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Effects of Handedness and Viewpoint on the Imitation of Origami-Making

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Abstract: The evolutionary origins of the human bias for 85% right-handedness are obscure. The Apprenticeship Complexity Theory states that the increasing difficulty of acquiring stone tool-making and other manual skills in the Pleistocene favoured learners whose hand preference matched that of their teachers. Furthermore, learning from a viewing position opposite, rather than beside, the demonstrator might be harder because it requires more mental transformation. We varied handedness and viewpoint in a bimanual learning task. Thirty-two participants reproduced folding asymmetric origami figures as demonstrated by a videotaped teacher in four conditions (left-handed teacher opposite the learner, left-handed beside, right-handed opposite, or right-handed beside). Learning performance was measured by time to complete each figure, number of video pauses and rewinds, and similarity of copies to the target shape. There was no effect of handedness or viewpoint on imitation learning. However, participants preferred to produce figures with the same asymmetry as demonstrated, indicating they imitate the teacher's hand preference. We speculate that learning by imitation involves internalising motor representations and that, to facilitate learning by imitation, many motor actions can be flexibly executed using the demonstrated hand configuration. We conclude that matching hand preferences evolved due to socially learning moderately complex bimanual skills.

Keywords: social learning; imitation; handedness; laterality; origami; evolution

1. Introduction

Handedness is a behavioural lateralization, defined as a species-level bias to use a certain hand configuration for most tasks. It is expressed in *Homo sapiens* as a species-universal behavioural bias (70–90%) towards using the right hand for fine manipulations and the left hand for stabilising actions [1–3]. Among vertebrates, 61 species (out of 119 measured) show population-level limb preferences, of which 25 species are mammals, 30 birds, and 6 amphibians, reptiles, and fish [4]. Some other animal species also have behavioural hand biases up to 90% at the species level [5–8], and many other species have individually stable hand preferences [9,10]. However, within our evolutionary clade, humans are the only great ape that shows strong, species-universal biases towards one direction of handedness. Non-human great ape hand preferences are characterized by high variability in their direction and a low magnitude of expression [4,11]. In particular, humans have much higher ratios of the dominant to non-dominant hand preference, compared to other apes [4,11,12]. Among the other great apes there are groups of individuals with a majority of right-handers, but there are also groups with a majority of left-handers [13]. In contrast, despite much cross-cultural research, no human group has been found with more than 30% left-handers [14]. The origins of handedness probably lie in brain lateralization [7]. The advantages to having lateralized brain functions, not only in the direction of laterality, but also in the strength of laterality, are ubiquitous in vertebrates [4,15]. In that case, we should ask why other ape species who engage in bimanual manipulations do not show a universal bias to either right- or left-handedness.

The obvious question concerning this bias to right-handedness is why most humans are lateralized in the same direction. Our recent ancestors had a similar majority of right-handers as today, judging by the proportion of right and left handprints and hand stencils in cave art [16,17]. Data on older, prehistoric handedness, from asymmetries in fossil brain endocasts, arm bones, and tooth cut-marks, show that 67–69% of hominins between 3 million and 30,000 years ago were right-handed with only 5–11% left-handed [18–20]. Interestingly, the same data also show a rate of 12% mixed-handedness in Neanderthals (a parallel species with whom we share a common ancestral species around 600,000 years ago). In contrast, present-day estimates for our species are around 4% mixed-handers [21,22]. Thus, *Homo sapiens* is characterised by a reduction of mixed-handers, and an equivalent increase in right-handers, compared to the Neanderthals.

A possible evolutionary driver of this directional bias in *Homo sapiens* is given by the Apprenticeship Complexity Theory [13,23,24]. This emphasizes the importance of the social learning environment of prehistoric hominins as they acquired complex tool manipulations [25]. It [26,27] proposes that group-level handedness biases in humans evolved to facilitate faster learning through imitation of complex tool manufacture. Stone tool-making changed over time towards requiring longer sequences and more subgoals, from the pre-Oldowan to the Late Acheulean [24,28,29]. Throughout the Pleistocene, as stone crafts and other essential survival tasks increased in difficulty, so did the pressure on children to learn those skills [24]. According to the Apprenticeship Complexity Theory, selective pressure for learning efficiently (i.e., quickly and accurately) favoured learners whose hand preference matched that of their teachers. This pressure was probably a factor for all individuals given that, for example, the archaeological evidence suggests that, for most of hominin prehistory, functional stone knapping skills were learned by all individuals in a group; the emergence of craft specialisation was a very recent invention linked to artistic production, reduced mobility, and complexification of human societies from the Mesolithic and Neolithic onward [30–35].

