

**A new modulator of cultural transmission:
congruence between learning and onward
transmission contexts**

The effects of context congruence on cultural
transmission

Aliki Papa^{1*}, Mioara Cristea¹, Nicola McGuigan², Monica Tamariz¹

¹School of social Sciences, Heriot-Watt University, Edinburgh, Scotland, United Kingdom.

²School of Education and Social Sciences, University of Western Scotland, Paisley, Scotland,
United Kingdom.

*Corresponding Author

E-mail: ap106@hw.ac.uk

Abstract

The adoption of cultural variants by learners is affected by multiple factors including the prestige of the model and the frequency and value of the different variants. However, little is known about what affects onward cultural transmission, or the choice of variants that models produce to pass on to new learners. This study investigated the effects on this choice of congruence between two contexts: the one in which we learn variants and the one in which we later transmit them on. We hypothesized that when we are placed in a particular context, we will be more likely to produce (and therefore transmit) variants that we learned in that same context. In particular, we tested the effect of a social contextual aspect: the relationship between model and learner. Participants learned two variant methods to solve a puzzle, one from an “expert” (in an expert-to-novice context) and one from a “peer” (in a peer-to-peer context). They were then asked to transmit one variant onward, either to a “novice” (in a new expert-to-novice context) or to another “peer” (in a new peer-to-peer context). Participants were, overall, more likely to transmit the variant learned from an expert, and this effect can be attributed to model-prestige bias. However, a significant interaction between context of learning and context of onward transmission supported our hypothesis: the expert’s variant advantage was clear when transmitting to a novice, but it disappeared when transmitting to another peer. We conclude that a context-congruence effect impacts cultural transmission.

1 Introduction and Literature Review

Human culture is extraordinary, and its complexity – highly attributable to its ratchet-like evolution [1,2] – renders it unique in the animal kingdom [3]. The social transmission of cultural traits has been extensively studied (see reviews by [4–7]) in the laboratory (e.g., [8–11]), through the use of mathematical models (e.g., [12–15]), though agent-based computer simulations [16–18], and even in real-world paradigms (e.g., [19,20]). The data gathered from these studies has allowed us to understand more fully the biases that influence the likelihood that a specific trait will be passed from a transmitter to a new learner [21–24]. Specifically, transmitters and learners can have different relationships, defined by different transmission pathways [15,17,25,26]. Depending on the trait, a learner might be more likely to adopt a vertically transmitted variant, i.e., one transmitted from parent(s), an obliquely transmitted variant, i.e., one transmitted from older individuals other than the parents (e.g., a teacher), or a horizontally transmitted variant, i.e., one transmitted from peer(s) [27–30].

Model-based Biases

Previous research supports that human cultural transmission is “highly biased toward particular representations” [31] (p.121). Studies have focused on revealing and examining such biases, as well as the strength of their effects on cultural transmission [11,32–35]. Pioneering research was conducted by Boyd and Richerson [15], who proposed, among others, content-based biases. According to these, an individual’s likelihood of copying a variant is affected by the intrinsic properties and characteristics of that variant.

Of relevance to the current study is the role of model-based biases in transmission [15]. Model-based biases operate in those instances where the behaviour adopted by a learner is influenced by characteristics of the transmitter. Such characteristics include status [36] (e.g., having a

position of authority [37]), age [38,39], knowledge [38], success [37] and homophily, or similarity of the model to the observer [40,41]. Henrich and Gil-White [38] concluded that individuals are biased to copy successful individuals who have real or perceived skill; a strategy which can prove adaptive, as those individuals will, potentially, be more successful than others in the same environment [42]. Social prestige, along with age, are cues used by learners to infer their model's expertise [38,43]. In support of this claim adults prefer to copy prestigious individuals - those who others spend more time observing [44]. Children are more likely to copy other children when their actions are effective [45], but they tend to copy adults over children [46,47], regardless of whether they report being experts or not [48].

Transmission Pathways

An important aspect of the model-based biases is the social relationship formed between transmitter and learner. Cavalli-Sforza and Feldman [25] distinguished between three cultural transmission pathways, each of which attributes different characteristics to the model/transmitter: vertical (from a member of one generation to a biologically related member of a succeeding generation), oblique (from a member of one generation to a biologically unrelated member of a succeeding generation), and horizontal (from a member of one generation to another member of the same generation). According to the developmental stage of the learner, a different pathway is dominant over the others [19,49,50], so the learner is more likely to acquire the traits of certain transmitters over others.

Vertical/Oblique Transmission

Vertical transmission is dominant during infancy and early childhood [51,52], and it is considered the most adaptive transmission pathway from an evolutionary perspective. The parents - the transmitters most likely for a child to learn from during this stage - are the most

motivated individuals in their child's social environment, transmitting variants they deem most beneficial [15], even at the cost of their own fitness [53]. As long as environmental conditions do not change to the point where a different variant becomes more adaptive [30], it is likely that, once that child becomes a parent, they will deem the same cultural variant transmitted by their parent as the most beneficial for their child, as well.

Studies exploring vertical transmission have shown that complex traits such as political tendencies [54–56], academic values [57], religion, entertainment, sports, superstitions and beliefs, customs and habits [29] tend to be transmitted vertically, thus leading to high degrees of attitude concordance between parents and their children [58–60]. This intergenerational congruence, facilitated by humans' capacity for faithful imitation and transmission of traits across generations [1,10], has allowed the continuity and preservation of cultural information for at least two biological generations [29], while it often leads to cultural products - such as traditions - that are passed on for many more generations [1,3,21,61,62].

