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ORIGINAL RESEARCH

Brain and psychological mediators of imitation: sociocultural versus physical traits

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Abstract The acquisition of cultural beliefs and practices is fundamental to human societies. The psychological and neural mechanisms underlying cultural acquisition, however, are not well understood. Here we used brain imaging to investigate how others' physical and sociocultural attributes may influence imitative learning, a critical component of cultural acquisition. While undergoing fMRI, 17 European American young adults imitated models from three different racial groups performing novel hand gestures. Participants learned that half the models shared

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their political ideology and half did not. We found that the model's political ideology—a sociocultural characteristic devoid of any physical correlates—was sufficient to influence imitative accuracy, and that this effect was mediated by changes in feelings of similarity to the model. Furthermore, the relationship between the imitative model's political ideology and imitation accuracy was mediated by brain regions associated with imitation and its control, as well as mentalizing. Finally, comparing these new data with those from one of our previous studies revealed that knowledge of a model's political ideology reduces the influence of the model's race on feelings of similarity to the model and imitation accuracy, as well as activity in brain regions typically activated during imitation. Taken together, these findings suggest that (1) others' sociocultural characteristics influence imitative biases more so than their physical attributes, and (2) that neural systems associated with imitation, imitation control, and mentalizing contribute to this cultural learning process.

Keywords Cultural transmission · Ethnic marker hypothesis · Race · Political ideology · fMRI · Medial prefrontal cortex

Introduction

The acquisition of cultural beliefs and practices is fundamental to human societies. Anthropological theories of cultural acquisition and transmission such as dual-inheritance theory (Cavalli-Sforza and Feldman 1973, 1981; Durham 1991; Feldman and Laland 1996) and culture-gene coevolutionary theory (Boyd and Richerson 1976, 1988) predict that humans should possess biases that enhance the efficiency of learning from others. One of these biases is that people preferentially imitate models whom they perceive as similar to themselves, or high in social status (Henrich and McElreath 2003). Both observational and experimental studies have provided evidence of imitative biases related to self-similarity (Bandura et al. 1961; Bussey and Bandura 1984; Mesoudi 2009) and social status (Chudek et al. 2012; Mesoudi 2009). How others' physical and sociocultural attributes contribute to these imitative biases, however, is still unknown. Even less is known about the neural mechanisms underlying cultural acquisition. We have proposed that brain regions associated with imitation (e.g., the inferior frontal gyrus, pars opercularis), mentalizing (e.g., the medial prefrontal cortex) and reinforcement learning

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(e.g. the ventral stratum) may act together to support cultural acquisition via imitation (Losin et al. 2009).

In a previous study, we used an explicit imitation paradigm in which participants imitated novel hand actions of male and female models from different racial groups while undergoing fMRI. Regardless of the participant's own race, imitating models from a racial group that participants associated with lower levels of social status (black vs. white or Asian) resulted in reduced imitation accuracy and greater activity within brain regions implicated in visual attention and imitation (Losin et al. 2013). We interpreted these findings as reflecting increased difficulty associated with performing a task that was incongruent with the cultural imitative bias toward high status models. In terms of the psychological mechanisms underlying cultural learning, our previous findings lead us to hypothesize that imitative biases related to race are likely to be based on the sociocultural (in this case social status) rather than the physical correlates of race. It remained unclear, however, whether these findings would generalize to other social categories, particularly those without any physical correlates.

In the present study, we further investigate these issues by comparing the influence of two independently manipulated social groupings, political ideology and race, on imitative biases. While race is associated with both sociocultural and physical characteristics, political ideology carries strong sociocultural associations but is not associated with any physical characteristics. This experimental design allowed us to test the following key predictions: (1) even though political ideology is not associated with any physical correlates, participants would be less accurate when imitating political outgroup members, because the task was incongruent with the cultural imitative bias towards self-similar models; (2) this decrease in imitative accuracy would be mediated by decreased perceptions of self-similarity (psychological mediator) and increased activity within brain areas relevant to cultural learning (Losin et al. 2009; neural mediators); (3) knowledge of the model's political ideology would attenuate the influence of the model's race on imitative behavior and brain areas relevant to cultural learning.