The nature of the social learning environment can also affect the efficiency of skill transmission. There is a broad spectrum of social learning strategies across human cultures and across animal species, ranging from unsupervised observation to interactive teaching [36–41]. Prehistoric hominins could have used any of these learning strategies [28,42–44]. Before the emergence of teaching, hominin children would have engaged in social learning through observation. Imitation is a form of observational learning that does not involve any teacher input, where the learner copies the actions of others.

Imitation is often seen as a goal-directed process involving knowledge and understanding on the part of the learner, rather than merely copying of a sequence of actions. Imitation requires learners to form an internal representation of the teacher's action sequence in order to reproduce it [45,46]. This action representation involves the mirror neuron system in Broca’s area [47,48]. Imitation also relies on the learners’ ability to adopt the visual perspective of others, in order to understand their actions [49–51]. Children’s learning by imitation in various human societies has a wide range of forms [52] such as helping with daily tasks [53] or third-party observation [40]. The learner’s position with respect to the demonstrator(s) will vary in different situations. For example, for participatory tasks, such as hunting, the child is most likely to be behind, or alongside, the demonstrator. In contrast, during observatory tasks, such as basket weaving, the child is more likely to be opposite, facing the demonstrator.

Viewing position during imitation tasks has attracted particular focus due to the transformation of visual perspective required to map between the reference frame of the imitator and the demonstrator [46]. When positioned beside a demonstrator (egocentric viewpoint), the observer’s viewpoint matches that of the demonstrator. In this case no mental transformation is needed to interpret the demonstrated action. However, when positioned opposite a demonstrator (allocentric viewpoint), the observer must compensate for the discrepancy between their viewpoint and that of the demonstrator. In this case a mental transformation of the input may be necessary, regardless of hand preferences. The brain processes actions differently depending on whether they are observed from beside, versus opposite, the viewer, with greater activation in the contralateral hemisphere in the former case but the ipsilateral hemisphere in the latter case [54], and with greater activity in the sensory-motor system in the former than the latter case [55]. In addition, visual object recognition is affected by the object's orientation [56,57]. People are better at action prediction for images of tools viewed from the perspective that they would see when using them [58]. Furthermore, in haptic (active touch) tasks, recognition is easier when objects are explored from the orientation typically used to manipulate them ([59], but see [60]). However, none of the previous studies on viewpoint also tested the interaction with handedness. In sum, there is some evidence showing that imitation is harder if there is a discrepancy in viewpoint that needs to be compensated for (though such viewpoint effects have not always been observed; for example, as described below, Reference [61] found no difference in an observer's ability to reproduce knot-tying dependent on their viewpoint). Furthermore, it is not known how handedness might affect the mental transformation required to process different viewpoints.

The Apprenticeship Complexity Theory predicts that the transmission of complex tasks is more efficient when the demonstrator and learner have the same hand preference. We define "complexity" here as motoric and conceptual difficulty, reflected in the learning time needed to acquire the skill [62]. In this sense, higher complexity is found in tasks with long learning times, narrow error tolerances, many components, and/or many steps in a sequence [63–65]. In particular, complementary bimanual tasks with asynchronous digit use rank high on the manipulative complexity scale [66] and thus are excellent models for testing the interplay of handedness and learning. We expected that folding origami, as used in the present study, would be a good example of such a task.

