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Is imitational learning a driving factor for the population bias in human hand preference?



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ABSTRACT

Lateral preference is a widespread organizational principle in human and nonhuman animals. In humans, the most apparent lateralized trait (handedness) is unique in the animal kingdom because of a very pronounced bias towards right-handedness on a population level. In this study, based on previous experiments, we test the hypothesis that this bias was-among other factors-shaped by evolution through the facilitation of social learning. We exposed 134 subjects to footage of right- or left-handed knot making and analyzed whether concordant handedness between instructor and student facilitated quicker and more successful imitation. We used a set of nautical knots of different difficulty levels in order to test whether the potential effect of concordance became stronger with increasing knot difficulty. For all three performance measures (time until correct completion, number of attempts needed and correct imitation), we found hand congruency and difficulty level to be significant predictors but not the interaction of the two. We conclude that concordance of handedness between teacher and student of a motor skill enhances the speed and accuracy of imitation, which may have been a beneficial trait for selection to act upon, thereby shaping the human population bias in handedness.

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1. Introduction

Lateral preference for using one hand or paw over the other seems to be a general organizational principle in animals, including humans (e.g., Bisazza et al., 1998; Bradshaw, 1988; McManus, 2004). Interestingly, human hand preference has by far the strongest bias both on the individual and population level. The function and evolution of this trait in humans are, despite its omnipresence, still not well understood, especially the strong bias of hand preference at the population level.

It is thought that in humans, the specialization and training of the motor cortex in one or both hemispheres allows a better specialization and precision of the corresponding contralateral hand (i.e. the left hemisphere controls the right hand because of the decussation of the pyramidal tracts; Vallortigara et al., 1999; Cochet and Byrne, 2013). This accounts for the bias of the individual. However, throughout human populations all over the world, a rough ratio of nine right-handers to one left-hander persists (e.g.,

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Llaurens et al., 2009; McManus, 2004), and from archaeological evidence, we can assume that it has been this way since up to 2 million years ago (Cashmore et al., 2008; Uomini, 2009). This has led to the question as to why and how this characteristically strong hand preference bias in a population has been shaped by evolution.

Cochet and Byrne (2013) give a good overview of the different theories on the evolution of handedness in humans, focusing on four core drivers for handedness bias, some of which we will describe in more detail below: Skilled, manipulative activity (e.g., tool use), communicative gestures, organizational complexity of action, and goal-directed action (Cochet and Byrne, 2013).

The hypothesis for skilled manipulative activity proposes that hand preference emerged from the specialization of both hands for different tasks (precision vs. power grip) and the subsequent development of right-biased gestural language in the right hand (precision grip). As a result, the dominance for language (first gestural and later vocal) became located in the left hemisphere and has further strengthened the asymmetry in preference between both hands. However, the gesture-language explanation for the human population bias for handedness has also been challenged. The reasoning is two-fold: Language is left-lateralized in 70% of







left-handers in humans (i.e., with right hemispheric dominance for hand coordination), and hand preference bias at the population level in wild chimpanzee behavior does not support the gestural origins of language lateralization since chimpanzees engage in gestural communication, yet did not develop a handedness bias. It is therefore unlikely that the common ancestor of humans and chimpanzees had a handedness bias due to gestural communication. At least, gestural communication might not be the complete explanation for the human population handedness bias (see Corballis, 2003, and discussions therein).

Additionally, an often-cited hypothesis is the so-called 'fighting hypothesis' (Faurie and Raymond, 2013) to explain the strong population bias in handedness. It proposes that left-handedness is associated with fitness-decreasing traits—such as higher vulnerability for several diseases—but is maintained in the population by negative frequency-dependent selection on co-occurring fitness benefits. For the latter, they propose a higher chance of winning fights due to a surprise effect. However, this hypothesis has received criticism. Direct evidence for the negative frequency-dependent selection process on winning fights has not yet been published, and other evidence in favor of the hypothesis has been challenged (for a review, see Groothuis et al., 2013).

