., occupation, practice of sport and music). We found that  
437 type of occupation had a significant effect on grip strength for males but not for females,  
438 which is consistent with the findings of Hossain et al. [76]. The female result could be  
439 explained by the relatively fewer number of females participants doing, for example,  
440 forceful manual labour (22 females against 36 males), which potentially can affect the  
441 analysis. In particular, we found that males engaging in forceful manual work were sig-  
442 nificantly stronger than those doing 'office work'. This result supports that of previous  
443 studies [52, 54, but see 76]. However, we found an effect only for the non-dominant hand.  
444 This result likely reflects the fact that manual labour occupations often involve using both  
445 hands more forcefully and frequently than office work does, thus increasing muscle  
446 strength [54]. Indeed, middle-aged males doing forceful manual work showed greater  
447 similarities in grip strength between the dominant and non-dominant hand compared to  
448 office workers (Table S1). We found similar results for the practice of manual sports,  
449 which significantly affected grip strength in the non-dominant hand for both sexes, while  
450 there was no effect of practicing a musical instrument. Together, these results suggest  
451 that middle-aged individuals practicing regular manual activities that require the force-  
452 ful use of both hands have less strength difference between the two hands (i.e., greater  
453 symmetry), while office and precision workers, who are doing more fine motor ma-  
454 nipulation and using general tools more often with their dominant hand, may have a  
455 greater asymmetry in grip strength between the two hands.

456 Our findings have interesting implications for the study of human evolution. Both  
457 hands are important for modern human daily activities, however experimental studies  
458 have demonstrated the importance of having two strong upper limbs, and hands in par-  
459 ticular, for prehistoric activities, such as tool production/use behaviours [1, 9-11, 97-99],  
460 carrying [100], hunting, picking fruit, or dismembering an animal carcass [101]. For some

461 hominins, powerful grip strength in both hands would be critical for climbing as well  
462 [102-104]. Thus, there would likely be negative selection for having weak hand grip  
463 strength throughout hominin evolution [105-107]. We found a significant influence of  
464 hand shape on grip strength such that individuals with wider hands were significantly  
465 stronger than those with longer hands. If this relationship held true in the past, there may  
466 have been increased selection for relatively shorter fingers and proportionally wider  
467 hands. Indeed, fossil evidence demonstrates that hand proportions have changed  
468 throughout human evolution [e.g., 103, 108] and that these changes likely improved  
469 dexterity [109-111] and potentially grip strength [112, 113].

470 In modern hunter-gatherer populations, greater grip strength in the dominant hand  
471 is associated with better hunting outcomes among Hadza males, but not for Yali males  
472 [114]. It would be interesting to also measure the strength of the non-dominant hand in  
473 hunter-gatherer populations to test the hypothesis of the importance of high grip  
474 strength in both hands for hunting and other manual activities. An increase of sedentism  
475 among recent (non-foraging) humans correlates with a decrease in cortical bone strength  
476 [reviewed in 115] and reduction in trabecular bone density [116-118] throughout the  
477 skeleton, including the hands [116, 1117]. Given bone's ability to reflect variation in  
478 loading throughout life via (re-)modelling, this research suggests that recent, more sed-  
479 entary humans have a reduced level of forceful manual activity compared with that of  
480 hunter-gatherers and/or that increased sedentism has resulted in systemic changes to  
481 bone structure throughout the skeleton.

482 It is possible that the population-level hand asymmetry or bias well-documented in  
483 modern human populations, inferred in Neandertals [28, 36] and potentially earlier *Homo*  
484 species [119], is related to advances in technological and cultural innovations [28, 120] or,  
485 more generally, to task complexity [24, 119, 121]. In turn, more frequent use of a domi-  
486 nant hand, rather than both hands, for diverse activities could have favoured an increase  
487 of hemispheric specialisation and vice versa. However, early hominins (e.g., *Australo-*  
488 *pithecus*, *Homo habilis*), and particularly those that likely still used their hands for loco-  
489 motion, may have been under stronger selection for bimanual manipulative ability and  
490 grip strength, such as in extant great apes [119]. Thus, it is important to investigate both  
491 hands in studies of grip strength and laterality to provide a broader evolutionary under-  
492 standing. In their research on lateralisation through prehistorical tools, Steele and Uo-  
493 mini [122] also highlighted the importance of studying the roles of both hands during  
494 bimanual activities (i.e., what they call a "Complementary Role Differentiation" model).  
495 We also require a greater appreciation of the effect of lateralization of specific behaviours  
496 on upper limb and hand bone morphology [123-127] to better understand the evolution  
497 of human dexterity related to strength of laterality.

498 There are some limitations of this study that should be considered. As these data  
499 were collected as part of the larger Me, Human project and within the rules of the Live  
500 Science scheme of London Science Museum, we were limited to a specific amount of time  
501 in which we could keep participants at any one experimental station. As a result, we were  
502 not able to collect more detailed data on daily hand use (e.g., number of musical instru-  
503 ments or specific sports played and for how long). Moreover, although participants were  
504 not selected and came voluntarily to the Live Science experiment, potential selection bias  
505 could be present and may have affected our results. First, we had more young partici-  
506 pants and parents accompanying their children compared to participants from 55 years  
507 and older. Moreover, the experiments took place during the summer months when the  
508 museum was more likely to attract international visitors. We did not record the ethnicity  
509 of the participants while previous, more targeted, studies have shown variation in grip  
510 strength across different populations [57, 74-76]. Future research on large and more di-  
511 verse groups of humans providing greater detail on ethnicity and specific hand use ac-  
512 tivities may provide a more nuanced understanding of the links between performance

(e.g., grip strength), hand asymmetry, and hand shape or how variation in hand shape and size impacts dexterity.

## 5. Conclusions

To conclude, we found that adult human grip strength was influenced by a variety of factors, including age, sex, hand shape, and hand dominance asymmetry (i.e., laterality), consistent with previous studies. We also demonstrate for the first time that (1) grip strength varies throughout the lifespan, with more pronounced differences at specific life stages and (2) that the practice of different manual activities through occupation and sport also influence grip strength, particularly in males. These results emphasize the importance of physical manual activities for the attenuation of age-related grip strength loss in a clinical context. These findings may also inform ergonomic research on modern anthropotechnical systems that rely on grip strength data [128-129]. Our results highlight the importance of studying the grip strength of both hands, rather than just the dominant hand, in relation to the above factors to better understand the link between form and function of the hand, in both modern populations and in our evolutionary past.

**Supplementary Materials:** The following are available online at [www.mdpi.com/xxx/s1](http://www.mdpi.com/xxx/s1), Figure S1: Distribution of participants used in the analyses according to ages groups and with right-handed (R) and left-handed (L) participants, Figure S2: Predictor effect plots for the fitting linear models of the interaction between age and hand shape for grip strength in female, for the dominant hand (A) and the non-dominant hand (B), Table S1: Details of the difference in percentage between hand grip strength in dominant and non-dominant hands for each sex (M = males; F = females) and ages groups, according to right and left-handers, practicing of sport and the different occupations.

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