Previous research on handedness and skill learning is very limited. Two studies found that a congruent hand preference between the demonstrator and observer resulted in more efficient learning than incongruent hand preferences. Reference [27] taught knot-tying to groups of right-handed and left-handed observers, with right- and left-handed demonstrators. They showed faster learning from same-handed demonstrators in both groups. Similarly, Reference [67] showed that same-hand demonstrations result in higher accuracy and speed for targeted hand movements than opposite-hand demonstrations (in right-handed observers). In early child development, imitation of the demonstrators' hand configuration is apparent. Infants are heavily influenced by the demonstrator's hand used when manipulating objects. When tested experimentally, although most infants showed right-hand preferences when first grasping an object, an action demonstrated by a left-handed researcher led all infants to subsequently use their left hand [68]. However, object recognition in the haptic modality is not affected by the hand used to explore the object, which suggests a constancy in object representations that generalises across the hands [60]. Thus, more work is needed to determine how learning and handedness are related.

Few studies have tested the effect of viewpoint on imitation. Reference [69] showed that imitation of body movements is easier when standing behind a teacher rather than opposite a teacher. Reference [70] found more accurate mirror imitation of body movements when the teacher faced the observer. Two other studies used a knot-tying task where participants reproduced knots after viewing demonstrations from different visual angles. Consistent with the body movement studies, Reference [71] showed that knots demonstrated in videos were learned more effectively if the teacher was shown from a position beside, rather than opposite to, the learner. Another study [61] used live knot-tying demonstrations from three different viewpoints (beside, opposite, and at right angles to the demonstrator) and found no difference in the mean number of trials to successfully replicate each knot. Reference [61] did, though, find that participants preferred to reduce the discrepancy in viewing angles by sitting beside the demonstrator when given the choice. These conflicting results mean that more work is needed to determine when viewpoint affects the learning of complex bimanual skills.

In order to disentangle the variables of hand preference and viewpoint on the acquisition of manual skills, we conducted a bimanual learning study involving making origami. We chose origami folding because it is a complex task that has been used in previous studies of learning [41,72,73]. Origami has several important advantages over "live" stone tool-making experiments: (1) the starting raw materials can be perfectly controlled so that all participants receive identical blank origami papers; (2) people already possess the motor skill to fold paper, so they can concentrate on learning the folding sequence, which was the focus of our experiment; (3) folding origami is clean and safe and does not require special equipment; (4) our experiment is reproducible by any scientist, not just the few who have access to specialist flint knapping resources. Following the method of [74], we showed participants demonstration videos of a teacher making nine different origami figures ranging from easy to hard. Learners were required to reproduce each figure by imitating the demonstrated actions. We manipulated the videos to show left-handed and right-handed teachers, and for the teachers to have either the same perspective as the participant (beside view) or a 180-degree rotated perspective (opposite view). We predicted that demonstrations of the origami figures would be harder to imitate if they showed an incongruent hand configuration, and if they showed the teacher opposite, rather than beside, the learner.

2. Materials and Methods

2.1. Participants

We recruited thirty-two participants (9 male) aged between 18 and 22 years. Participants were University of Liverpool undergraduate students, with no restriction on hand preference. All subjects gave their informed consent before they participated in the study. The study was conducted in accordance with the Declaration of Helsinki, and the protocol was approved by the Ethics Committee of the University of Liverpool (Project identification code PSYC-1011-075).

2.2. Stimuli

Videos were created demonstrating nine asymmetric origami figures being folded. A right-handed teacher folded all of the origami figures using a 21 cm^2 piece of orange paper. The teacher was video recorded from above, at a height of 42 cm from the desk (see Supplementary Video S1 for full videos). Four versions of each of these nine videos were created varying the hand configuration and viewpoint. Following [74], we rotated each video 180 degrees in the picture plane to create the alternate viewing positions and mirror-flipped the video to create a left-handed version in both viewpoints (Figure 1). The camera was placed directly above the teacher's hands to ensure both that the same visual information was available for the two viewing positions and that both viewing positions could occur in actual viewing (this would not be the case if an angled camera angle had been used).