It is important to note that, when cultural evolutionary studies refer to “vertical” transmission, they often conflate vertical and oblique transmission under that label (e.g., [63–65]). In some of these studies, the effects of the model-based “vertical” bias are evident - i.e., the preference to copy an older, a more prestigious, or a more expert model. Children in these studies are more inclined to copy the actions of adults as opposed to those of other children [39,66,67]. For instance, when witnessing the performance of novel actions by both adults and peers, children imitated the actions of the adult models over those of the child models [68]. Moreover, Nagle [69] found that children would more readily imitate the actions of a highly competent teacher model than those of a highly competent peer model. Zmyj et al. [70] also found that fourteen-month-old infants' imitative tendencies increased as the age of the model increased; imitating adults more often than younger models. Finally, Cheng and Chartrand [71], found that adults were more likely to imitate the actions of those whom they perceived as their superiors.

Horizontal Transmission

On the other hand, less complex traits such as taste in clothes and hair [72], consumer socialisation [73], social skills [27], drinking behaviours [74–76], smoking [77–79] and eating behaviours [28,80] have been associated with horizontal cultural transmission - a pathway which can only guarantee the conservation of the transmitted information for one biological generation [25]. In fact, Rogers [81], argues that homophily - i.e., the tendency to imitate those who are similar to oneself - allows for more efficient communication, and it is more likely to lead to behaviour change.

As children age, horizontal transmission becomes the dominant pathway [50], with learners becoming more likely to acquire the traits of their peers than those of adults [25]. Seehagen and Herbert [66] have shown that children’s tendency to imitate peers more readily than adults increases as a function of age, with the older infants in their study retaining significantly more often the information they learned from their peers than from adults. Zmyj et al. [68] found that a child’s association of a model with herself can have a significant effect on the probability that she will copy that model (even in the absence of communicative context), as identifying a model as “like me” [82] leads to the “peer model advantage in infant imitation” (p. 2; see also [83]). Similarly, children tend to copy children over adults in a novel toy task [39] and, generally, tend to imitate their peers’ behaviours, as part of their ingroup identity [84].

The effects of a model-based “horizontal” bias have also been observed in adolescents and adults [85–87], with peers in these developmental stages deploying similar behaviours – i.e., showing behavioural congruence. Yabar, Johnston, Miles, and Peace [88] found that, when participants perceived a model as part of their group (i.e., similar to themselves), they were more likely to imitate their gestures than the gestures of a model whom they perceive as someone outside their group, even if both models performed the same gestures. Cheng and

Chartrand [71] have also found that participants were more likely to imitate the gestures of a confederate, when they perceived her to be a peer. Finally, Webb and Sheeran [89] found that behaviour-change interventions delivered by research assistants (non-experts) had a larger impact on behaviour than when they were delivered by experts.

In sum, much research has focused on which cultural variants learners will adopt and how cognitive biases – such as a model-based biases – may affect that choice, but it has produced conflicting results. Some studies suggest that a model-based vertical bias affects the learner’s choice, leading to a tendency to adopt the variants of older, more expert, or more prestigious transmitters. Others suggest that a model-based horizontal bias has a stronger effect on that choice, with learners preferring to adopt the variants of the transmitters who are most like themselves – i.e., who are identifiable as “peers”.

Associative Learning

The inconsistencies in these results could be addressed by considering the role of associative learning [90,91] during cultural transmission. Associative learning takes place when a learner connects two events, where one event refers to, signals, co-occurs with, or causes the other [92–95]. It has previously been suggested that associative learning could account for imitation – i.e., a learner’s reproduction of a model’s observed behaviour [96] – and be involved in the acquisition of complex traits, such as word-learning [97]

Heyes and Pearce [98] have argued that associative mechanisms “make learning selective” (p. 6) and they can be viewed as learning strategies. Thus, a learner may use social (and asocial) cues to “decide” which traits to acquire. During cultural transmission, specifically, learners could be associating the variant they deem best to acquire for themselves with the transmitter who has a specific relationship with them. For example, an individual will acquire the political

orientations of his parent(s) [54,56], because of their parent-child relationship, while that same individual will acquire the social skills of a peer [27], because of their peer-peer relationship.

As such, a congruence in cultural traits could arise between two consecutive “generations” (the transmitter and the learner) – whether these are vertical (e.g., parent-child) or horizontal (peer-peer) generations – and this determines the nature and complexity of the traits [29]. In general, the traits that are more relevant to our survival – such as subsistence and childcare skills – tend to be transmitted vertically [50,99], thereby persisting for generations. Vertical cultural transmission can sometimes be from just one parent to the child. Specifically, evidence suggests that there exists a higher behavioural congruence in the mother-daughter and father-son dyads than the father-daughter and mother-son dyads (e.g., [100–102]). It may be that these patterns are due to the impact of the context of acquisition, whereby a woman transmits to her daughter cultural variants she acquired from her mother, or a student transmits to a classmate something acquired from another classmate and so on.

Yet, we do not fully understand the factors influencing what the learners transmit onwards once they become transmitters. Over the course of our development, we learn different strategies to solve problems. For instance, to socialise with others and form new friendships, one might have learned from one individual that it is a good strategy to ask interesting questions and from another individual that it is effective to make jokes and share anecdotes. Or a child might have learned from her mother that, to keep a boiling egg from cracking, a good strategy is to pour some vinegar in the water, whereas another strategy learned from a friend of hers would be to add a lemon wedge in the water. So, from enhancing our bonds with others to boiling eggs, we are often exposed to more than one variant of the same trait. But which variant is chosen to be transmitted onward and which factors may influence this choice?

Current study

To understand how information is transmitted over social networks in the long term, we do not only need to determine the process of the learner's choice of cultural variants to adopt; we also need to examine which cultural variants that learner transmits onward to others. This question is extremely important, and yet has been severely understudied: if a learner has acquired more than one variant of the same cultural trait (e.g., two different strategies to solve a problem) in different contexts - one from an expert and one from a peer - does that learner choose to transmit different variants in different onward transmission contexts (see Fig 1).