A third hypothesis addresses the fact that humans are exceptional tool makers and tool users within the animal kingdom-a trait that has evolved to this extent through the social transfer of these skills (Legare and Nielsen, 2015). For maintaining the skill of tool fabrication in a population, it needs to be transferred to younger generations, thus making the efficiency of acquiring this skill a potential factor for the fitness of an individual and at the same time for speed of its transmission in a population (Morgan et al., 2015). Imitation, i.e., the copying of behavior towards a goal or an end product, reduces errors and increases copying fidelity in comparison to the copying of merely the end product (i.e., emulation; Schillinger et al., 2015). Copying others would have been a crucial strategy for Paleolithic stone tool makers to develop and perfect their craft to produce hand axes or scrapers from flint and other materials (Geribàs et al., 2010; Schillinger et al., 2015). Even today, human societies rely heavily on tool making for many aspects of survival, both in preindustrial and postindustrial societies. In the vast majority of cases, the skills for manufacturing tools or learning how to use them are not developed de novo but through social transfer via imitation and instruction (Legare and Nielsen, 2015). These traits have, among others, contributed to the vast growth of human knowledge and cumulative culture over time (Vaesen, 2012).

Imitation (direct copying of movement sequences performed by others) in contrast to emulation (copying the product of a behavior but not the movements themselves) has been shown to decrease copying error in the reproduction of a stone tool shape (Lycett, 2015). The propensity to imitate readily, frequently, even actions that clearly have no direct function, is already present in children from a very young age, indicating the importance of this trait in the ontogeny of human behavior (Horner et al., 2005; Vaesen, 2012; Legare and Nielsen, 2015). With regard to hand preference and imitation, it intuitively makes sense that the same-sided hand preference of teacher and student has the potential to speed up the process of the transmission of skills for tool production and tool use. This, in turn, could establish the selection pressure necessary to shape a strong population bias towards the same handedness, also called the 'apprenticeship complexity theory' (Michel and Harkins, 1985; Bradshaw, 1988; Uomini, 2009). Nonetheless, like for the previous hypothesis, it would not explain whether it would be either a right- or left-handedness bias.

Surprisingly, there is only a small body of literature on the topic of learning from models with different hand preferences, specifically when it comes to experimental evidence for the hypothesis that learning from a concordantly handed instructor is easier than from a discordantly handed one. In the study by Michel and Harkins (1985), the efficiency of imitation was tested for three different knots, as demonstrated by either a left- or right-handed model. They found that concordance of handedness between model and imitator vielded a higher success rate in learning the knots. In an additional analysis of one knot specifically, they found a significant interaction between handedness of imitator and teacher on the time needed to learn the knot. Right-handers learned better from a right-handed demonstrator and slower from a left-handed demonstrator, and vice-versa for left-handers. However, a problem with this study might be that only one demonstrator was used per hand preference. Demonstrators could have differed in other aspects than being left- or right-handed, or they could have produced knots of identical chirality rather than mirrored knots.

In a similar and extended setup, a study of origami-making tested if imitation performance was influenced by the handedness of the demonstrator and the viewpoint of the instruction (first-person view or a 180° rotated version) but found that neither had an effect (Uomini and Lawson, 2017). In another study, Rohbanfard and Proteau (2011) tested the influence of perspective (trainee facing the trainer or assuming the same perspective as the trainer), using a protocol of a simple single-hand tapping movement sequence. They did not find an effect of the demonstrator's handedness on imitation in a sample of only right-handers. However, this might be due to the fact that the task did not require the coordination of both hands, which is often needed in tool use. Another imitation study for very simple motor tasks showed that reaction times in right- and left-handers were shorter when action had to be imitated from a concordantly handed stimulus. This was found in right- and left-handers, when the movement had to be executed with the dominant hand, and when the instruction was administered in egocentric view (as if one would look on top of one's own hands from above (first-person view; Mori et al., 2015). In this study, however, the task was simply to imitate a tapping movement as opposed to learning an entirely new movement sequence; therefore, the accuracy of the imitated movement was not assessed. Interestingly, in an experiment with users of sign language, it was found that although both left- and right-handed signers (in the role of the recipient) reached a higher accuracy in comprehension of words signed by right-handed demonstrators, left-handed participants showed faster response times to lefthanded demonstrators (Watkins and Thompson, 2017). Perhaps left-handers are so well-adapted to a right-handed environment that they do not experience it as a hindrance, but they would potentially do better in a left-handed environment.