The first video shown to participants was an easy practice stimulus and it was the only one that required the use of scissors. Each participant created all eight origami figures once. They created two figures in each of the four viewpoint conditions (Left-Handed Opposite, Left-Handed Beside, Right-Handed Opposite, and Right-Handed Beside), so that each participant received all conditions. The assignment of the two figures to each condition, and the order of presentation of conditions, was counterbalanced using a Latin Square procedure to reduce order effects. Two participants were assigned to each of the 16 counterbalancing conditions.

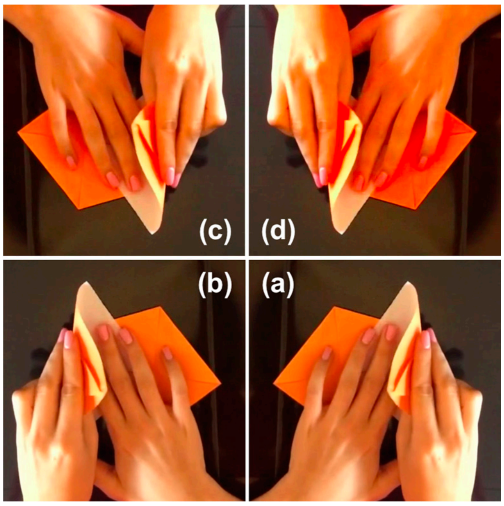

Figure 1. Still images from each of the four conditions created for the "Fish" video showing (**a**) right-handed beside; (**b**) left-handed beside; (**c**) left-handed opposite; and (**d**) right-handed opposite teachers.

2.3. Procedure

Participants initially read an information sheet that stressed that they had to reproduce the origami figures as similarly as possible to the example shown in the video. They were not informed about the different experimental conditions. Participants were given nine 21 cm^2 pieces of paper (one was orange for the practice trial; with two red, yellow, purple, and green papers each assigned to each experimental condition). The demonstration videos were presented to participants on an Apple MacBook Pro 13″ using QuickTime player. Participants were free to interact with the video while they reproduced the figures, by pausing with the pause button, and rewinding by dragging the progress bar backwards.

Participants were first shown the practice demonstration video. After the practice reproduction, any queries were resolved before the experiment began. Participants then did the eight experimental trials. While participants were watching the demonstration videos, the experimenter discreetly recorded the number of times the video was paused and was rewound, and also recorded the time taken to complete the figure, using a stopwatch.

After all nine figures were completed, participants were asked a series of questions:

1. Do you know what the experiment is testing?
2. Did you notice anything about the position of the hands in the videos?
3. Did you notice anything about the hands themselves in the videos?
4. Did you find any of the trials particularly hard?

Participants then completed a Short Form Edinburgh Handedness Inventory [75].

2.4. Analyses

Performance at origami folding was coded with respect to preferred hand dominance. For left-handed participants, left-handed demonstrations were coded as congruent and right-handed demonstrations as incongruent. The reverse coding was used for right-handed and mixed-handed participants. We included mixed-handers in the right-handed category because they all had positive scores (range +25 to +62.5) on the Short Form Edinburgh Handedness Inventory (left-handers had scores ranging from −50 to −100). Since human hand performance is not categorical but rather on a continuum [76], we focus here on hand preference, that is, the categorical choice of hand dominance when doing a task.

The efficiency of reproducing origami figures was measured in two ways: first, the time taken to complete the figure divided by the length of the demonstration video; second, the total number of pauses and rewinds for each video.

The accuracy of reproducing origami figures was also measured in two ways. First, subjective ratings were made of the completed origami figures. Two naïve raters who did not take part in the experiment independently rated the similarity of the produced origami figures to the originals. As training, the two raters were initially shown all 32 practice figures and were asked to rate these using the full scale from 1 for figures which looked 'unlike the original' to 10 for figures which looked 'exactly like the original'. Zero was given to incomplete figures. Raters were required to assign at least three figures to each number on the scale to ensure that they used the full scale. Raters then rated each set of eight experimental figures created by each participant using the same scale. The eight demonstration figures were laid out in front of them together with the set of eight figures from one participant. After completing ratings for all 32 participants, the figures from the first two participants that they had rated were re-presented (without informing the raters) for rating to check for the stability of ratings. The raters completed their ratings of participants in reverse orders with respect to each other.