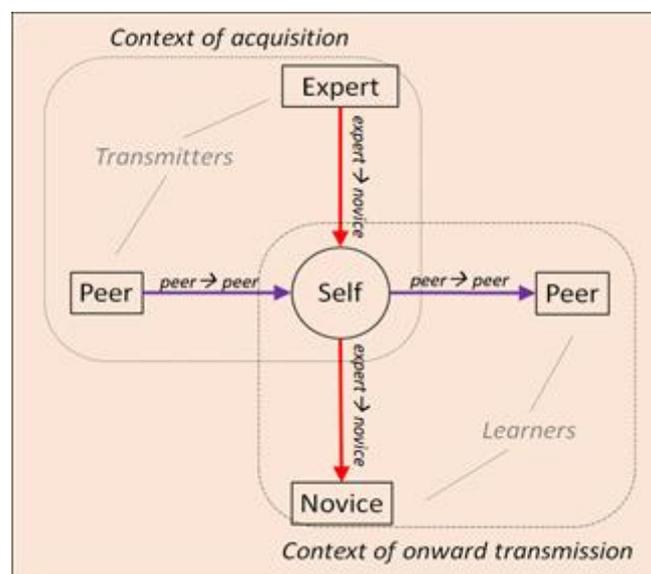


Figure 1: Social Relationships. This figure presents the social relationships between transmitters and learner (Expert-to-Novice / Peer-to-Peer) in the acquisition context, and between that learner and others (Expert-to-Novice / Peer-to-Peer) in the onward transmission context.

The aim of the current study was to test whether the likelihood that a cultural variant was transmitted onward was affected by the social relationship between the participant and the learner during acquisition (i.e., the Participant is an Expert and transmits onward to a Novice, versus the Participant is a Peer and transmits onward to another Peer).

Hypotheses

Our first hypothesis concerned model-based bias. It was predicted that a model-based vertical bias would influence the strategy that the participants transmitted onwards. Specifically, the participants would be more inclined to transmit the expert's strategy, irrespective of whether they were transmitting to a novice or to a peer.

Our second hypothesis concerned associative learning [90,92], during which our participants connect two events [92–95]. We predict that cultural variants will become associated with the context in which they were learned, and therefore their onward transmission will be affected by congruence between the contexts of acquisition and transmission. Specifically, we hypothesise that participants who learn two distinct variants, one from a peer (in a peer-to-peer context) and one from an expert (in an expert-to-novice context) will be more likely to transmit the former variant when transmitting to another peer (in a new peer-to-peer context), and more likely to transmit the latter variant when they once they have become an expert transmitting to a novice (in a new expert-to-novice context).

To test the above, we employed a novel experimental design that allowed us to manipulate the context of acquisition by introducing two variants of the same trait to each participant. One trait was introduced by an expert (who represented a vertical transmission pathway), and the other by a peer (who represented a horizontal transmission pathway). We also manipulated the context of the onward transmission by asking the participant to transmit the trait to either a novice or a peer.

As we included two different strategies (traits) in our experiment, there were two confounding variables that could potentially impact upon what trait the participants transmitted onward: (i) the content of the strategy itself and (ii) the order in which the two strategies were acquired by the participant. The order of acquisition has previously been shown to affect learning via

primacy and recency effects [103–106]. For instance, the ability to recall brand names is more strongly affected by primacy than by recency [107], as is the ability to learn the attributes of a repeated stimulus [108]. Therefore, to counter such confounds we fully counterbalanced both the strategy variant that was transmitted to the participants and the order in which the strategies were learned.

2 Methods

This study was granted ethical approval from Heriot-Watt University’s School of Social Sciences Ethics Committee, and it was pre-registered with the Open Science Foundation (link: <https://osf.io/6q4bn>).

2.1 Participants

Sixty-four adults (33 female, $M = 21.17$ years, $SD = 2.19$ years; range = 18-28 years) were recruited from the student population at Heriot-Watt University (UK). Participants were recruited in one of two ways, either by the experimenter approaching the participant directly in a University social space, or via an advert posted around the University campus.

Five additional students, all female and aged between 19 and 21 years (two second years, one third year, and two final years), acted as the confederates for the experiment.

All participants were entered into a raffle to win one of two Amazon vouchers (£25 each), with any participating psychology undergraduate students also receiving course credit for their participation.

2.2 Materials

2.2.1 Task

Using gargenerator.com we created a linear sequence of seven interconnected gears (Fig 2). The gears were presented on a computer display (sequence frozen at first) and participants were asked to predict the direction (clockwise or anti-clockwise) in which the last gear in the sequence would turn, if the first gear turned clockwise. To highlight that the final gear was the central focus of the problem it was coloured blue to as opposed to black for the other six gears. This task was chosen as it was readily understandable and had two alternative solutions that seemed equivalent in difficulty and took the same time to complete.

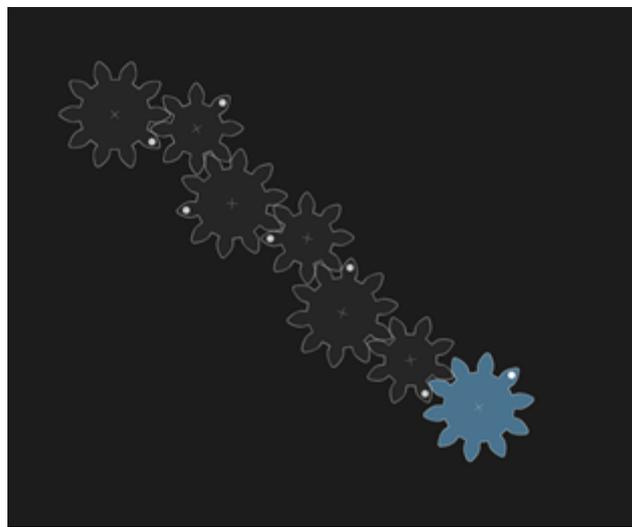


Figure 2: The seven-gear sequence. This figure presents the sequence of the seven gears as they appeared on the computer screen for each participant to see. The participants saw the sequence frozen, and, after having heard the solutions, the experimenter pressed ‘Play’ and the gears started to move.