Methods

Participants

Participants were 18 (8 male) right-handed, European American young adults (mean age 23.57, SD age 3.63). In order to ensure that our political ideology manipulation was highly salient to participants, participants were recruited from political groups on the University of California, Los Angeles (UCLA) campus and Los Angeles Craigslist using the following criteria: Participants had to report (1) participating in at least one political activity; (2) having a political ideology that was either strongly liberal or strongly conservative [i.e., on a scale from 1 (strongly conservative) to 7 (strongly liberal), rate themselves as a 1–2, or 6–7]; and (3) that their political ideology was highly central to their self-identity [i.e., on a scale from 1 (not at all central) to 7 (extremely central) rate themselves 5 or above]. Seventeen participants

Table 1 Participant demographics and imitation task-related measures by study

Measure	PL		Non-PL		*p*
	Mean	SD	Mean	SD	
Age (years)	23.70	3.57	23.06	2.14	0.51
Handedness (1 = right, −1 = left)	0.56	0.32	0.69	0.18	0.14
Socioeconomic status	45.33	6.72	48.79	7.11	0.14
Mean imitation accuracy (0–1)	0.96	0.07	0.95	0.09	0.31
Mean relative displacement (mm)	0.08	0.03	0.08	0.04	0.46
Max. relative displacement (mm)	0.69	0.43	0.65	0.62	0.69
Motion excluded volumes	5.94	6.53	5.26	6.39	0.55

Handedness scores are from the (Edinburgh Handedness Inventory; Oldfield 1971). Socioeconomic status scores were calculated by converting a participant's self-reported job and level of education to a numerical score using the nine job categories and seven education categories in the Barratt simplified measure of social status (Barratt 2005) and adding them to together (scores could range from 8 to 66). For imitation accuracy, the *p* value comes from a statistical linear mixed model in R (command: lmer) with imitation accuracy as the dependent measure, study as the fixed factor, and subject and imitative model as crossed random factors. The *p* value is calculated using Satterthwaite approximated as implemented in the package lmerTest. All other *p* values are the result of 2-tailed independent sample *t*-tests between the political and non-political study participants

reported being liberal and one reported being conservative. Given the growing literature suggesting psychological and neural differences between liberals and conservatives (Amodio et al. 2007; Hibbing et al. 2014; Kanai et al. 2011), we excluded the conservative participant from the present analyses; thus, our analyses are based on 17 strongly liberal participants (7 male). For some analyses, we compared these participants to a prior sample of 20 (10 male) right-handed, 18–26 year old European American participants (referred to here as the Non-Political Study) whose data were previously reported in (Losin et al. 2011). Participants in the two studies were also matched in age, handedness (Edinburgh Handedness Inventory; Oldfield 1971), socioeconomic status (Barratt 2005), and imitation task accuracy. See Table 1 for study demographics and between-group comparisons and Supplementary Methods for more details about participants' demographics in both studies. Participants in both studies had normal or corrected-to-normal vision and reported using no medication or drugs (other than oral contraceptives), no heavy use of alcohol, and no prior or concurrent diagnosis of any neurological, psychiatric, or developmental disorder. The study was approved by the UCLA Institutional Review Board.

Political ideology training

In both the present study, as well as in the prior Non-Political Study (Losin et al. 2011) the same hand sign imitation task was used during fMRI scanning. In this task, participants were presented with 12 imitative models (6 male), from three different ethnic groups (European American, African American, and Chinese American). For the remainder of the paper we will refer to these groups by the broader racial

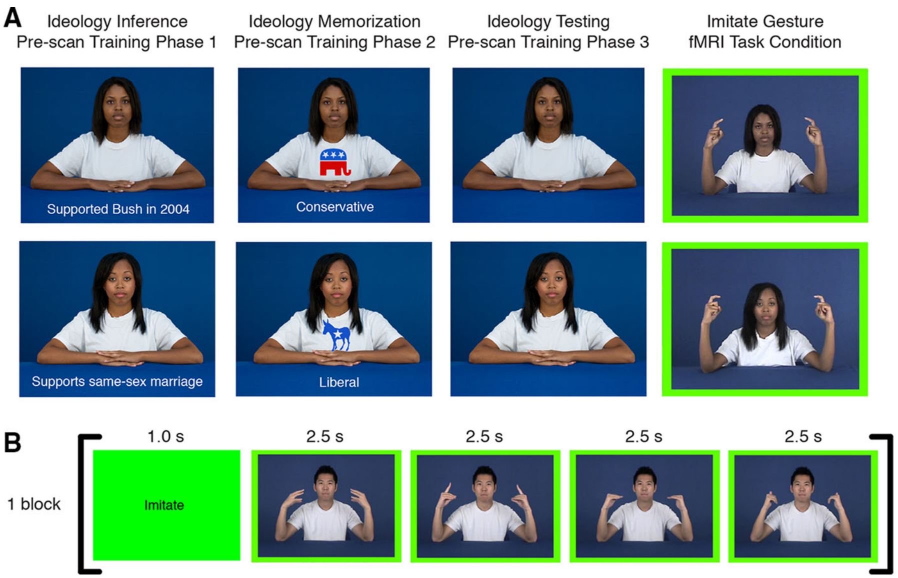

Fig. 1 Political ideology training and fMRI task structure. **a** Example stimuli from the three phases of the pre-scan political ideology training paradigm and imitate gesture condition of the fMRI task. **b** Structure of a block from the imitate gesture condition during the fMRI task

categories—white, black and Asian —that participants likely perceived based on the visual stimuli used in the scanner. The critical difference between the present study and the previous studies using this paradigm (Losin et al. 2013, 2009, 2011) is that in the present study participants learned about the imitative models' political ideologies prior to scanning: half of the models were liberal and half were conservative. Thus, half of the imitative models (one from each gender-race category, counterbalanced across participants) shared the participants' political ideologies and half did not.