Second, the experimenter recorded the symmetry of all eight figures produced by each of the 32 subjects in turn. Each figure was categorised as having matching asymmetry to the original (MA), having the opposite asymmetry to the original (OA), as being incorrectly folded to be symmetrical rather asymmetrical (IS), or as being uncodeable due to the poor quality of the reproduction.

3. Results

The Short Form Edinburgh Handedness Inventory scores revealed three left-handed participants (scores −100 to −50), five mixed-handers (scores +25 to +62.5), and 24 right-handed participants (scores +75 to +100). Our sample was similar to the usual human distribution of hand dominance with 9% left-handed, 16% mixed and 75% right-handed participants.

Participants were asked questions prior to debrief in order to assess whether they were aware of the aims of the experiment. None of the 32 participants reported the correct overall aims of the experiment. When prompted, only two participants had noticed that the hand configurations in the video changed in some way, and only three noticed that the viewpoint of demonstrations changed.

For the subjective ratings of figures' similarity to originals, inter-rater reliability between the two raters revealed a fair agreement between the two raters, k = 0.35 ($p < 0.001$), 95% CI (0.414, 0.284), as well as moderate agreement within rater 1, k = 0.56, ($p < 0.001$), and substantial agreement within rater 2, k = 0.64, ($p < 0.001$).

3.1. Effect of Viewpoint and Handedness of Demonstrator on the Efficiency of Making Origami Figures

The data were analysed using an ANOVA with two within-subjects variables, viewpoint (Beside or Opposite) and handedness of demonstrator relative to the participant (Congruent, where, for example, a right-handed participant watched a right-handed demonstrator; or Incongruent, where, for example, a left-handed participant watched a right-handed demonstrator) and reaction time as the dependent variable. There was no effect of viewpoint, $F(1,31) = 0.06$, $p = 0.8$, partial $\eta^2 = 0.002$, with similar time to complete figures for Beside (Mean = 231 s, SD = 10.9) and Opposite (Mean = 225 s, SD = 10.2) videos. There was also no effect of handedness, $F(1,31) = 1.16$, $p = 0.3$, partial $\eta^2 = 0.04$, with similar time for Congruent handedness (Mean = 227 s, SD = 10.9) and Incongruent handedness (Mean = 229 s, SD = 11.66) videos. Finally, there was no interaction between viewpoint and handedness, $F(1,31) = 0.35$, $p = 0.6$, partial $\eta^2 = 0.01$.

Repeating this ANOVA using the sum of pauses and rewinds as the dependent variable revealed the same pattern of results. Again, there was no effect of viewpoint, $F(1,31) = 0.07$, $p = 0.8$, partial $\eta^2 = 0.002$, with a similar number of pauses and rewinds for Beside (Mean = 7.9, SD = 0.53) and Opposite (Mean = 7.8, SD = 0.66) videos. There was also no effect of handedness, $F(1,31) = 0.40$, $p = 0.5$, partial $\eta^2 = 0.01$, with a similar number of pauses and rewinds for Congruent handedness

(Mean = 7.7, SD = 0.59) and Incongruent handedness (Mean = 8.1, SD = 0.67) videos. Finally, there was no interaction between viewpoint and handedness, $F(1,31) = 0.03$, $p = 0.9$, partial $\eta^2 = 0.001$.

3.2. Effect of Viewpoint and Handedness of Demonstrator on the Accuracy of Making Origami Figures

The ANOVA was repeated with ratings of accuracy of reproduction of the origami figure as the dependent variable. Here, there was no effect of viewpoint, $F(1,31) = 3.06$, $p = 0.09$, partial $\eta^2 = 0.09$, with similar ratings for figures produced from Beside (Mean = 6.2, SD = 0.37) and Opposite (Mean = 5.8, SD = 0.44) videos. There was also no effect of handedness, $F(1,31) = 1.46$, $p = 0.2$, partial $\eta^2 = 0.05$, with similar ratings for figures in the Congruent handedness (Mean = 6.2, SD = 0.42) and Incongruent handedness (Mean = 5.8, SD = 0.42) conditions. Finally, there was no interaction between viewpoint and handedness, $F(1,31) = 0.002$, $p = 0.9$, partial $\eta^2 = 0.00$.