The first and last gears always turned clockwise.

2.2.2 Problem and strategies for solving it

All participants were presented with the same problem: to state correctly which way the last gear in a chain would turn given that the first gear is turning in a particular direction. Next, the experimenter (expert) and the first confederate (peer) each provided a verbal description of one

of two strategies (counterbalanced across the expert and the peer) that could be used to solve the problem:

Strategy A: Counting the gears. *“First, you count all the gears. If we have an even number of gears, then the last gear will turn in the opposite direction from the first. If we have an odd number of gears, then the last gear and the first gear turn in the same direction”*.

Strategy B: Alternate direction of the gears. *“You can go clockwise, anticlockwise, clockwise, anticlockwise... clockwise [pointing to each consecutive gear in turn] when you point at the last gear, you will be saying whether it will turn clockwise or anticlockwise”*.

2.3 Design

Throughout the study the verb *“to teach”* was used to describe those instances where an expert transmitted to a novice, and the verb *“to show”* was used to describe those instances where a peer transmitted to another peer.

The study employed a between groups design in which participants were randomly allocated to one of two conditions (expert-to-novice condition or peer-to-peer condition). Each condition began with an identical acquisition phase in which participants were presented with both strategies (A and B) for solving the gear task, before undertaking a second, onward transmission phase, in which the participants were asked to either *teach a novice* (expert-to-novice) or *show a peer* (peer-to-peer) how to solve the same problem. Thirty-two participants were tested in each condition.

The experimental design is summarised in Fig 3 below.

<u>1. Acquisition Phase</u> (All participants trained in both contexts*)	<u>Expert (Exp)</u> teaches participant (P) (P is a novice to Exp) <i>Strategy A or B</i> AND <u>Peer (C1)</u> shows participant (P) (P is a peer to C1) <i>Strategy B or A</i>
<u>2. Onward Transmission Phase</u> (1/2 participants tested in each context)	Participant (who is now an expert) <i>teaches</i> strategy to a <u>novice (C2)</u> OR Participant (who is a peer) <i>shows</i> strategy to another <u>peer (C2)</u>
Note. Order (Expert-to-Novice, Peer-to-Peer) and Strategy (A, B) were fully counterbalanced.	

Figure 3. Illustration of the experimental design employed. First, in the acquisition phase participants were trained by an expert and a peer on strategy A and strategy B. Next, in the onward transmission phase, participants were told either they were now an expert and had to *teach* a novice how to solve the gear task (expert-to-novice condition) or that they now had to *show* another peer (peer-to-peer condition) how to solve the gear task. The ‘expert’ in the acquisition phase (underlined) was the experimenter and the underlined ‘novice’ and ‘peers’ were three different confederates (fellow students).

The dependent variable was the strategy produced in the context of onward transmission, either the strategy that was taught by a novice in the context of acquisition or the strategy that was shown by a peer. The order of presentation of the two variants (A and B), and the transmitter from which each of them was learned (expert or peer) was fully counterbalanced (see S1).

2.4 Procedure

The experimenter led the participant to the waiting area, where they were introduced to the first confederate (C1), who pretended to be another participant (i.e., a peer of the participant). The experimenter explained that the experiment would be conducted in pairs and led both the participant and C1 to the testing lab. On entry to the testing lab the participant and C1 read a participant information sheet and signed a consent form each. Next, they were given the

following instructions: *“I will present you with a problem and then I will teach you the solution. If you look at the computer screen, you’ll see some gears connected to each other and (experimenter hits ‘play’) move each other. Now see, the first gear turns clockwise (experimenter points at the gear on the left top corner; then hits ‘stop’). The problem is to figure out which way the last gear of the sequence turns”*. After that, one of four different dialogues occurred, according to the condition in which the participant was assigned (see S2 for all dialogues). Below is an example of one of the dialogues:

E.g., expert’s strategy first, participant teaches novice:

Phase 1: Acquisition

Experimenter – I will teach you the solution I’ve taught many people before as part of my experiment. [Teaches strategy].

C1 (Peer) – I’ve played this before, I know another solution. [Shows alternative strategy].

Experimenter – [Initiates Phase 2]: Oh okay, that’s interesting! So now you both know two different solutions to this problem. Okay, for the next part I need you both to teach your solution to two other participants who don’t know how to solve the problem, yet. So, I’ll need one of you in this lab and the other one to the other lab. Who would like to come with me to the other lab?

C1 (Peer) – I’ll come.

The experimenter leads C1 out and, after approximately ten seconds, brings in a different confederate (C2): the novice.

Phase 2: Onward Transmission

Experimenter – (looks at C2) Okay so, the problem is to figure out which way the last gear turns... [Participant] is now an expert at this, and he/she will now teach you his/her solution to the problem.

Following the above, the experimenter left the testing lab. Both she and the first confederate were absent during the onward transmission phase (i.e., from participant to a different confederate) to remove demonstrator presence-related pressures [4,109,110]. After approximately thirty seconds (and after listening through the door to make sure that the participant had finished teaching/showing their solution) the experimenter returned to the testing room and asked C2 to go back to the waiting area (from where she supposedly brought them) to await debriefing. The confederate then left the testing room and noted the solution that the participant chose to pass on (so that they could inform the experimenter after the participant left).