Participants learned this information through a three-stage training paradigm (Fig. 1a). In the first stage of the training paradigm, participants were presented with a picture of each model three times in random order along with a statement about that model's support of a politically polarizing issue (2×; e.g., "Supports same-sex marriage") or their voting behavior in the last two elections (1×; e.g., "Supported McCain in the 2008 election"). On each presentation, they had to push a mouse button to indicate whether they thought that the imitative model was liberal or conservative based on the statement and were then presented with correct/incorrect feedback. In the second stage, participants saw a still portrait of each imitative model with their ideology written below the picture and a political party symbol on their t-shirt (donkey for liberal and elephant for conservative). In this stage, participants were told to just look at the person and try to remember their ideology. In the final stage, participants were presented with the same portraits devoid of any ideology information and had to correctly identify all 12 imitative models' ideologies three times in a row before testing would terminate. Participants were told that the political statements and ideologies were based on the imitative models' answers on a questionnaire they filled out about their political views when they came to the lab. In reality, the statements were chosen as those most strongly associated with liberal (N = 12) or conservative (N = 12) viewpoints by a prior sample of 19, mixed race, moderately liberal (mean 3.5 on a scale from 1-strongly liberal to 7-strongly conservative) college students.

Participants were told that the purpose of the political ideology learning phase of the study was to investigate how people learn information about others and that we chose political information because people typically regard it as important. In order to decrease the chances of explicitly altering participants' behavior during the imitation task, they were also told that the imitation paradigm in the scanner was unrelated to this learning task, but that they would be tested on their retention of the ideology information after the scanning session.

Hand sign imitation paradigm

The in-scanner imitation paradigm was identical for all participants and did not include any indicators of imitative models' political ideologies. The same imitation paradigm was previously described, see (Losin et al. 2013, 2009, 2011) or Supplementary Methods for more details. Briefly, throughout the course of the task participants imitated each model performing each of 16 novel, meaningless hand signs in waist-up color videos while lying in the MRI scanner. Stimuli were presented in blocks consisting of four hand signs from the same model per block (Fig. 1b). The task was divided into four balanced runs so that each model was seen an equal number of times in each run. The task also included a rest condition in which participants fixated on a black crosshair on a white screen, which was used as the baseline in some analyses.

Self-report and behavioral measures

In order to verify the importance of the manipulated social grouping variable (political ideology) to participants, as well as the success of our manipulation, we administered the following post-scan self-report measures: participants rated (1) their political ideology on a scale from −5 (extremely liberal) to +5 (extremely conservative), (2) the centrality of this political ideology to their identity, (3) their level of support for each political view and presidential candidate that was paired with imitative models during the training phase on a scale from −5 (strongly oppose) to +5 (strongly support), and (4) how often they were thinking about the imitative models' political views while imitating and observing them in the scanner on a scale from 1 (never) to 10 (always).

We further quantified the influence of the political ideology manipulation on participants' overall perceptions of the imitative models using an implicit association test (IAT; Greenwald et al. 1998). During the IAT, participants saw pictures of the liberal and conservative imitative models' faces and had to pair them with either self-related words (i.e., first person pronouns) or other-related words (i.e., third person pronouns) in a strategy similar to that used by (Mitchell et al. 2006). The difference between the average matching speed for the (self/liberal imitative models and other/conservative imitative models) pairings and the (self/conservative imitative models and other/liberal imitative models) pairings yielded the IAT score, which was used as a measure of implicit perceptions of similarity to imitative models with shared political ideology.

In order to assess participants' overall performance on the imitation task and to test whether knowledge of the imitative model's political ideology influenced imitation accuracy, we rated the accuracy of participants' imitation of each hand sign while in the scanner (17 of the political participants, and 16/19 of the non-political participants). Signs imitated correctly were rated as "0" representing zero mistakes, and signs imitated with a mistake or not imitated during the imitation condition were represented as one mistake. This scale allowed for the calculation of the proportion of signs imitated correctly for each imitative model (0–1), which was used as the metric of imitation accuracy in all accuracy analyses.