In addition to studies of imitation directly, there is compelling positive evidence for the imitation hypothesis from the field of medicine where tool use and training are of exceptional importance, showing that hand preference plays an important role in the learning of tool use to this day. Lee and colleagues (Lee et al., 2013) demonstrated in a study with medical students learning basic suturing and knotting techniques that, indeed, when trained under a concordantly handed instructor, left-handers performed just as well as right-handers. Participants learning in a discordantly handed curriculum were performing significantly worse compared to those trained in a course concordant to their handedness. This was regardless of the hand preference of the subject, indicating that left-handers are not intrinsically worse at learning or executing these techniques but suffer from a learning environment that puts them at a disadvantage. However, as the authors themselves state, the sample size was very small (9 vs. 10). In conclusion, three studies indicate that imitation is easier from a model with the same handedness, two studies did not find this effect, and one study

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found ambiguous results, with some of the studies having potential methodological problems.

In the present study, we replicated the experiments of Michel and Harkins (1985), which in our opinion, is the best set-up because of its evolutionary-relevant task and straightforward concept while correcting for the potential weakness mentioned above (only one live demonstrator for each handedness). We aim to examine if concordant handedness between teacher and student facilitates faster and/or more successful learning of manual skills. To test this, we used different (nautical) knots since these require coordination between both hands and fine motor manipulation while being a skill that is not commonly practiced in an average population (around 5%, according to Chisnall, 2010). In addition to the factors analyzed in the original study, we took the difficulty of the knots into account to examine if the benefit of concordant handedness is more pronounced in demanding tasks where better visual-spatial insight and motor planning of the hands is required. Knot making can be described as a sequence of bimanually coordinated actions that need to be learned (motor sequence learning). We chose to use instructional videos similar to Rohbanfard and Proteau (2013), as opposed to live demonstrations of the knot making because they allow for each participant to receive the instruction with identical timing and precise movement sequences of both the left-handed and right-handed versions (Rohbanfard and Proteau, 2013).

We predict that subjects will learn faster and more successfully from a concordantly handed instructor and that the benefit of concordant handedness will increase with the difficulty of the knot. We discuss the outcomes in terms of fitness advantage and frequency-dependent selection for hand preference in the population.

2. Methods

2.1. Participants and materials

We collected data on imitation in the context of a practical course from a student sample (85 females, 49 males, aged 18–24 years). Students were informed about the testing procedure and provided with written instruction and an informed consent form, which they signed. Students were offered alternative practicals, in the event they did not feel completely comfortable in completing the imitation tests and handedness questionnaire, but none used this opportunity.

Participants were seated in a room in groups of approximately 15, each student at an individual desk with a computer, a piece of cotton rope (diameter 5 mm, length 50 cm), and a stopwatch. Author B.R. produced the instruction videos in the first-person view by rigging a camera above his hands, then carrying out the steps to produce the following specific knots: granny knot, bowstring knot, artillery loop, a bowline (all instructions for the demonstrator and assistants obtained from http://www.realknots.com). The knots were included in this sequence in all four versions of the instructional videos, which differed only in the randomization of the rightand left-handed demonstrations. All films contained two lefthanded and two right-handed demonstrations. Left-handed demonstrations were artificially produced by mirroring the videos of a right-handed demonstrator, so the right side appeared left and vice versa. This produced a left-handed demonstrator while preserving the demonstrator and dynamic aspects of the knot making.

2.2. Protocol

Participants were asked to play a movie file on the computer. In this movie, a text explained the task (reproducing a knot after a video

instruction), the nature of the video instruction, and the steps they had to take according to the protocol of the experiment (as described below). Following the text instructions, participants viewed a video clip showing two hands in the first-person view tying a specific knot in a rope, first in slow-motion and then repeated twice at real-time speed. After each video, the screen went to black with the instruction to pause the movie (see Supplementary Online Material [SOM] S1 and SOM Fig. S1 for detailed text and example). As instructed, the participants were required to start a stopwatch, reproduce the knot they had seen in the movie, stop the stopwatch when finished, and record the time on paper. The knot was then presented to a trained assistant, who evaluated the knot for its correctness. If a knot had been tied incorrectly, students were allowed two more attempts. Each attempt, including the first one, had to be completed within 90 seconds; attempts longer than 90 seconds were scored as failed. Three failed attempts indicated failure to reproduce the knot and was recorded as such. Four different types of knots had to be reproduced in total. The variables thus recorded were (1) the number of attempts needed to reproduce a knot, either correctly or incorrectly; (2) the duration it took to successfully reproduce a knot; and (3) whether the knot could be reproduced successfully at all.