3.3. Check That Results Were Not Influenced by the Inclusion of Participants Who Were Not Right-Handed

In order to ascertain that the results reported above were not contaminated by the inclusion of the three left-handed participants and five mixed-handed participants, these three ANOVAs were repeated but only including the 24 right-handed participants. These ANOVAs produced the same pattern of results, with no signficant main effects of viewpoint or of handedness congruency and no significant interactions between these two factors.

3.4. Analysis of Symmetry of Reproduced Origami Figures

Participants produced similar numbers of figures with matching asymmetry to the original (MA; 90 figures, 35%), as figures with the reverse asymmetry to the original (RA; 76 figures, 30%). The remainder of figures were incorrectly reproduced as symmetrical (IS; 30 figures, 12%) or were too poorly reproduced to be coded (60 figures, 23%). The IS and uncodeable responses occurred at similar rates across the four conditions (5–10/condition for IS; 13–17/condition for uncodeable).

Of primary interest was the proportion of figures produced with matching (MA) versus reverse (RA) asymmetry across the four conditions. Considering only these two types of responses, for the Beside viewpoint, when handedness was congruent, as expected most figures had matching asymmetry (MA = 38/46 responses, 83%). Critically, when handedness was incongruent, most figures continued to have matching asymmetry (MA = 29/40 responses; 73%). Thus participants continued to fold using the same hand configuration as the teacher even when the teacher had the opposite handedness as them. A similar, but weaker, pattern occurred for the Opposite viewpoint. Here, when handedness was congruent most figures had, as expected, matching asymmetry (MA = 26/39 responses, 67%). Crucially, when handedness was incongruent most figures again continued to have matching asymmetry (MA = 26/41 responses; 63%). Thus people usually used the same hand configuration to fold as shown by the teacher, whether or not the teacher had the same hand preference as them, with this preference being rather weaker for demonstrations shown from the Opposite viewpoint.

4. Discussion

Contrary to our predictions, there was no effect on performance of either viewing position of the participant relative to the teacher or of handedness of the participant relative to the teacher. Performance was assessed in terms of efficiency of reproduction of each figure, as measured both by the amount of time taken to complete the figures and by the number of pauses and rewinds of the demonstration videos needed to finish the figures. Performance was also assessed in terms of the quality of reproduction of each figure using subjective ratings of the figures' similarity to the originals and coding of the asymmetry of each figure relative to that of the original.

Our experiment provides no evidence for an effect of viewing position on performance, with no difference between viewing demonstration videos from the same visual perspective as the demonstrator, or from a 180 degree rotated viewpoint. This result is in line with [61] who found that a change in viewing position did not perturb imitation performance. It goes against [56], that visual object recognition is faster for objects viewed from a beside orientation. One possible explanation is that our participants were able to interpret the opposite viewpoints by mentally rotating their body relative to the object, rather than by mentally rotating the origami figures themselves. Mental object rotation is more difficult than mental body rotation [77] and is more sensitive to angle of rotation. Therefore, it is possible that people imitate origami folding using the easier strategy of copying the hand movements, rather than by trying to reproduce the shape of the origami figures directly. Future work could test this by investigating whether viewpoint affects performance in the visual recognition of origami figures. In addition, for our video stimuli we elected to use the overhead view, rather than the angled views that would be more characteristic of live demonstrations, in order to better control for visual differences across the four conditions. It is possible that an angled view would give learners a stronger cue to the differences in hand configurations, as most of our participants did not notice any change in the hands between conditions. Again, this possibility could be tested in future studies.