Next, the experimenter asked the participants a series of questions that aimed to determine why a particular solution was transmitted and whether the participant suspected that C1 and C2 were confederates:

1. Why did you teach/show that solution?
2. What did you think happened in this experiment?
3. What did you think of the people who were with you in this experiment?

Finally, the experimenter debriefed the participants and thanked them for their participation.

2.5 Coding

For each participant, we coded their ID, gender and age, and the following variables:

- V1. Control factor 1. Order of strategy (A or B first)
- V2. Control factor 2. Order of acquisition context (Expert or Peer first)

V3. Factor: Context of onward transmission (Expert-to-Novice or Peer-to-Peer)

V4. Dependent variable: Strategy transmitted onward by the participant (Expert or Peer strategy).

2.6 Analysis

To confirm that the strategy variant (A or B) and the order of acquisition (controlled; see design) were not associated with the transmitted variant (Expert or Peer strategy) two Chi-squared tests of independence were conducted.

To test the effects of our factor variable on the transmitted strategy, we constructed a generalised linear mixed effects model (binomial family) using R (R Core Team, 2012). The model was fit using `glmer` from the `lme4` package [111,112] and the `bobyqa` optimiser. The dependent variable was the transmitted variant (Expert or Peer strategy); the fixed effect was the context of onward transmission (Expert-to-Novice or Peer-to-Peer), and we included random intercepts for participant ID and participant gender. The full model (Transmitted variant ~ Context of onward transmission + (1 | Participant) + (1 | Gender)) was tested against the null model, which contained only the random effects, using the `anova()` function.

3 Results

Two male participants (both from the expert-to-novice condition) were excluded from the analysis, as the post-test questionnaire revealed that they suspected the presence of confederates. No other participants indicated that they suspected this during the post-test questions.

The Chi-squared tests of independence indicated that the strategy variant (A or B) was not associated with the transmitted variant (Expert or Peer strategy), $\chi^2(1) = 0.13$, $p > 0.1$, and neither was the order of acquisition (first from Expert or first from Peer), $\chi^2(1) = 0.52$, $p > 0.1$.

Table 1: Chi-squared test results.

Context of onward transmission	Variant transmitted onwards		Total N	Chi-squared (df = 1)	p value
	Expert's strategy N (%)	Peer's strategy N (%)			
Expert → Novice	27 (90%)	3 (10%)	30	19.20	.000
Peer → Peer	14 (43.8%)	18 (56.3%)	32	0.50	.480
Total (%)	66.1%	33.9%			
<i>Chi-squared</i>	4.12	10.71			
<i>p value</i>	.043	.001			

This table presents the results of the Chi-squared tests for each comparison of contexts of onward transmission (Expert → Novice / Peer → Peer) and acquisition (Expert's strategy / Peer's strategy).

In the condition when onward transmission was expert to novice (Table 1; First row), twenty-seven participants transmitted the expert strategy (congruent) and three the peer's strategy (incongruent). This difference is highly significant ($\chi^2(1) = 19.20$, $p = .000$). In the condition when onward transmission was peer to peer (Table 1; Second row), fourteen participants transmitted the expert strategy (incongruent) and eighteen the peer's strategy (congruent). This difference is not significant. The expert's variant (Table 1; First column) was produced twenty-seven times in the expert-to-novice transmission context (congruent), and fourteen times in the peer-peer transmission context (incongruent); this difference is significant. The peer's variant (Table 1; Second column) was produced three times in the expert-to-novice transmission context (incongruent), and eighteen times in the peer-peer transmission context (congruent); this difference is highly significant.

3.2 GLMER

The full model containing the fixed effects (context of acquisition and context of onward transmission) was significantly better than the null model ($\chi^2 = 16.02$, $df = 1$, $p < 0.001$; see Table 2 below).

Table 2: Summary of our full GLMER model.

Model: Context of acquisition + (1 Participant) + (1 Gender)				
	Estimate	SE	z-value	p-value
Context of Onward Transmission (Peer-to-Peer)	2.45	0.71	3.45	< 0.001***
Marginal R^2 : 0.31, Conditional R^2 : 0.31				

The context of onward transmission significantly affected the participants' choice of which variant to transmit, with those in the Peer-to-Peer condition being more likely to transmit the peer's variant onward (see Fig 4).

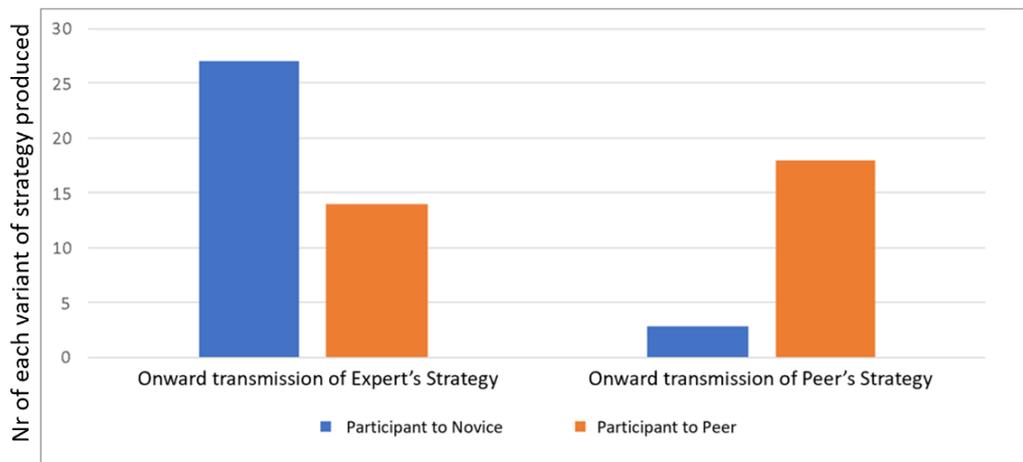


Figure 4: Number of each variant of strategy produced by acquisition context and onward transmission context.