In order to determine whether the political ideology manipulation influenced our psychological variables of interest (i.e., participants' perceptions of self-similarity and social status of the imitative models), we administered another series of post-scan self-report and behavioral measures. Participants provided ratings of how similar they felt to each imitative model overall, and the level of subjective social status they perceived that imitative model to have (i.e., their perception of that imitative model's position in society akin to the community version of the MacArthur Scales of Subjective Social Status; Adler et al. 2000). To make these ratings, participants viewed portraits of each imitative model in a randomized order, once for each type of rating, and provided a rating using a visual analogue scale depicted under each portrait that ranged from 1 "very dissimilar to me" or "very low in status" to 9 "very similar to me" or "very high in status", with "average" as the scale mid-point.

To test the predicted relationships between the political ideology manipulation, imitative behavior (imitation accuracy), and the potential psychological mediators—self-similarity and social status, we computed a series of linear mixed effects statistical models in R (Development Core Team 2010) between the different pairs of variables (ideology-accuracy, ideology-similarity, and similarity-accuracy). Statistics were calculated using the command lmer from the package lme4 and the package lmerTest to estimate degrees of freedom and *p* values using Satterthwaite approximation. All statistical models had subject and imitative model as crossed random factors to allow results to generalize beyond individual participants and individual imitative models.

We also tested this relationship between all three variables using a multi-level mediation analysis based on a 3-variable path statistical model (Baron and Kenny 1986) using the Mediation Toolbox (http://www.wagerlab.colorado.edu/tools) (Atlas et al. 2010; Wager et al. 2008). In this analysis, imitative model political ideology was the predictor (X) variable, imitative model imitation accuracy was the outcome (Y) variable, and ratings of imitative models' self-similarity served as the mediator (M) variable (see path diagram in Fig. 2d).

To test whether knowledge of the imitative models' political ideologies decreased the effect of the imitative models' race on imitative behavior (accuracy) and its psychological mediators (perceptions of imitative model self-similarity), we

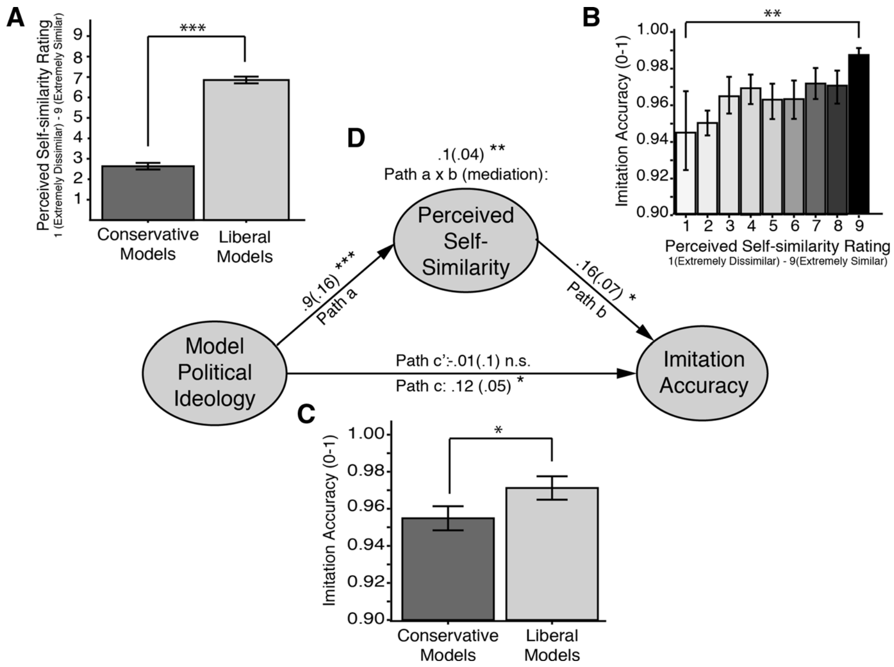

Fig. 2 Relationships between imitative model political ideology, imitative model self-similarity, and imitation accuracy. **a** Mean self-similarity ratings for conservative and liberal imitative models (made while looking at model portraits) on a scale from 1 (very dissimilar to me) to 9 (very similar to me). **b** Mean imitation accuracy levels (proportion of signs imitated correctly for each imitative model from 0 to 1) for each model self-similarity rating. **c** Mean imitation accuracy rating for liberal and conservative imitative models. **d** Path model for multi-level mediation analysis between model political ideology (X), model self-similarity (M) and model imitation accuracy (Y). Path coefficients are listed for each path with standard errors in parentheses. For **a–d** $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. *Error bars* represent within-subject standard error of the mean, calculated with Cousineau's adaptation of Loftus and Masson's method with Morey's correction (Cousineau 2005; Loftus and Masson 1994; Morey 2008)

computed another series of linear mixed effects statistical models comparing race effects in the present study (Political Study) to those in the Non-Political Study. As before, all statistical models were computed using the lmer command in R, and included subject and imitative model as crossed random factors.

fMRI analyses

Data were collected using a 3 Tesla Siemens Trio whole-body MRI scanner. See Supplementary Methods for details of MRI data acquisition and preprocessing.