The participants were asked to complete a short questionnaire stating their sex, year of birth, and the Edinburgh Handedness Inventory (EHI; Oldfield, 1971) offered in a Dutch translation (Strien, 1992, 2003). Participants were asked to mention the hand they use to perform a certain task (e.g., ball throwing) and were given the choice to answer 'left', or 'right', coded as 0 or 1, respectively. The sum of the coded answers represents the hand preference score (EHI score). The EHI score ranged from 0, representing complete left-handedness, to 10 (complete right-handedness). Based on this scale, we classified participants in one of three groups: left-handed (0-1), ambidextrous (2-8), and right-handed (9-10); for a review and discussion of cut-offs, see Edlin et al., 2015). We only included left-handers (n = 15) and right-handers (n = 119) in the analysis, while excluding ambidextrous participants (n = 14). Based on the subject's handedness and that of the demonstration, we labeled each trial as a matching or mismatching condition.

As performance measures for imitation, we analyzed whether and how quickly a knot was learned by analyzing the following three parameters:

- Time per knot(seconds): the time that it took to complete a knot, by adding up the number of seconds for each of the three attempts until the knot was correct;
- 2) Attempts per knot: the number of attempts (1, 2, or 3) it took to successfully imitate a knot (when all three attempts failed, a score of 4 was given); and
- 3) Successful imitation: whether a knot could be successfully replicated at all.

2.3. Statistical analyses

All participants imitated knots under both conditions (concordant and discordant demonstrator), and these conditions were randomized over the trials while the sequence of knots of varying levels of difficulty stayed the same. The participants were prompted to record cases in which they were familiar with the knot. As only one individual was familiar with one of the knots, we did not exclude any subjects based on this information. We analyzed the data with a generalized mixed modeling approach in IBM SPSS Statistics v. 22 (Armonk, New York). For the three variables (time per knot, attempts per knot, and success of imitation), respectively, we used a linear regression. For each of the three variables, subject identity was added as a random effect. Hand preference congruency and knot difficulty, and the interaction term of the two, were added as fixed factors in the model. In a stepwise backward regression approach, the interaction term was removed from the model if it was not significant; the main factors remained in the model regardless of their significance level. The difficulty of the knots was assessed by the success rate at which they were reproduced, resulting in the following ranking: granny knot (easy, 95% success rate), artillery loop (medium, 61% success rate, respectively). Mean scores for the three dependent variables in the three difficulty categories are given in SOM Table S1. Alpha was set at 0.05.

3. Results

In all analyses of imitation performance, knot difficulty was significant (all *p*-values <0.001) and will thus only be reported in the tabular results.

Analyzing the time needed per knot revealed a significant effect of hand preference congruency, but not for the interaction of hand preference congruency and knot difficulty (full model, Table 1). The interaction term was removed in the final model, and hand preference congruency was revealed as a significant main factor (final model, Table 1).

For the performance measures 'attempts per knot' and 'success of imitation', neither hand preference congruency nor the interaction of hand preference congruency and knot difficulty were significant (full model, Table 1). When the interaction term was removed in the final model, hand preference congruency was significant for both performance measures (final model, Table 1).

We can summarize that in the concordant condition, time taken per knot was shorter, the attempts per knot were fewer, and imitation success was greater (Table 2; Fig. 1). Parameter estimates of the factors can be found in SOM Table S2).

Despite the fact that the interaction term was removed from all models because it was not significant, Figure 1 indicates that knots of higher difficulty (medium and difficult ones) produced a pronounced difference in medians where the concordant handedness between the model and the student led to less time needed to reproduce a knot.