Congruent results – in which the variant acquired from an expert was taught to a novice or the variant acquired from a peer was shown to another peer ($N = 45$) – were significantly more frequent than instances in which the variant acquired from an expert was shown to a peer or the variant acquired from a peer was taught to a novice ($N = 17$) ($\chi^2 = 18.95$, $df = 2$, $p < 0.001$) (leftmost and rightmost bars in Fig 4).

4. Discussion

The main objective of the current study was to determine whether the context of acquisition and onward transmission affected what trait the transmitter chose to pass on to the learner. Two models, an expert and a peer, each taught the participant a different strategy for solving a problem, before the participant was allowed to transmit onward only one of the strategies. Of interest was how often each strategy was transmitted onward by the participants and whether their choice was affected by the participant→learner relationship (Expert→Novice; Peer-to-Peer). Our results yield three major conclusions, each of which are discussed below.

4.1 Model-based Biases

As predicted, the participants demonstrated a general tendency to transmit the expert's variant onward. We, therefore, suggest that - in accordance with previous studies [36,39,44,66,67] - a model-based *vertical* bias affected transmission, with the expert being the transmitter whose strategy was more likely to be transmitted onward to the learner.

Generally, the model-based biases [15] (see also [113]) posit that the likelihood of a learner copying one variant over its competing one(s) is affected by the specific attributes of the model/transmitter who exhibits that variant [48,114,115]. It has previously been shown that an expert may be a more influential model to copy, with attributes including perceived skill and

knowledge [37,38] increasing this influence. The experimenter - i.e., the expert model in our design - explicitly displayed these attributes, by presenting herself as the “*teacher*” who has “*taught many people before*” in “*her*” experiment. In contrast the peer model (C1) and learner (C2) were presented as another participant about to learn something and “*a participant just like*” the participants themselves, reinforcing the perceived homophily and equality in skill and knowledge.

4.2 Associative Learning and Context-congruence effect

However, despite the expert appearing to have a stronger influence on transmission than the peer, the findings show that learners do not copy experts unconditionally. In the context of a Peer-to-Peer relationship, participants transmitted onward the strategy acquired from another peer significantly more often than those instances where there was an Expert-to-Novice relationship. As this tendency cannot be attributed to a model-based horizontal bias - because only a small fraction of our participants in the Expert-to-Novice transmission context transmitted onward the peer’s strategy - we suggest that there exists another factor which impacted upon social transmission.

Our results suggest that, in addition to model-based biases, a context-congruence bias operates on transmission. In the context of onward transmission to a peer, we tend to pass variants learned in a peer-to-peer acquisition context, while in the context of onward transmission to a novice, we tend to pass variants learned in an expert-to-novice acquisition context (Fig 1). So, the relevant feature of the transmitter, which affects social transmission, is his/her *relationship* with the learner - as formed by the context of onward transmission - and not simply the attributes of the transmitter during acquisition [15], such as expertise and knowledge [38], or familiarity and homophily [68].

By saying to the participants that they were “now an expert”, we constructed an expert-to-novice onward transmission context; here, participants tended to produce the variant they learned in the Expert-to-novice acquisition context. Conversely, by asking to participants to “show a peer” how to solve the puzzle, we constructed a peer-to-peer onward transmission context; here, participants tended to produce both variants equally. For a participant at the moment of onward transmission, beside model-based bias, the only difference between the two variants is which context with which they were associated during acquisition. Therefore, we can infer that the context-congruence effect we found is due to associative learning [92–95].

Although previous studies have also demonstrated the intergenerational congruence of traits during vertical - e.g., parent-to-child [85–87], and horizontal transmission - i.e., peer-to-peer [116,117], the cognitive processes in operation leading to that congruence had not been sufficiently explored. This might be due to the narrower scope of focus of social transmission studies, which attempts to answer questions such as how the behaviour of peers affects the behaviour of participants [118], or how the closeness of a parent and child affects their behavioural congruence [119–121].

In our study, we have widened that scope, by examining how relationships between the contexts of acquisition and onward transmission affect the social transmission of cultural traits. This illustrates the important role of associative learning in social transmission and the resulting congruence between transmitted behaviour in acquisition and transmitted behaviour in onward transmission. The cancellation of the model-based bias effect when participants were transmitting to a peer suggests that the magnitude of the acquisition context congruence effect is at similar to that of the model-based bias. To estimate the magnitude of each force with more precision, future studies could include a control condition in a neutral context of transmission that serves as a baseline against which either force can be compared separately.

4.3 Onward Transmission effects

In turn, then, we have shown – for the first time – evidence for a factor which affects not only the adoption of behaviour by a learner, but, also, the *onward* social transmission of said behaviour by that learner: context-congruence. This has important implications for cultural evolution, as it explains the continuity of vertical transmission of traits and their subsequent conservation [29], and the lower continuity of horizontal transmission of traits and the fast cultural changes to which this can lead [122].

The context-congruence effect we found entrenches the reliance of cultural variants on a particular transmission pathway. So, we can infer that the parents' tendency to transmit to their children - the learners at time t - their political orientations [123,124] will lead to the children's tendency to transmit onward the same orientations to their children at time $t + 1$ independently of whether they acquire different ideologies from their peers in the meantime. By extension, we can assume that all traits – including gender ideology, religious values, academic values and so on – previously found to be transmitted from parent to child [29,57–60], will continue to follow that same vertical pathway, thus conserving such traits for many generations to come [10,21,125].

Similarly, traits which were found to be horizontally transmitted (from peer to peer) will also continue to follow the congruent pathway. Despite only guaranteeing the persistence of behaviours for a maximum of one cultural generation, horizontal transmission can lead to vast cultural change [3,10,21,25,29,62,125], especially in the Information Age. The context-congruence bias could be operating behind the increasing peer-to-peer transmission of traits through social media [126–128]. This would explain the continuity of transmitting maladaptive traits such as fake news and disinformation [119–121]. More importantly, it could be the key

to identifying ways of tackling problems arising from such phenomena, such as the worsening of disease outbreaks [129,130] and the flourishing of racist attitudes [128,131].