Single-subject analyses

Statistical analyses were performed at the single subject level using a general linear model (GLM) with FSL's fMRI Expert Analysis Tool (FEAT). The time courses of blocks during imitation of each of the 12 imitative models were convolved with a canonical double-gamma hemodynamic response function and included as regressors in the GLM. The five 22.5-second rest (fixation) blocks were used as the implicit baseline.

General linear model analyses

In order to investigate the influence of the imitative models' political ideologies on neural activity during imitation, comparisons between imitating liberal and conservative imitative models were estimated (e.g., imitate gesture liberal > imitate gesture conservative). Imitation of each group of imitative models was also compared to the fixation baseline (e.g., imitate gesture liberal > baseline). In order to investigate whether the neural correlates of the imitative model's race during imitation differed between the Political and Non-Political Studies, for both sets of data, all possible pairwise contrasts of imitating the models from the three racial groups were estimated (e.g., imitate gesture white > imitate gesture black) and imitation of each racial group of imitative models was also compared to the fixation baseline (e.g., imitate gesture white > baseline). See Supplementary Methods for further details of single-subject and group GLM analyses.

Multi-level mediation analyses

In order to test which neural systems mediated the influence of the imitative models' political ideologies and perceptions of model self-similarity on imitation accuracy, we conducted whole-brain multi-level mediation analyses (Baron and Kenny 1986) using the Mediation Toolbox (http://wagerlab.colorado.edu/tools) (Atlas et al. 2010; Wager et al. 2008, 2009). Mediating brain regions are candidates for links in functional pathways that relate brain activity in multiple regions to behavior and other outcomes. In the current study, we used either the imitative models' political ideologies or participants' self-similarity ratings to each imitative model as the "X" variable and imitation accuracy for each imitative model as the "Y" variable. Thus, the X–Y relationships (Path *c*) in these mediation models were the previously tested linear associations between the imitative models' political ideologies or self-similarity ratings and imitation accuracy. This analysis allowed us to look for the brain systems mediating these demonstrated behavioral relationships. Additionally, in order to further investigate brain activity associated with perceptions of model self-similarity during imitation, we investigated the results of the Path *a* analysis from the similarity-brain-accuracy mediation, which is equivalent to an analysis using model self-similarity ratings as a parametric regressor. See Supplementary Methods for more details on the whole-brain mediation analyses.

Results

Verification of political ideology manipulation

Participants reported being strongly liberal (mean −4, SD 0.61, with −5 representing strongly liberal), and that their political ideologies were highly central to their personal identities (mean 8.41, SD 1.42, with 10 representing extremely central). Participants also reported more support for the political issues paired with the liberal imitative models (mean 4.43, SD 0.67, with 5 representing strongly support) compared to those paired with the conservative imitative models (mean −2.38, SD 0.84, with −5 representing strongly oppose, $t(16) = 24.23$, $p < 0.0001$), suggesting that the ideology training procedure resulted in half of the imitative models having more similar political views to participants than the other half, as intended. Using an IAT, we also found that participants were quicker to pair first person pronouns with the faces of the liberal imitative models and third person pronouns with the faces of the conservative imitative models than the opposite pairing (mean D score 0.65, SD 0.38, $t(14) = 6.73$, $p < 0.0001$), suggesting that the political ideology training also resulted in participants forming an implicit 'self' association with the liberal imitative models and an implicit 'other' association with the conservative imitative models. We found that participants reported thinking of the imitative models' political ideologies most of the time (mean 7.2, SD 2.8, with 10 representing "the entire time") while imitating and observing them in the scanner, despite the fact that they were told that the political facts were not connected to the in-scanner imitation task. Finally, we found that all participants recalled all 12 models' political ideologies with 100 % accuracy when tested after the scanning session. Together, these findings underscore the salience of political ideology to the present participants and the effectiveness of our political ideology manipulation.