The medians and means for the three performance measures (averaged across all difficulty levels) show that participants needed, on average, 50 seconds longer and more attempts to imitate a knot in the mismatching condition (demonstrated by a model of the opposite handedness based on the median values; Table 2; Fig. 1).

Note that the variance of the medium and difficult categories is much higher than of the easy category. Subjects were also slightly more often successful in imitating the knot when the demonstration was given by a model who matched their handedness (Table 2).

4. Discussion and conclusions

The fact that all three measurements of imitation performance (time to make a knot, attempts needed, and the correctness of the end result) are significantly better for matching handedness between model and imitator confirms our hypothesis and successfully replicates the results from the original experiment (Michel and Harkins, 1985). As in their study, participants in the discordant condition were less often successful in the imitation and needed more time to learn a knot.

Additionally, the number of attempts and the time needed to reproduce a knot for all three levels of difficulty confirms that concordant handedness between model and imitator facilitates quicker learning. With respect to the second research question, we did not find that the benefit of concordant handedness increases with greater difficulty of the task. However, visualization of the data (Fig. 1) suggests that this effect might be present when comparing difficult and easy knots. The high variance present in the data of the medium and difficult knots (concordant and discordant condition) likely explains the nonsignificant effect. This high level of variance may be due to our experimental set-up, in which we established a cut-off time for how long an attempt could last (90 seconds). Thus, if a participant was unable to replicate a knot successfully within the given 90-second timeframe, they were forced to begin again in the next trial when they might have solved the task if given a slightly longer time span in the first trial. As a consequence, the next attempt for the same knot, being often somewhat shorter because of the learning effect from the previous attempt, would include this second time interval plus the previous 90 second (the maximum time allowed in the first interval). For example, if 120 seconds were needed in the first trial while only 90 seconds were allowed, and if 70 seconds were needed in the second trial, then the total time until success would be 90 + 70 = 160 seconds, rather than 120. Therefore, the cut-off time of 90 seconds enlarged the variation between successful and unsuccessful students.

The fact that imitational learning is easier with matching hand preference makes it a candidate hypothesis to explain the maintenance of the strong population bias in the direction of hand

Table 1

Results of analyses of three measurements of imitation performance, including all factors (Full model) and only the main factors (Final model).

Performance	Factor	F	df	<i>p</i> -value
Full model				
Time per knot (s)	hand preference congruency	9.906	530	0.002
	knot difficulty	149.919	530	< 0.001
	hand preference congruency*knot difficulty	0.923	530	0.398
Attempts per knot	hand preference congruency	2.160	527	0.142
	knot difficulty	63.899	527	< 0.001
	hand preference congruency*knot difficulty	2.006	527	0.136
Success of imitation	hand preference congruency	0.156	530	0.693
	knot difficulty	41.325	530	< 0.001
	hand preference congruency*knot difficulty	0.905	530	0.405
Final model				
Time per knot (s)	hand preference congruency	12.351	532	< 0.001
	knot difficulty	150.038	532	< 0.001
Attempts per knot	hand preference congruency	5.468	529	0.020
	knot difficulty	63.448	529	< 0.001
Success of imitation	hand preference congruency	4.905	532	0.027
	knot difficulty	43.355	532	<0.001

Table 2

Median (upper and lower 95% confidence interval) and mean (SEM) scores per condition for the time taken per knot, attempts per knot, and successful imitation (average number of knots reproduced successfully).

<i>n</i> = 134	Time per knot (s)		Attempts	Attempts per knot		Successful imitation	
Condition	Concordant	Discordant	Concordant	Discordant	Concordant	Discordant	
Median Mean	46 (86–109) 97.3 (5.8)	96 (108–133) 120.6 (6.2)	2 (2.2–2.5) 2.3 (0.8)	3 (2.5–2.8) 2.6 (0.8)	1 (0.56–0.68) 0.62 (0.03)	1 (0.46–0.58) 0.52 (0.03)	



Figure 1. Boxplot of the time needed (in seconds) to complete a knot over the three different difficulty levels. White boxes indicate the concordant condition, and grey boxes indicate the discordant condition. For reasons of clarity, outliers are not shown in this graph, although they were included in the statistics (outliers were only present in the easy condition n = 18). Error bars represent a 95% confidence interval.

