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Are right- and left-handedness relevant as general categories in a non-industrialized country?

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Abstract Whether right- and left-handedness are defined as a function of individual tasks or represent general categories across tasks has been long debated. However, the literature on handedness primarily concerns industrialized societies in which manual work has been extensively automated, and the majority of individuals in those countries do not use their arms and hands intensively for highly specialized tasks on an everyday basis. Thus, the question remains whether results from those countries regarding handedness are transferable to countries where the majority of individuals are still exploiting their lateralized skills. Here, we sampled 506 individuals from 143 locations on the islands of Flores and Adonara, Indonesia, to assess their hand preference for and hand performance on several tasks in order to evaluate, in a non-industrialized country, the level of manual specialization and the relevance of right- or left-handedness as general categories. Generalized-declared handedness was consistent with task-declared handedness across 10 specific tasks and with a measure of strength and a measure of skilfulness, suggesting that general handedness is a valid concept. This hand specialization for tasks is discussed in the context of intense and daily tool use in this agricultural society.

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Introduction

Manual specialization, when the same hand is used for different unimanual tasks, describes handedness at the individual level (Marchant and McGrew 2013). When manual specialization extends to most tasks, an individual is either right- or left-handed, and a generalized handedness is a meaningful concept. When an individual uses one hand for a task and the other hand for another task (referred to as ambidexterity across tasks, or ambilaterality), the concept of generalized handedness weakens. There is an abundance of literature concerning handedness in contemporary humans (McManus 1996; Llaurens et al. 2009), and two contrasting results are emerging.

First, there are no two clear categories such as left- and right-handers: for a given manual action, each individual shows a preference for the use of one hand, and it is not always the same hand for two different actions (Salmaso and Longoni 1985). This suggests that right- or left-handers are not general categories, but rather are defined as a function of the tasks. This justifies the use of continuous index across various tasks to quantitatively measure handedness, such as the classical Edinburgh Handedness Inventory (Oldfield 1971). However, much of the research is concerned primarily with industrialized populations (Marchant et al. 1995; Cavanagh et al. 2016). This is a pivotal point, as manual work, particularly in agriculture, has been extensively automated in industrialized countries. There are still some specific professional activities requiring high manual specialization, such as surgery, butchery, stone-masonry, hairdressing, some sports, and others. However, the majority of individuals in those countries, comparatively to non-industrialized countries, are probably not using their arms and hands intensively on highly specialized tasks on an everyday basis (usage of keys, mouse, comb, airdryer, phone etc. does not require a very high and intense manual specialization). This general decrease of specialized and demanding manual tasks in the daily life of modern societies probably explains the secular decline of handgrip strength, and more generally of muscular strength components, observed during the last century in e.g. US, Canada, Denmark, and Spain (Malina 2004; Silverman 2011; Moliner-Urdiales et al. 2010).

Second, when the tasks considered are highly skilled and complex, and the individuals tested are specialized in these tasks, there is a very strong correlation between the different tasks (Bryden 1977; Wood and Aggleton 1989; Marchant and McGrew 1998), suggesting right- and left-handedness are useful categories in this context. Interestingly, when asked whether they consider themselves right- or left-handed, many people from western countries respond according to the hand they use to write, as writing and related activities are probably now the most common uni-manual task considered as skilled and complex.

Thus the question remains on the level of hand specialisation in non-industrial countries. If mechanisation, by massively decreasing the need for intense manual work, has decreased manual specialisation, then a higher level of hand specialisation is expected on those countries not affected by the process of extended mechanisation. On the opposite, if mechanisation does not affect the level of hand specialisation, no difference are expected when comparing industrialised and non-industrialized countries. Comparison with studies measuring handedness in traditional or non-industrialized society is not straightforward, as the various measures of handedness developed in modern countries are not always useful for a cross cultural analysis. Questionnaires are often unsuitable (such as the classical Edinburgh Handedness Inventory which considers non-universal tasks such as tooth-brushing, holding a golf club, or using a broom, see Oldfield 1971), unreliable as indicators, and/or biased toward Western cultural frameworks (Marchant et al. 1995; Steele and Uomini 2005; Cochet and Byrne 2013). Additionally, to our knowledge, only seven publications on handedness from traditional populations have been published (excluding studies focused on subadults), corresponding to 12 studies on 11 populations (Table 1). Manual specialization could not be evaluated in these populations, because only one task was studied (5 cases), or individual data for more than one task were either not recorded or not reported (6 cases). The only remaining study (Connolly and Bishop

Table 1 Handedness studies from traditional populations. The year when the data was recorded (Year), the sample size (N), whether or not manual specialization and a sex effect could be studied, and an estimated reliability are shown.