The context-congruence effect we have revealed affects long-term cultural evolution. In the extreme, cultural variants that are learned purely horizontally, among age-peers, are locked in a particular generation and die out with it (an example of this are slang words that characterise a generation; see [132]), and variants that are transmitted purely vertical will be very long-lasting as they will be preserved over generations. Knowing which variant of cultural variants tend to be passed on from parents to children or among peers, therefore, allows us to predict the cultural fate of those variants. Cavalli-Sforza et al. [29] found, for example, that religion tends to be passed on from mother to child, political ideology from father to child, while social skills tend to be transmitted between peers [27]. Knowing the strength of these effects could be used to fit parameterised evolutionary models and help predict the longevity of cultural traits.

The congruence effect does not mean that cultural traits will be deterministically trapped in a particular transmission pathway. Just as context congruence interacts with model-based biases – as shown in our results – it can also interact with content-based, or direct biases, whereby more adaptive traits are preferentially transmitted. For instance, if a variant learned from a peer is very adaptive, it may overcome the congruence effect and be preferentially transmitted onwards both horizontally, to peers, and vertically, to children and novices.

4.4 Experimental design issues and future work recommendations

Our experiment used a complex design, part of which was the creation of three cultural generations that employed confederates. For success, it was essential that the participants believed that the confederates were co-participants in the experiment. The post-experiment

questions revealed that two participants suspected that the confederates were, in fact, part of the experiment. Although none of the remaining participants appeared to have realised the presence of confederates, one could argue that we cannot expect that the transmitter-confederate was someone with whom the participants would associate with to the point that they felt she was their peer. Her additional knowledge regarding the experiment may have hindered somewhat the participant's ability to see her as their peer. In real-world situations a learner acquires cultural information from a peer-transmitter who possesses knowledge that the learner does not. Yet, the transmitter will still be identifiable as a peer, albeit being more knowledgeable. In our study, the difference of knowledge between the participants and the confederates did not preclude their perceiving the confederates as similar to themselves, or their associating the peer's strategy with the one deemed best to transmit onward to them. Thus, even with this potential limitation, we observed context congruence. In the case of real peers and real experts (or real parents) the effect may be stronger.

The participants' perception of their knowledge status in relation to their perception of both the transmitter and the learner's knowledge status was an essential tool in our design. When participants were introduced to the "*novice*", the experimenter referred to them as "*experts*" to facilitate the perception of their difference in knowledge/expertise, and when introduced to the "*peer*", the experimenter referred to that confederate as "*another participant just like you*", to strengthen the perception of peer status. However, it would be difficult to ascertain the dynamics of the participant→learner relationship during onward transmission, as we had no way of measuring the increase or decrease in perceived expertise and/or peer status. Despite that, we assume that the participants experienced analogous situations in their everyday lives, in which they felt like "*experts*" (e.g., when teaching a younger cousin how to win at a game or teaching a sibling how to solve their math problem etc.) and "*peers*" in relation to others (e.g., when helping a classmate with homework, when showing a friend how to play a game

they like etc.). In these situations, their perceived role as transmitters was not always apparent (as in our experiment), but it was implied.

Although our study provided evidence for the context-congruence bias of transmitter and learner relationship as formed by expertise versus peer status, other characteristics could also be shaping this relationship during acquisition and onward transmission. For instance, it is a consensus in the literature that mothers and daughters share higher levels of behavioural and attitude concordance than do mothers and sons or fathers and daughters [119–121]. Gender could, then, be another extension of the transmitter-learner relationship which leads to congruency in their choice of trait transmission. In our study, all the transmitters during acquisition (i.e., the experimenter and the confederates), as well as the learners during onward transmission (confederates) were female, so we could not test for a gender congruence, though it would be an interesting aspect which future research could investigate. Other characteristics that should be explored as they could be significantly affecting the relationship between transmitters and learners can include race [133,134] and social class [135]. In general, there could be multiple dimensions of the context whose congruency could affect transmission including place, time of day, time of year, and language spoken (for multilingual individuals) among many others.

Finally, our study suggests that the model-based bias and context-congruence effects interact with each other. An interesting next step would be to examine how these interactions occur with different actors (e.g., mothers, fathers, teachers, peers, experts) at different ages and for different cultural traits. Quantifying the relative strength of different effects and biases is another interesting avenue to be explored.

4.5 Conclusions

In sum, we have provided evidence for a novel factor in cultural transmission that links acquisition and onward transmission that is mediated by associative learning. In our study, cultural variants were more likely to be passed on if aspects of the current context were also present in the context in which the variant was acquired. Specifically, if we learn different variants of a trait from a peer and an expert, we tend to transmit the former to other peers and the latter when we become experts. Extending beyond our study, the context-congruence effect may account for the conservation of cultural traits - such as language, religion, tradition, and habits - which are transmitted vertically from parent to child within a population, as well as the assumption that, such traits, will continue to follow a vertical pathway of transmission. In parallel, context-congruence explains the cultural change brought forth by the transmission of traits from peer to peer, as transmitters will continue to pass on their horizontally acquired knowledge preferentially to other learners - given these learners are perceived peers - using means which enable and support fast horizontal transmission, such as social media.

To conclude, our work makes a key contribution to cultural evolutionary theory: for the first time, it links learning and adoption of cultural traits on one hand to their subsequent production and onward transmission on the other. This will allow us to better understand the overall process of cultural transmission in individuals and populations and the fate of cultural traits over different timescales. In turn, it will allow us to ensure the conservation of target traits and behaviour, even, intercept and disrupt the transmission of maladaptive information, such as political extremities, disinformation, and inequality.