Political ideology effects on the psychological and neural mediators of imitation

Consistent with the importance of the model's sociocultural characteristics in guiding imitation, we found that the model's political ideology did influence imitative behavior. Participants were more accurate when imitating liberal compared to conservative models ($F(1185.61) = 5.98$, $p = 0.01$; Fig. 2c), despite the fact that all imitative models performed the same hand signs. Next, we tested the influence of the model's political ideology on the two psychological mediators proposed to guide cultural learning: perceptions of the imitative model's self-similarity and social status. We found that the participants reported feeling more similar overall to imitative models who shared their political ideology than to those who did not ($F(1181.99) = 632.93$, $p < 0.0001$; Fig. 2a). As mentioned previously, we also found the same pattern using an implicit measure of self-similarity (IAT), suggesting participants' reports of feeling more similar to liberal than conservative imitative models were not merely the result of self-presentational biases. Interestingly, we did not find an effect of the imitative models' political ideologies on the level of social status that participants associated with the different imitative models ($p > 0.2$). This finding suggested that political ideology may influence imitative learning primarily through changes in the perception of self-similarity rather than social status. Indeed, we found that participants were more accurate when imitating models whom they reported feeling more similar to ($F(1188.18) = 6.39$, $p = 0.01$; Fig. 2b). Finally, consistent with our prediction, the mediation analysis revealed that perceptions of similarity to the imitative models fully

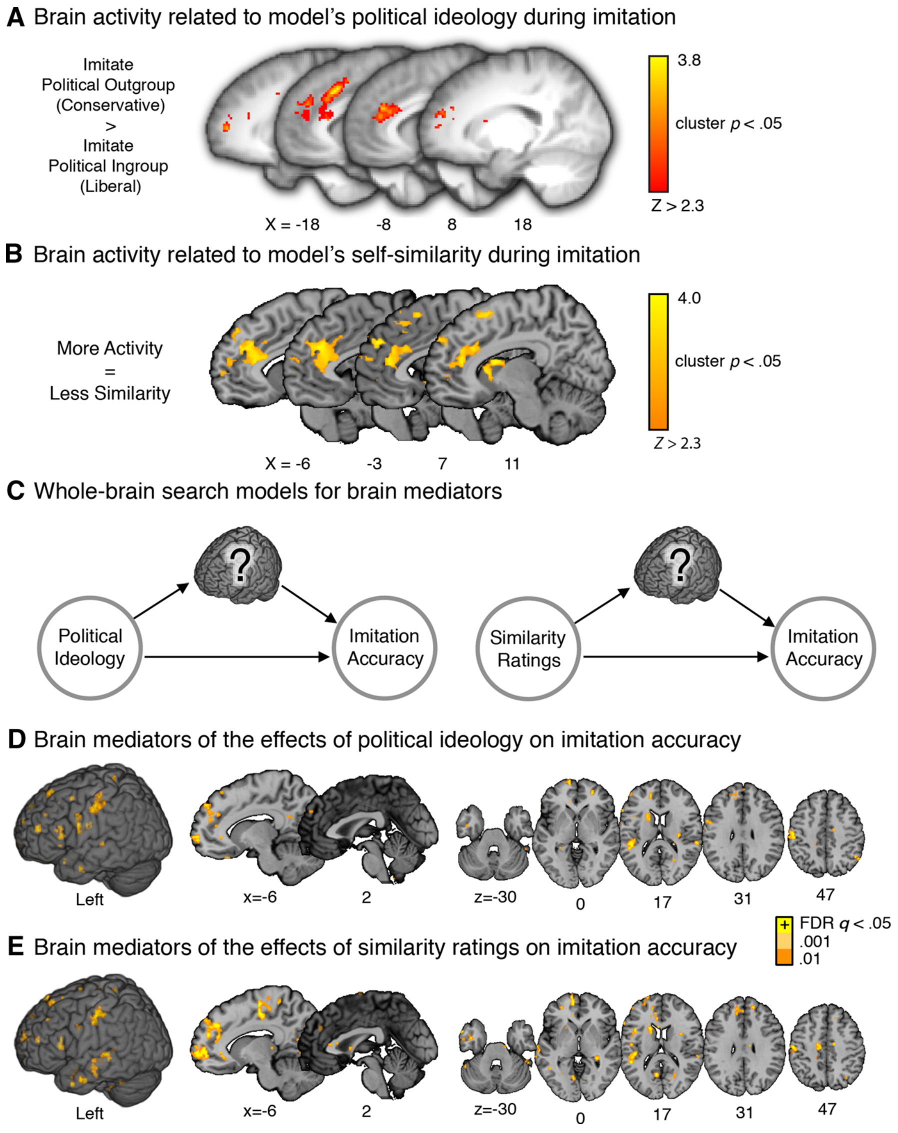

Fig. 3 Brain regions related to imitative model political ideology during imitation. **a** Results of a GLM analysis comparing imitation of conservative versus liberal imitative models. Results are thresholded at $Z > 2.3$, corrected for cluster extent by controlling familywise error at $p < 0.05$, and displayed on a group average structural image (MPRAGE). **b** Path a from the similarity-brain-accuracy mediation analysis, equivalent to a parametric analysis using model self-similarity. Results are thresholded at $Z > 2.3$, corrected for cluster extent by controlling familywise error at $p < 0.05$. **c** Path diagrams for two whole brain multi-level mediation analyses. **c–d** Positive mediators (Path $a \times b$) of the relationships between **d** imitative model political ideology (X) or **e** model self-similarity (X) and imitation accuracy (Y) from whole brain multi-level mediation analyses conducted using Mediation Toolbox (http://wagerlab.colorado.edu/tools). Multi-level mediation analyses were thresholded using the false discovery rate (FDR) at $q < 0.05$ and displayed on the Colin 27 average brain