Population	Year	*N*	Possibility to study		Reliability	Reference
			Manual specialization	Sex effect		
Inuit	1892–1971	211	No[a]	Yes	Yes[e]	Faurie et al. 2005
Eipo	1974–1980	1295	No[b]	No[c]	Yes[e]	Faurie et al. 2005
G/wi	1976	41	No[a]	No[d]	Yes[e]	Marchant et al. 1995
Yanamomö	1989	31	No[a]	No[d]	Yes[e]	Marchant et al. 1995
Himba	1990	37	No[a]	No[d]	Yes[e]	Marchant et al. 1995
Jimi Valley	1990	185	Yes	Yes	?[f,g]	Connolly and Bishop 1992
Ntumu	1998	246	No[b]	Yes	Yes[h]	Carrière & Raymond, 2000
Dioula	2001	346	No[b]	Yes	Yes[h]	Faurie et al. 2005
Baka	2002	403	No[b]	Yes	Yes[h]	Faurie et al. 2005
Kreyol	2003	333	No[b]	Yes	Yes[h]	Faurie2005
Hadza	2005–2009	42	No[a]	No[d]	Yes[e]	Cavanagh et al. 2016
Eipo	2010	621	No[a]	Yes[c]	?[f]	Schaafsma et al. 2012
Flores	2015–2016	480	Yes	Yes	Yes[h]	This study

[a] Individual data for more than one task were not recorded or reported
[b] Only one task was recorded
[c] Only one sex studied
[d] Sample size too low
[e] Individual laterality recorded from photos or movies made for another purpose
[f] Solicited behaviour with audience
[g] Some tasks culturally meaningless
[h] Interviews partially cross-checked with spontaneous performance

1992), performed in the Western Highlands of Papua New Guinea, used solicited performance from people seated on the ground in the focal centre in the villages, thus in the presence of a social audience (plus a foreign scientist), thus introducing social interferences, as described in the authors: “there was a certain shyness and reluctance made all the more significant by the inevitable crowd of spectators who were almost always in attendance. The spectators were invariably jolly, laughing and joking amongst themselves about the activities and the person performing the tests. One very striking feature was the dramatic change in demeanour when a spectator was persuaded to become a subject; the laughing and interactions with others stopped and an air of focused concentration took over”. In addition, the solicited task performance included manipulation of unknown items, such matches, pencils, spoon, playing cards, etc., thus questioning the ecological validity of the data (Cochet and Byrne 2013). In conclusion, to our knowledge, there are no sufficient published data from which to evaluate the level of manual specialization (within subjects, across tasks) in non-industrialized societies. Thus, the question remains regarding whether the results for handedness from industrialized countries are transferable to populations where the majority of individuals are still exploiting their lateralized skills.

Here, we sampled individuals born on the island of Flores, Indonesia, to assess their hand preference for or hand performance on several tasks to evaluate, in a non-industrialized country, the level of manual specialization and the relevance of right- or left-handedness as general categories.

Materials and methods

Participants

The study was performed in January 2015 and January 2016 on the island of Flores (and the small and adjacent island of Adonara), Indonesia. A total of 143 locations were sampled from most of the regencies (Kabupaten) on the islands. Locally, groups of at least 3 individuals were targeted, often resulting in a larger sample due an unavoidable social snowballing effects. Most of the time the people in groups outside homes were males, and the social snowballing effect concerned mainly males, resulting in a male biased sample. Sampling was performed independently to the proportion of left-hander, although the snowballing effect resulted in a higher proportion of left-handers (left-handers neighbours were sometimes solicited by participants as soon as the purpose of the study was disclosed). These non-randomly sampled participants were kept in the final sample, as no population-level inferences were sought. At the beginning of each interview, the participants were informed of the general aim of the study, the type of data collected and that the data would only be used anonymously for a scientific purpose. A written voluntary agreement was obtained prior data collection. The interviews were conducted in the Bahasa Indonesia language in the presence of one Indonesian researcher. No financial incentive was provided.