Our results also show that participants were no more efficient at completing the task when observing the folding demonstration by the congruent-handed teacher compared to the incongruent-handed teacher. This contradicts previous studies by [27,67] which both showed improved learning with congruent handedness. Our study is, instead, consistent with the results of [58] that handedness congruence had no effect on performance in a tool action prediction task. Our findings are also in line with [60], who suggest that handedness does not affect object representations. Further support for this conclusion comes from the analysis of the asymmetry of the figures produced. This indicated that participants preferred to fold using the hand configuration demonstrated by the teacher whether or not the teacher had the same hand preference as them. We do not know if participants achieved matching symmetry in origami figures by imitating the teacher's hand configuration itself, or by imitating the direction of folding only. Future work could test this directly by video-recording the participants to see exactly how their hands move during the task. Follow-up studies should also recruit more left-handed and mixed-handed participants in order to test a balanced sample of groups with a range of hand dominances.

We interpret our findings as indicative that learning by imitation involves internalising observed motor representations in order to execute them, as [78] found in their study of brain activation during imitation of Mousterian stone knapping actions. An earlier study [73], presented origami folding instructions as a sequence of written instructions with pictures of the folding shown from the Beside viewpoint. They found that when people learn to fold origami from such pictorial-verbal instructions, they creatively interpret the instructions by reformulating them into spatial terms and adding information. Hand configurations were not specified in this study, but the direction of folding was (e.g., "fold the tip diagonally to the left"). They measured folding success by subjective ratings of figure similarity, and found that people who read fewer instructions aloud were more successful [73]. This result suggests that internalising visual representations is a key process in action imitation [78], and that verbal instructions can actually hinder learning. During learning by imitation alone, as in the present study, no explicit teaching occurred and there were no verbal instructions, so the learner was not instructed to use a particular hand configuration. In this case, the internalised motor representations allowed the learner to use any hand configuration. Our results suggest that these motor representations are hand-independent, consistent with what has previously been found by [60]. This enabled learners to flexibly match their hand preference to that used by the demonstrator.

Our finding that incongruent handedness between demonstrator and learner did not affect performance, was thus, we argue, because learners effectively preferred to remove the handedness incongruence by adopting the hand configuration of the demonstrator. Support for this claim comes from our finding that learners preferentially produced origami figures that matched the direction of asymmetry demonstrated by incongruent-handed teachers. The conflicting results found in previous studies could be explained by participants finding it harder to reproduce stimuli created by incongruent-handed teachers, but being able to compensate for this by changing their handedness to be congruent with that of the teacher.

If, as we have suggested, the preferred configuration of hand use is flexible when people learn a complex bimanual task, this indicates that social learning by imitation can be a powerful determinant of handedness. Despite having established hand preferences, our adult participants behaved the same as the infants in [68] who imitated the hand configuration of the demonstrator. We speculate that an ability to facilitate learning by rapidly and temporarily adopting a demonstrator's hand configuration evolved due to the pressure for efficient social learning of complex tasks. Similarly, [79] proposed that hominins were the only species who engaged in sufficiently complex manual tasks to trigger the expression of a handedness bias.

Our evolutionary scenario is as follows: prior to the evolution of complex tool manufacture, hand preferences were evenly distributed among human populations, as is the case in other species of living apes, which we take to reflect the ancestral condition. Thus, some groups would have had a left-hand bias, some groups a right-hand bias, and other groups no bias. During social learning of simple skills such as many foraging tasks like picking fruit or pounding nuts, there was no need to conform to any particular hand configuration. This was because the tasks were simple enough to allow easy mental transformations so that each individual could use their preferred hand. This situation still exists among non-human apes. We propose that human imitation of manual skills began to require congruent handedness only once a certain level of tool complexity was reached. At this stage, learners found it beneficial to flexibly adopt the hand configuration of their teachers, in order to minimise the difficulties of mental transformation for such tasks.

Importantly, if, as we have argued, learners can efficiently imitate their teacher's hand preference, then we would have no reason to expect a drive for dominance of any particular hand preference. Thus, our species-level directional bias towards right-handedness still needs to be explained. We suggest that a combination of, first, functional brain laterality and, second, task expertise effects could be the evolutionary driver for the dominance of right-handedness in *Homo sapiens*.

First, regarding brain laterality, the two brain hemispheres have specialised, complementary roles in controlling the contralateral hand and arm [2]. Evidence from vertebrate lateralization indicates an evolutionarily ancient hemispheric specialisation was already in place before the hominin lineage emerged [5,79,80]. We believe the persistence of 10% left-handers in humans today is due to both a minority advantage in combat (Fighting Hypothesis) [20] and to atypical functional brain lateralization patterns which occur naturally in the population [81].