mediated the influence of the imitative models' political ideologies on participants' accuracy when imitating them (Path $a \times b$ $\beta = 0.1, t = 2.51, p < 0.01$; see Fig. 2d for path diagram as well as other path coefficients and significance levels).

Brain mediators of imitative model's political ideology on model imitation accuracy

Using a standard GLM analysis, we found differential activity related to the imitative models' political ideologies in three brain regions. More activity was present when participants imitated models who did not share their political ideology (i.e., political outgroup members; conservatives) compared to those who did (i.e., political ingroup members; liberals) in the dorsomedial prefrontal cortex (dmPFC), the dorsal anterior cingulate cortex (dACC), and early visual cortex (V1, V2) (Fig. 3a; Table S1). In contrast, there were no brain regions that exhibited greater activity during imitation of political ingroup models compared to political outgroup models. This finding suggested that the dmPFC may play a role in encoding the imitative models' political ideologies during imitation, as predicted. The presence of increased dmPFC activity combined with decreased accuracy during imitation of political outgroup models further suggested that this dmPFC activity might reflect increased processing load due to the difficulty of imitating political outgroup members, a task that was incongruent with the cultural imitative bias toward self-similar models.

To directly test this hypothesis, in a second analysis, we used a multi-level mediation approach to conduct a whole-brain search for positive mediators of the relationship between imitative models' political ideologies and imitation accuracy (see Fig. 3c for path diagram). One of the largest and strongest clusters of activity was located in the dmPFC (Fig. 3d), just as we had found in the GLM analysis (see Fig. S1a for cluster overlap). Other positive mediators of the relationship between political ideology and imitation accuracy included brain regions associated with imitation (e.g., precentral gyrus, and inferior frontal gyrus, pars opercularis), and the left caudate and right orbitofrontal cortex, implicated in goal directed action and reward learning (Dayan and Balleine 2002). All of these positive mediators exhibited both negative Path *a* and negative Path *b* relationships (i.e., greater activity associated with imitating political outgroup members and lower imitation accuracy). This finding provides direct support for the interpretation of increased dmPFC activity during imitation of political outgroup members as relating to the difficulty participants experienced when imitating political outgroup members.

In order to more directly investigate the role of perceptions of self-similarity in brain activity during imitation and imitation accuracy, we also conducted a whole brain search for brain regions that varied in response to imitating models associated with different levels of perceived similarity (Path *a* in a similarity-brain-accuracy mediation model), and for mediators of the relationship between imitative models' levels of self-similarity and imitation accuracy (see Fig. 3c for path diagram). We found a cluster in the dmPFC that exhibited increased activity in response to imitating less self-similar models (Fig. 3b). We found a similar dmPFC cluster that positively mediated the relationship between perceived similarity and imitation accuracy such that this region was most active when similarity and accuracy were lowest (negative Path *a* and negative Path *b*; Fig. 3e and see Fig. S1b for cluster overlap). Given the large amount of variance in perceptions of the model's self-similarity explained by the model's political ideology ($R^2 = 0.74$), the similarity of these results to those from the ideology-brain-accuracy mediation analysis is not surprising; however, these findings further support the interpretation that the dmPFC may play a role in self-similarity imitative biases.

The connection between dmPFC activity and imitation accuracy further suggests that the dmPFC may not only play a role in encoding the imitative models' political ideologies during imitation, but it may also play a functional role in translating these model characteristics into imitative biases, consistent with our recent findings of the dmPFC being associated with imitation control (Cross et al. 2013). The only brain region exhibiting positive Path *a* and Path *b* relationships was the left postcentral gyrus. The positive relationship between this postcentral gyrus activity and both