Handedness measures

We designated interviewed subjects as focal respondents. They were asked whether they were overall left- or right-handed. These focal individuals also provided hand preference information for their close kin and other family members (reported elsewhere). Next they were asked about their specific hand preference (right, left, both) for ten tasks based on Rife (1940): ball throwing, racquet holding during badminton (a popular game in Indonesia), the use of three distinct large tools (knife/machete, hammer, saw), marble play, writing, and the use of three distinct small tools (spoon, scissors, needle). According to the anatomical and functional analysis by Napier (1956), these tasks are further classified as requiring either a power grip (the object is held as if in a clamp between the flexed fingers and the palm, and counter pressure is applied by the thumb lying more or less in the plane of the palm), corresponding to the first five tasks, or precision grip (the object is pinched between the flexor aspects of the fingers and that of the opposing thumb), corresponding to last five tasks. As handedness measured from questionnaires are known to be not fully correlated with performance (e.g. Raczkowski et al. 1974; Cavill and Bryden 2003), behavioural cross-validation was sought and two measures of hand performance were recorded. The writing-declared handedness was cross-checked by recording the hand used to sign the voluntary agreement sheet: in all cases recorded ($N = 324$), an exact concordance with writing-declared handedness was observed. Handedness could sometime be observed during an unsolicited behaviour (e.g., after the interview an individual resumed his manual work using a tool): in all cases ($N = 14$), an exact concordance with the declared handedness for the corresponding action was observed. Hand-grip strength was measured using a hand dynamometre “Grip–D”, T.K.K 5401 series (Takei Scientific Instrument, Niigata, Japan). The mean of four consecutive grips was recorded for each hand (G_R and G_L), and the relative hand difference was computed as $(G_R - G_L)/(G_R + G_L)$. Which hand (R or L) was used as the starting hand for this measure was recorded as a potential confounding variable. Hand skill was measured using a peg-moving task. The respondents were asked to move the pegs with tweezers, along a line of holes, from the first hole to the next hole one by one until the pegs were moved to the last hole (five steps for each line, three lines concerned, see Fig. S1). This movement was performed with one hand and was repeated 3 times for each hand, alternating between hands. The mean of three trials was computed for each hand (S_R and S_L), and the relative hand difference was computed as $(S_R-S_L)/(S_R + S_L)$. The starting hand was also recorded.

Statistical analyses

The influence of sex and age on handedness was evaluated using logistic regression. The influence of sex, handedness, their interaction, and confounding variables (age, starting hand of the measure) on relative handgrip or relative hand skill was evaluated using linear regression. The concordance of handedness over the tasks was measured and tested using Fleiss's Kappa for categorical data (Fleiss 1971), via the R package irr. The ability of each handedness variable, or of a group of handedness variables, to correctly assign the generalized-declared handedness of an individual was evaluated using linear discriminant analysis. The R package MASS (version 7.3–44) was used, with the option leave-one-out cross-validation, for the results (classes and posterior probabilities). The resulting percentage of correct classification was compared to the percentage obtained under random assignment, i.e. the percentage of the most frequent handedness class (RH, 79.2%). Exact confidence intervals of binomial proportions were computed using the R package binom (version 1.1–1). All analyses were performed using R version 3.3.0.

Results

Sample description

A total of 506 individuals were directly interviewed (focal), corresponding to 145 females and 361 males. Individuals ($N = 26$) not born on Flores or Adonara were removed from the sample, resulting in a final sample of 480 focal individuals (Table S1): 135 females and 345 males. For the age distribution (from 13.3 to 76.4 years old), the mean was 37.3 years (34.8 years for women and 38.4 years for men), the median was 36.0 years (33.6 years for women and 37.3 years for men) and the standard deviation was 13.7 years (13.1 for women and 13.8 for men).