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Supporting information

S1: Design

In order to control our confounding variables, we counterbalance the strategy variant – counting-the-gears (strategy A) versus alternate-directions (strategy B) – and the order of the presentation of the two strategies to the participants (expert’s first, peer’s last, versus peer’s first, expert’s last) all participants were allocated to one of two different subgroups, so that each subgroup had sixteen participants (see also table S1 below):

1.a. Expert-Peer-Novice: All sixteen participants in this group were asked to *teach a novice* (a confederate) how to solve the problem. Eight of the participants in this group were first taught by the expert strategy A, and then they were shown by a peer strategy B. The remaining eight participants were first taught by the expert strategy B, and then they were shown by a peer strategy A.

1.b. Peer-Expert-Novice: All sixteen participants in this group were asked to *teach a novice* (a confederate) how to solve the problem. Eight of the participants in this group were first shown by a peer strategy A, and then they were taught by the expert strategy B. The remaining eight participants were first shown by a peer strategy B, and then they were taught by the expert strategy A.

2.a. Expert-Peer-Peer: All sixteen participants in this group were asked to *show a peer* (a confederate) how to solve the problem. Eight of the participants in this group were first taught by the expert strategy A, and then they were shown by a peer strategy B. The remaining eight participants were first taught by the expert strategy B, and then they were shown by a peer strategy A.

2.b. Peer-Expert-Peer: All sixteen participants in this group were asked to *show a peer* (a confederate) how to solve the problem. Eight of the participants in this group were first shown by a peer strategy A, and then they were taught by the expert strategy B. The remaining eight participants were first shown by a peer strategy B, and then they were taught by the expert strategy A.

S1 Table. This table presents the two conditions and their subgroups, in which the participants were allocated.

	CONDITION 1		CONDITION 2	
	Group a	Group b	Group a	Group b
Phase 1	Expert (Experimenter) teaches strategy A (or B)	Peer (Confederate 1) shows strategy A (or B)	Expert (Experimenter) teaches strategy A (or “B)	Peer (Confederate 1) shows strategy A (or B)
Phase 2	Peer (Confederate 1) shows strategy B (or A)	Expert (Experimenter) teaches strategy B (or A)	Peer (Confederate 1) shows strategy B (or A)	Expert (Experimenter) teaches strategy B (or A)
Phase 3	Participants are asked to teach a strategy to a novice (Confederate 2).		Participants are asked to show a strategy to a peer (Confederate 2).	

In Condition 1, the participant assumes the role of an expert, and is asked to teach a strategy to a novice. In condition 2, the participant assumes the role of a peer, and is asked to show a strategy to a peer. The groups within each condition are formed to counterbalance the strategy variants and the order of presentation to the participant.

S2: Procedure according to each condition

Expert's strategy first, participant teaches novice:

Phase 1: Acquisition

Experimenter – I will teach you the solution I've taught many people before as part of my experiment. [Teaches strategy].

C1 (Peer) – I've played this before; I know another solution. [Shows alternative strategy].

Experimenter – [Initiates Phase 2]: Oh okay, that's interesting! So now you both know two different solutions to this problem. Okay, for the next part I need you both to teach your solution to two other participants who don't know how to solve the problem, yet. So, I'll need one of you in this lab and the other one to the other lab. Who would like to come with me to the other lab?

C1 (Peer) – I'll come.

The experimenter leads C1 out and, after approximately ten seconds, brings in a different confederate (C2): the novice.

Phase 2: Onward Transmission

Experimenter – (looks at C2) Okay so, the problem is to figure out which way the last gear turns... [Participant] is now an expert at this, and he/she will now teach you his/her solution to the problem.

Peer's strategy first, participant teaches novice:

Phase 1: Acquisition

C1 (Peer) – I've played this before; I know a solution. [Shows strategy].

Experimenter – Oh okay, that’s interesting! I will also teach you the solution I’ve taught many people before as part of my experiment. [Teaches alternative strategy, then initiates Phase 2].

The experimenter leads C1 out and, after approximately ten seconds, brings in a different confederate (C2): the novice.

Phase 2: Onward Transmission

Experimenter – (looks at C2) Okay so, the problem is to figure out which way the last gear turns... [Participant] is now an expert at this, and he/she will now teach you his/her solution to the problem.

Expert’s strategy first, participant shows to peer:

Phase 1: Acquisition

Experimenter – I will teach you the solution I’ve taught many people before as part of my experiment. [Teaches strategy].

C1 (Peer) – I’ve played this before; I know another solution. [Shows alternative strategy].

Experimenter – [Initiates Phase 2]

The experimenter leads C1 out and, after approximately ten seconds, brings in a different confederate (C2): the peer.

Phase 2: Onward Transmission

Experimenter – (looks at C2) Okay so, the problem is to figure out which way the last gear turns... [Participant] is a participant just like you, and he/she will show you his/her solution to the problem.

Peer's strategy first, participant shows to peer:

Phase 1: Acquisition

C1 (Peer) – I've played this before, I know a solution. [Shows strategy].

Experimenter – Oh okay, that's interesting! I will also teach you the solution I've taught many people before as part of my experiment. [Teaches alternative strategy, then initiates Phase 2].

The experimenter leads C1 out and, after approximately ten seconds, brings in a different confederate (C2): the peer.

Phase 2: Onward Transmission

Experimenter – (looks at C2) Okay so, the problem is to figure out which way the last gear turns... [Participant] is a participant just like you, and he/she will show you his/her solution to the problem.

S3: Data availability

The datasets generated during and/or analysed during the current study are available in the Zenodo repository, <https://zenodo.org/record/6463741#.Y1m19DfMJS5>.