preference in human populations, although it is likely not the exclusive factor. On the other hand, our results cannot explain why the population bias is toward right-handedness vs. left-handedness. It also does not dismiss the fighting hypothesis (Faurie and Raymond, 2013), as negative frequency-dependent selection and facilitation of motor learning through handedness concordance need not be mutually exclusive. Both theories can explain how the right-handed bias is maintained: while the fighting hypothesis represents a benefit for left-handedness (at low frequencies), the imitation hypothesis represents one aspect of the costs that makes up an essential part of the fighting hypothesis.

Specifically, apart from negative frequency-dependent selection, the fighting hypothesis requires increased costs for lefthanders explaining why left-handers are in the minority in the first place. Increased health costs for left-handers have been proposed to be the reason for this (e.g., reduced longevity and delayed sexual maturity, as reviewed in Llaurens et al., 2009). Costs due to health risks for left-handers can also explain why the strong population bias needed for facilitation of imitation is in favor of righthandedness. This would hold true even if the fighting hypothesis is not supported. Since recent literature has begun to question the differential health costs for left- and right-handers (McManus and Wysocki, 2005; Zickert et al., 2018; van der Feen et al., 2020), it might be feasible to search for other factors explaining the righthanded bias. Alternatively, a small bias toward right-handedness might have been established by chance, after which it became stronger as being at a disadvantage for imitative learning (or being taught for that matter) might pose as a disadvantage for lefthanders in a right-handed world.

We chose to test the imitation of a motion sequence that is ecologically relevant and which entails different roles for both hands, using videos of a single right-handed instructor and mirror images thereof as a proxy for the left-handed demonstrator. This brings the large advantage of eliminating all variability in behavior and kinematics of knot making that is introduced by having different demonstrators for left and right. In a study on the perception of videos of hand and arm movements from egocentric and allocentric perspectives that were mirrored in the same way as in our experiment (trainee assuming the same perspective as the trainer, seeing hands from above), observers reported only unmirrored right-handed grasping as looking natural (Neal and Kilner, 2010). Although mirrored images were perceived as unnatural (as opposed to non-mirrored images), we cannot exclude the possibility of an effect of using mirrored videos in our own experiment since the mirrored version of a right-handed instruction was used (i.e., the one perceived as more unnatural). Despite the actual effect of perception on imitation being unknown, it is unlikely to have any influence. This is supported by the origami-making study of Uomini and Lawson (2017), which used mirrored films to create differently handed demonstrators and viewing angles. The results showed no effect on imitation performance based on viewing angle or hand concordance. Further studies should take this into account and include left- and right-handed teachers, control for movements (kinematics) and other confounding factors by mirroring, and assure unified knot chirality (i.e., similar knots that mirror each other should be counted as two distinct knots) between instructors (see below). Moreover, to test the influence of hand preference alone, it is probably advisable to use instructional videos that show hands in the perspective of the learner (first-person view) since this configuration seems to facilitate the easiest imitation (Mori et al., 2015; Nishizawa et al., 2015; Sebastianutto et al., 2017).

Additionally—and for examining the relevance of the imitation hypothesis—it should be determined in diverse human populations if an alignment that results in a first-person view for a learner of a manual task is indeed the preferred one, as opposed to a teaching style in which the instructor is opposite of the learner. This is particularly relevant for (experimental) archeological research on the transfer of flint-knapping and other tool-production methods (Lycett and Eren, 2019). Observations in indigenous cultures, which do not use tables or other support structures that could limit the free choice of the learner's viewpoint, should most resemble the conditions in the past and give us vital insights on which to build further studies. There have already been efforts to trace down the neurological bases of the acquisition of Paleolithic tool-making (Stout and Chaminade, 2007), which could be very useful in tying together behavioral research and neuroscience in the context of the evolution of learning and handedness. Lastly, one aspect, which has not yet been taken into account as far as we are aware, is the level of novelty of the task for a student. One can safely assume that university students have some degree of experience with tying knots or folding paper-even hammering two objects with a purpose-so the tasks in previous studies have tested the performance of these tasks only on a higher level of complexity while the basic requirements of motor coordination for those tasks are presumably already present and well practiced. A stronger influence of differences in handedness between teacher and student might be seen when testing actual novices of a praxis, e.g., children tying their shoes for the first time or adults who have never knitted.