Declared hand preference

A total of 478 individuals declared their general handedness: 101 left-handed (31 females and 70 males) and 377 right-handed (104 females and 273 males), resulting in an overall sample frequency of 21.1% left-handers, see Table 2 (no population inference was possible, due to an over-sampling of left-handers). Generalized-declared handedness was used as a response variable in a binomial regression to assess the influence of sex and age. The males and females did not differ significantly ($P = 0.82$) for the declared hand preferred. Generalized-declared right-handedness was significantly ($P = 0.0082$) associated with older age, with a 0.024 increase of linear unit (i.e., log of odd ratio) for each additional year.

Table 2 Number of individuals reporting hand preference for general handedness and for ten specific tasks

Reported handedness	R	L	%L (sample frequency)
General	377	101	21.1
Specific tasks:			
Throwing	376	98	20.7
Racquet holding	374	99	20.9
Marbles	376	97	20.5
Knife/machete	371	103	21.7
Spoon	380	94	19.8
Hammer	373	101	21.3
Saw	373	101	21.3
Sewing	380	94	19.8
Writing	421	52	11.0
Scissors	378	96	20.2

A total of 480 individuals declared their handedness for up to 10 tasks, resulting in a total of 4737 reports. From these reports, 15 (or 0.32%) were declared as ambidextrous. For any given task, the frequency of ambidextrous reports was between 0 (for 4 tasks) and 0.8%. Due to their low frequency, those ambidextrous reports were further coded as left-handed. Overall, the sample percentage of task-declared left-handedness ranged from 11.0 to 21.7% (Table 2). A total of 472 individuals reported their hand preference for all ten tasks. Concordance over the 10 tasks was significant (Fleiss's Kappa = 0.884, $z = 129$, $P < 10^{-4}$), and was even stronger when writing handedness, which is prone to cultural influences, was omitted (Fleiss's Kappa = 0.935, $z = 122$, $P < 10^{-4}$). Generalized-declared handedness was significantly correlated with each of the 10 tasks-declared handedness (with writing handedness: $r = 0.68$, $P < 10^{-10}$; with all others: $r \geq 0.93$, $P < 10^{-10}$).

To assess the link between general and task-specific handedness, the number of individuals reporting a left hand preference for a given number of specific tasks was computed for both general right- and left-handedness (Table 3). Independence between general and specific hand preference was significantly rejected (Fisher exact test on a contingency table, $P < 10^{-10}$). Only 49 individuals (or 10.4%) declared a left-handed preference for all the specific tasks and general left-handedness. However, when writing handedness was removed, this number rose to 82 (or 17.4%). Overall, 32 individuals (6.8%) declared a hand preference for at least one specific task (writing excluded) that was different from their generalized-declared handedness. The figure dropped to 13 individuals (2.8%) when this discrepancy occurred for at least two specific tasks, and it dropped to 7 individuals (1.5%) for at least three specific tasks. Only 2 individuals (0.4%) declared

Table 3 Number of individuals reporting a left-hand preference for specific tasks (writing handedness excluded) according to generalized-declared handedness

	Generalized-declared handedness	
Number of specific tasks with a left-hand preference	Right-handed	Left-handed
0	356	0
1	10	0
2	4	1
3	0	0
4	1	1
5	1	1
6	0	2
7	0	2
8	0	9
9	0	82