Second, this hemispheric specialisation could be critical when undertaking a highly complex bimanual task such as stone tool-making. Specifically, the brain's motor control specialisations mean that typically the dominant (right) arm controls movement direction and shape, while the non-dominant (left) arm maintains a stable position [2,82,83]. During direct, hand-held percussion for stone tool-making, these are precisely the bimanual complementary roles required of the two hands [13,17]. The non-dominant hand firmly holds the stone core at an appropriate angle while the dominant hand strikes the core with a fast, accurate, aimed motion. In this task, the hand role differentiation is extreme. In contrast, our origami task required quite similar and sometimes overlapping roles for the two hands. It is likely that the behavioural asymmetries were not salient in this task, as evidenced by the fact that most participants did not notice the change in conditions. Furthermore, the differentiation in difficulty between the motor skill required to, for example, hold the paper flat on the table (typical for the non-dominant hand) while folding one corner (typical for the dominant hand) was much less than for stone tool-making. In addition, task learning is much faster, in part because there is ongoing visual feedback and the error tolerances are much wider than in stone knapping. We suggest that the relative difficulty of the movements required by the two hands during origami-making is likely not enough to cause differential activation of the brain's hemispheric specialisations, as previously proposed by [7]. In contrast, given that the acquisition of stone tool-making skills was both essential for survival and very difficult, we speculate that the most efficient learning strategy used the brain's existing hemispheric specialisations. For example, archaeological evidence from Neanderthals living 80,000 years ago, at the site of Buhlen in Germany, suggests that they experienced childhood pressure to become right-handed through social learning of extremely difficult "Keilmesser" stone tool manufacturing techniques [84].

We thus argue that the level and nature of manual expertise required to master a task may be crucial in determining whether the handedness of a demonstrator influences task performance. In experimental psychology, origami-folding and knot-tying are considered complex tasks. Indeed, 23% of origami figures produced by our participants were poorly formed, indicating that the task was challenging. However, humans can learn to reproduce a particular knot or origami figure in about an hour. For this type of task, flexible imitation of incongruent handers may be sufficient to support successful performance. In contrast, proficient Oldowan stone knapping needs weeks of practice and most stone tool types take years to master [85–87]. While the basic gestures and concepts of stone tool production can be learned in an hour with active teaching ([42], N. Uomini pers. obs.), learning this task by imitation alone is much less efficient [28]. The non-verbal social learning of stone knapping skills requires close attention to fine details of hand postures, stone core geometry, selection of where to strike, and striking direction and speed. It is likely that these essential details are easier to perceive and to reproduce when watching a congruent hander. This prediction could be tested by measuring the frequency of handedness congruence between masters and their apprentices learning modern-day crafts such as stone carving (we are not aware of any published data).

Our experimental findings are consistent with the evolution of concordant hand preferences due to social learning by imitation of complex bimanual skills such as stone tool manufacture. In our study, learners flexibly adapted their hand configuration to match that of the demonstrator, resulting in no decrease of performance for the incongruent-handedness conditions or from viewpoints requiring mental transformation. This result partly supports the Apprenticeship Complexity Theory, at least for origami imitation. We suggest that our origami task was not sufficiently challenging to cause obligate use of the brain's preferred right/left hand specialisations. As a consequence, using an incongruent hand configuration did not disrupt learning. Future work should focus on acquiring difficult craft skills that require extended learning periods and precise motor control. This would allow a check of whether there is a cost to incongruent-handedness and viewpoint on more complex and ecologically valid tasks. More work is also needed to establish how objects are represented during tool creation tasks that require mental transformation, particularly for difficult sequential bimanual actions such as stone knapping.

incorrect link; TBA

Supplementary Materials: The following is available online at https://oc.gnz.mpg.de/owncloud/index.php/s/ORKxdiaA7dvNQpw, Video S1: Full videos of origami-folding stimuli.

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