As illustrated in Figure 1 and reported in Michel and Harkins (1985), the difficulty of a task is an important factor that needs to be considered in follow-up experiments. The present study found that for easy knots, learning from congruent or discordant teachers does not differ significantly, whereas, for higher levels of difficulty, it does. It is especially interesting to investigate bimanual tasks that require different levels of coordination between both hands. In concordance with previous studies, we can assume that concordance of hand preference becomes more important the more the roles between both hands differ from each other (Uomini and Lawson, 2017). In the same vein, it might be interesting to see if there is a difference between the acquisition of motor skills that build on familiar motor sequences (such as knot-making while learning an unfamiliar knot) and the learning of completely new motion sequences.

In sum, using a design controlling for the confounders in an earlier study, we confirmed previous findings that concordance of handedness between teacher and student of a motoric skill does enhance the speed and accuracy of learning in an extended design over a range of difficulty levels.

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Appendix A. Supplementary Online Material

Supplementary online material to this article can be found online at https://doi.org/10.1016/j.jhevol.2021.103045.

References

- Bisazza, A., Rogers, L.J., Vallortigara, G., 1998. The origins of cerebral asymmetry: A review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. Neurosci. Biobehav. Rev. 22, 411–426.
- Bradshaw, J.L., 1988. The evolution of human lateral asymmetries: New evidence and second thoughts. J. Hum. Evol. 17, 615–637.
- Cashmore, L., Uomini, N., Chapelain, A., 2008. The evolution of handedness in humans and great apes: A review and current issues. J. Anthropol. Sci. 86, 7–35.
- Chisnall, R.C., 2010. Knot-tying habits, tier handedness, and experience. J. Forensic Sci. 55, 1232–1244.
- Cochet, H., Byrne, R.W., 2013. Evolutionary origins of human handedness: Evaluating contrasting hypotheses. Anim. Cognit. 16, 531–542.
- Corballis, M.C., 2003. From mouth to hand: Gesture, speech, and the evolution of right-handedness. Behav. Brain Sci. 26, 199–208 discussion 208-60.
- Edlin, J.M., Leppanen, M.L., Fain, R.J., Hackländer, R.P., Hanaver-Torrez, S.D., Lyle, K.B., 2015. On the use (and misuse?) of the Edinburgh handedness inventory. Brain Cognit. 94, 44–51.
- Faurie, C., Raymond, M., 2013. The fighting hypothesis as an evolutionary explanation for the handedness polymorphism in humans: Where are we? Ann. N. Y. Acad. Sci, 1288, 110–113.
- Geribàs, N., Mosquera, M., Vergès, J.M., 2010. What novice knappers have to learn to become expert stone toolmakers. J. Archaeol. Sci. 37, 2857–2870.