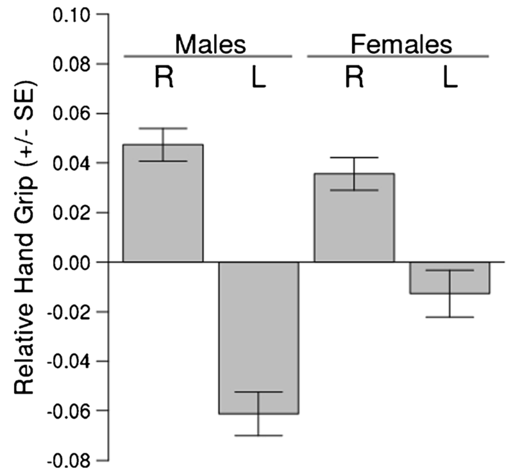

Fig. 1 Fitted relative difference in hand-grip strength according to sex and declared general handedness. Error bars are plus/minus one standard deviation

an equal number of right and left preferences across the specific tasks: one declared general right-handedness and the other declared general left-handedness. If a (arbitrary) criterion of concordant laterality for at least seven of the specific tasks is used to assign handedness, then generalized-declared handedness is consistent with assigned handedness for 98.5% (or 463/470) of the cases, corresponding to 99.5% (370/372) right-handers and 94.9% (93/98) left-handers.

Hand performance

Relative hand grip (RHG) was computed for 469 individuals. RHG was not influenced by age ($P = 0.59$) or whether individuals started using their preferred hand ($P = 0.17$). Sex, generalized-declared handedness and the interaction between the two had a significant effect ($P = 0.0023$, 3.9×10^{-7} and 0.00078, respectively). For both sexes, individuals who declared a right-hand preference had higher hand-grip strength for the right hand (Fig. 1). Individuals who declared a left-hand preference had higher hand-grip strength for the left hand, although this was significant only for males (Fig. 1).

Relative hand skill (RHS) was computed for 457 individuals. RHS was not influenced by age ($P = 0.15$), sex ($P = 0.68$), or by the interaction between generalized-declared handedness and sex ($P = 0.26$). The starting hand had an effect for right handers (RHS was lower when individuals started the peg-moving test using their non-preferred hand, $P = 1.8 \times 10^{-5}$) but not for left-handers ($P = 0.69$). The participants were significantly ($P = 1.9 \times 10^{-11}$) faster on the peg-moving task with their preferred hand than with their non-preferred hand (Fig. 2).

RHG and RHS were negatively correlated (Pearson's correlation = −0.32, $t = -7.2$, df = 451, $P = 2.1 \times 10^{-12}$), thus low values of RHS (skilled right handers) are associated with high values of RHG (strengthful right handers).

Predicting generalized handedness from specific tasks

Each of the 10 specific hand-preference variables was evaluated for its ability to predict declared-generalized handedness above chance level (Table 4). Each of the variables was able to predict at least 97.8% of generalized-declared handedness. The only exception was writing handedness, which predicted only 90.1% of the cases. Taken simultaneously, these 10 specific handedness variables significantly ($P < 10^{-10}$) predicted the general handedness above chance level. Distinguishing tasks requiring either a power grip or a precision grip did not

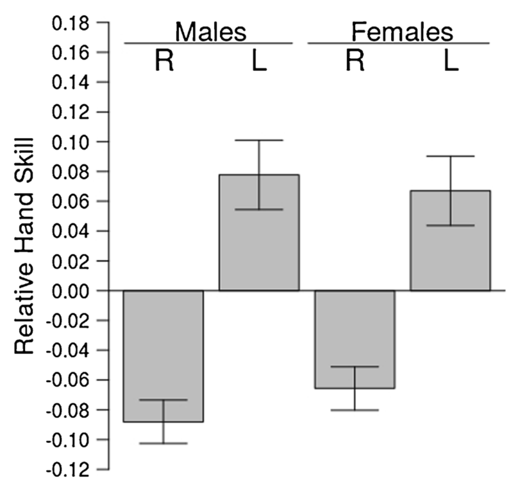

Fig. 2 Fitted relative difference in hand skill according to sex and declared general handedness. Error bars are plus/minus one standard deviation

Table 4 Accuracy of prediction of generalized-declared handedness for each individual handedness variable and for different groupings. CI refers to confidence interval. *P*-values refer to a two-sided exact binomial test of departure from random assignment (baseline of 80.3%). Italic characters indicate significant ($P < 0.05/12 = 0.0042$) values, taking into account multiple testing

Handedness variables	Prediction accuracy (%)	95% CI	*P* value
Power grip tasks			
Throwing	98.4	96.8–99.4	$< 10^{-10}$
Racquet holding	98.7	97.1–99.5	$< 10^{-10}$
Knife/machete	98.7	97.1–99.5	$< 10^{-10}$
Hammer	98.7	97.1–99.5	$< 10^{-10}$
Saw	99.3	98.1–99.9	$< 10^{-10}$
All	99.3	98.1–99.9	$< 10^{-10}$
Precision grip tasks			
Marble play	98.7	97.1–99.5	$< 10^{-10}$
Spoon	98.0	96.2–99.1	$< 10^{-10}$
Sewing	98.8	97.4–99.6	$< 10^{-10}$
Writing	90.1	87.0–92.8	$9.4\ 10^{-10}$
Scissors	97.8	95.9–98.9	$< 10^{-10}$
All	99.1	97.7–99.7	$< 10^{-10}$
All ten tasks	99.1	97.7–99.8	$< 10^{-10}$
Performance			
Hand grip	82.1	78.2–85.5	0.14
Hand skill	83.0	79.2–86.4	0.05
All	86.1	82.6–89.2	$1.9\ 10^{-4}$
All variables	99.1	97.7–99.7	$< 10^{-10}$

significantly improve prediction accuracy. The same procedure was applied for the two measures of relative hand performance (hand grip and hand skill). Neither was able to predict handedness above chance level (Table 4). Taken simultaneously, the 2 performance variables predicted generalized-declared handedness significantly above chance level, although 13.9% individuals were incorrectly assigned. When all the handedness variables (the 10 specific handedness variables, hand grip and hand skill) were considered simultaneously, 99.1% of the individuals were correctly assigned. There were 4 individuals incorrectly assigned (or 0.9%).

Discussion

Handedness is usually viewed from three different aspects: (a) the relative preference for one hand in the execution of various unimanual tasks, (b) the greater skilfulness of one hand in the performance of these tasks, or (c) the greater strength of one hand (Annett 1970; Chau et al. 1997; Peters 1998). These aspects are not exclusive, as higher skilfulness or higher strength explain relative preference, and vice-versa. In the present sample, declared-generalized handedness was overall consistent with task-declared handedness across 10 specific tasks for each individual, and with a measure of strength and a measure of skilfulness, suggesting that general handedness seems to be a valid concept in this population.

When a participant declared their general handedness, right or left, this meant that most daily lateralized tasks were performed with the declared hand. The 10 tasks used were all familiar to the population sampled. Most of them are farmers and use a knife, machete, saw, and hammer frequently; many of the women on Flores are weavers and are familiar with sewing and the use of scissors. Writing is common because education until elementary school is compulsory. In a traditional society based on agriculture, heavy daily tool use is common for both sexes. In addition, as the market economy is limited on Flores, many items such as fishing boats, fences, beams, floorboards, handles, and others are still self-made. During the interviews in the villages, we came across several individuals using a tool (machete, axe, saw, needle, knife, spoon, etc.) while working, cooking or playing. Even though a precise quantification remains to be done, hand specialization is probably an adaptation for this intense and daily tool use, generating a general manual handedness. Additionally, some tasks are probably functionally redundant: it seems logical that if one hand is specialized for cutting, the same hand will also be specialized for sawing. This is because some features, such as muscle strength and mass, developed for a particular specialization could also be mobilized for other similar tasks (Gritsenko et al. 2016). This process may explain why the frequent performance of several different unimanual tasks generates a general hand specialization.

Handedness for the ten tasks was measured using self-reporting, rather than observing hand-use. Observation of unsolicited hand usage is not frequently reported, and generally corresponds to analysis of ethnographic video footages, providing a low sample size (G/wi, Hadza, Himba and Yonamamö, Table 1). Observation of solicited behaviours is also reported (Jimi valley and Eipo, Table 1), although an ecological validation is required, particularly when the solicited behaviour introduces social interferences, as it is often the case in traditional settings. In industrialized countries, questionnaire and performance-based measures of preference on adults are correlated (e.g. agreement of 98% for throwing, Raczkowski et al. 1974) and test-retest questionnaires on e.g. throwing and hammering handedness have produced 100% concordant responses (Coren and Porac 1978). Here, whenever the validity of self-reporting was evaluated by the observation of unsolicited lateralized tasks, observed handedness was 100% consistent. Similarly, declared-generalized handedness was fully concordant with observed handedness in Bobodioulasso area, Burkina Faso (Faurie et al. 2005). Apparently, one's own handedness is confidently known, suggesting that biases are minimal for handedness information collected through self-declarations.