- Groothuis, T.G.G., McManus, I.C., Schaafsma, S.M., Geuze, R.H., 2013. The fighting hypothesis in combat: How well does the fighting hypothesis explain human left-handed minorities? Ann. N. Y. Acad. Sci. 1288, 100–109.
- Horner, V., Whiten, A., Horner, V., Whiten, A., 2005. Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). Anim. Cognit. 8, 164–181.
- Lee, J.Y., Mucksavage, P., McDougall, E.M., 2013. Surgical skills acquisition among left-handed trainees—true inferiority or unfair assessment: A preliminary study. J. Surg. Educ. 70, 237–242.
- Legare, C.H., Nielsen, M., 2015. Imitation and Innovation: The dual engines of cultural learning. Trends Cognit. Sci. 19, 688–699.
- Llaurens, V., Raymond, M., Faurie, C., 2009. Why are some people left-handed? An evolutionary perspective. Philos. Trans. R. Soc. Lond. B Biol. Sci. 364, 881–894.
- Lycett, S.J., 2015. Cultural evolutionary approaches to artifact variation over time and space: Basis, progress, and prospects. J. Archaeol. Sci. 56, 21–31.
- Lycett, S.J., Eren, M.I., 2019. Built-in misdirection: On the difficulties of learning to knap. Lithic Technol. 44, 8–21.
- McManus, I.C., 2004. Right Hand, Left Hand: the Origins of Asymmetry in Brains, Bodies, Atoms, and Cultures. Harvard University Press, Cambridge.
- McManus, I.C., Wysocki, C.J., 2005. Left-handers have a lower prevalence of arthritis and ulcer. Laterality 10, 97–102.
- Michel, G.F., Harkins, D.A., 1985. Concordance of handedness between teacher and student facilitates learning manual skills. J. Hum. Evol. 14, 597–601.
- Morgan, T.J.H., Uomini, N.T., Rendell, L.E., Chouinard-Thuly, L., Street, S.E., Lewis, H.M., Cross, C.P., Evans, C., Kearney, R., de la Torre, I., Whiten, A., Laland, K.N., 2015. Experimental evidence for the co-evolution of hominin toolmaking teaching and language. Nat. Commun. 6, 6029.
- Mori, H., Yamamoto, S., Aihara, T., Uehara, S., 2015. The role of handednessdependent sensorimotor experience in the development of mirroring. Neurosci. Lett. 584, 119–122.
- Neal, A., Kilner, J.M., 2010. What is simulated in the action observation network when we observe actions? Eur. J. Neurosci. 32, 1765–1770. Nishizawa, H., Kimura, T., Goh, A.-C., 2015. The effect of different imitation models
- Nishizawa, H., Kimura, T., Goh, A.-C., 2015. The effect of different imitation models on the accuracy and speed of imitation of movement. J. Phys. Ther. Sci. 27, 3417–3420.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9, 97–113.
- Rohbanfard, H., Proteau, L., 2011. Effects of the model's handedness and observer's viewpoint on observational learning. Exp. Brain Res. 214, 567–576.
- Rohbanfard, H., Proteau, L., 2013. Live vs. video presentation techniques in the observational learning of motor skills. Trends Neurosci. Educ. 2, 27–32.
- Schillinger, K., Mesoudi, A., Lycett, S.J., 2015. The impact of imitative versus emulative learning mechanisms on artifactual variation: Implications for the evolution of material culture. Evol. Hum. Behav. 36, 446–455.
- Sebastianutto, L., Mengotti, P., Spiezio, C., Rumiati, R.I., Balaban, E., 2017. Dual-route imitation in preschool children. Acta Psychol. 173, 94–100.
- Stout, D., Chaminade, T., 2007. The evolutionary neuroscience of tool making. Neuropsychologia 45, 1091–1100.
- Strien, J.W. Van, 1992. Classificatie van links- en rechtshandige proefpersonen (Classification of left- and right-handed subjects.). Ned. Tijdschr. Psychol. haar Grensgebieden 47, 88–92.
- Strien, J. van, 2003. Vragenlijst Voor Handvoorkeur. Retrieved from. http://hdl. handle.net/1765/955.
- Uomini, N.T., 2009. The prehistory of handedness: Archaeological data and comparative ethology. J. Hum. Evol. 57, 411–419.
- Uomini, N., Lawson, R., 2017. Effects of handedness and viewpoint on the imitation of origami-making. Symmetry 9, 182.
- Vaesen, K., 2012. The cognitive bases of human tool use. Behav. Brain Sci. 35, 203–218.
- Vallortigara, G., Rogers, L., Bisazza, A., 1999. Possible evolutionary origins of cognitive brain lateralization. Brain Res. Rev. 30, 164–175.
- van der Feen, F.E., Zickert, N., Groothuis, T.G.G., Geuze, R.H., 2020. Does hand skill asymmetry relate to creativity, developmental and health issues and aggression as markers of fitness? Laterality 251, 53–86.
- Watkins, F., Thompson, R.L., 2017. The relationship between sign production and sign comprehension: what handedness reveals. Cognition 164, 144–149.
- Zickert, N., Geuze, R.H., van der Feen, F.E., Groothuis, T.G.G., 2018. Fitness costs and benefits associated with hand preference in humans: A large internet study in a Dutch sample. Evol. Hum. Behav. 39, 235–248.