Hand-grip strength is known to decrease with age and to be higher in men than in women (Innes 1999). Interestingly, relative hand grip strength is independent of age and is thus a useful comparative measure of handedness. On Flores, the right-handed participants of both sexes had higher hand-grip strength for the right hand (RHG > 1, Fig. 1). This result seems robust, as it has been reported for other Asian populations (e.g. Singapore: Incel et al. 2002) and western countries (e.g. Germany, Greece, Switzerland: Günther et al. 2008; Mitsionis et al. 2009; Werle et al. 2009). The converse was true for the left-handers, who displayed a higher hand-grip strength for the left hand (RHG < 1, Fig. 1) for both sexes, although the effect for females was smaller. Hand skill, as measured by a peg-moving task, is known to be influenced by age and sex (Grice et al. 2003; Mathiowetz et al. 1985). Here, however, relative hand skill was independent of age and sex and is thus a useful comparative measure of hand skill. When the participants used their preferred hand, they were faster than when they used their non-preferred hand (RHS < 1 for right-handers, and RHS > 1 for left-handers, Fig. 2).

The 12 measures of handedness (10 tasks, RHG, and RHS) were overall consistent with generalized-declared handedness (Table 4), suggesting that ambidexterity is reduced in this population. True ambidexterity (being able to use both hands with equal ease for a specific unimanual task) is uncommon, particularly when the task is specialized. For example, only one ambidextrous pitcher (or hand-switcher) able to perform at a championship level has ever been recorded during 110 years of history of baseball, despite such strategy to have a higher payoff than either only right or left pitchers (Goldstein and Young 1996). Similarly, only 1.5% ambidextrous writers have been recorded from a sample of 1355 individuals from New Zealand (Corballis et al. 2008). In this sample from Flores and Adonara, true ambidexterity was also uncommon: for any given task, its frequency was lower than 0.9%. This low frequency of ambidexterity is consistent with hand specialization in a context of frequent tool usage in order to increase precision and efficiency. Precision is essential when potentially dangerous tools are used, such as a knife, machete, hammer, or saw, in order to reduce self-injury and bodily harm. Ambidexterity across tasks, when an individual uses one hand for a task and the other hand for another task, is more common (referred to as ambilaterality). When only two tasks are considered (writing and throwing), 5.3% of men are mixed-handed according to a large sample ($N > 300{,}000$) of American men aged 20–50 years old (Gilbert and Wysocki 1992). When more tasks are considered, as in the classical Edinburgh Inventory (10 tasks) and its variants (Edlin et al. 2015), this proportion is approximately 30–50%, depending on the criteria used to define mixed-handedness (e.g., Oldfield 1971; Dellatolas et al. 1991.; Millencovic and Dragovic 2012). The frequency of ambilaterality in this sample from Flores and Adonara is less than 1%, corresponding to 4 individuals. This percentage cannot be considered a population estimate, as some left-handers were non-randomly sampled in order to increase the frequency of left-handedness for comparison purposes. Thus, considering that ambilateral people are probably declaring a left preference more frequently than a right one, this percentage is therefore a maximum value for a population estimate. No special characteristics seem to be associated with the four individuals who did not have a clear general lateralization across tasks: all were farmers (except one whose occupation was not recorded), they represented both sexes (three males and one female), they were between 33 and 52 years old, and they lived in different villages.

The results of this study indicate that for Indonesian men and women from Flores and Adonara, right- and left-handedness are meaningful categories. Thus, in these traditional populations, generalized-declared handedness seems to be a valid and sufficient source of information to identify handedness category as it was ascertained by handedness for various specific tasks and relative hand performance and skill.

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