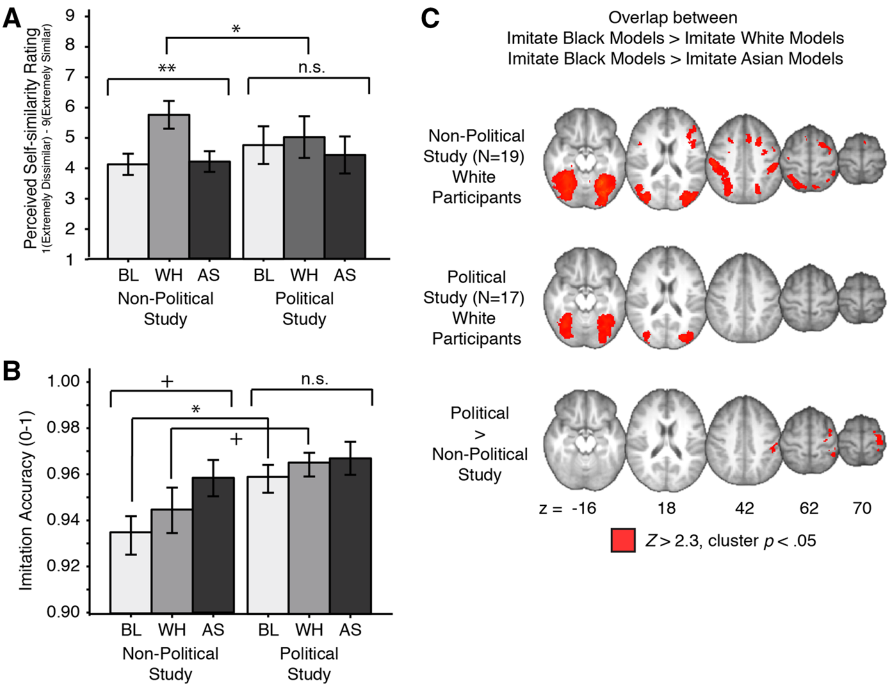

Fig. 4 Influence of the imitative model's political ideology on psychological and neural effects of imitative model's race during imitation. **a** Mean self-similarity ratings for imitative models from each of the three racial groups *black* (BL), *white* (WH), and *Asian* (AS) on a scale from 1 (very dissimilar to me) to 9 (very similar to me) from both the Non-Political and Political Studies. **b** Mean imitation accuracy (0–1) for imitative models from each of the three racial groups from both the Political and Non-Political Studies. For **a**–**b** $+p < 0.1$, $*p < 0.05$, $**p < 0.01$. *Error bars* represent within subject standard error of the mean, calculated with Cousineau's adaptation of Loftus and Masson's method with Morey's correction (Cousineau 2005; Loftus and Masson 1994; Morey 2008). **c** Results from GLM analyses looking at effects of the imitative model's race in the Non-Political Study (line 1), the Political Study (line 2), and directly comparing these effects between studies (line 3). For ease of display, activity shown is the overlap between the (imitate black models > imitate white models) and the (imitate black models > imitate Asian models) contrasts, as these contrasts produced very similar results. Results are thresholded at $Z > 2.3$, corrected for cluster extent by controlling familywise error at $p < 0.05$, and displayed on a group average structural image (MPRAGE)

imitating liberal models and increased imitation accuracy, suggests it may somehow play a facilitatory role in imitating models with shared political ideologies, perhaps via the postcentral gyrus' role in providing proprioceptive feedback (London and Miller 2013).

Influence of imitative model's political ideology on psychological and neural correlates of the imitative model's race during imitation

We first investigated the influence of the imitative model's race on perceptions of imitative model's self-similarity. We found a main effect of the imitative model's race in the Non-Political Study ($F(2206.98) = 24.716$, $p < 0.001$) such that participants reported feeling more similar to white imitative models than either black or Asian imitative models. In contrast, we found no main effect of the imitative model's race in the Political Study ($F(2200.99) = 0.978$, $p > 0.3$; Fig. 4a). Consistent with our prediction, we also found that the effect of the imitative model's race was significantly greater in the Non-Political compared to the Political Study ($F(2391.98) = 4.0475$, $p = 0.02$; Fig. 4a). We did not find a main effect of study on feelings of similarity to the imitative models ($F(133.99) = 0.0165$, $p > 0.8$), suggesting that overall between-study differences in feelings of similarity to the imitative models did not contribute to the observed differential effects of race.

Next, we investigated the influence of the imitative model's race on imitation accuracy. In the Non-Political Study, we found a trend towards a main effect of race on imitation accuracy ($F(2173.74) = 2.25$, $p = 0.11$) such that participants were more accurate when imitating Asian compared to black imitative models, with mean accuracy for imitating white models falling the middle of these two groups. We previously attributed the higher levels of accuracy associated with imitating Asian and white models compared to black models to the higher levels of social status participants associate with Asian and white individuals (see Losin et al. 2013 for a full explanation of these findings). In contrast, we did not find a main effect of the imitative model's race on imitation accuracy in the current (Political) study ($F(2184.62) = 0.60$, $p > 0.5$; Fig. 4b). The race × study interaction was not significant. However, post hoc pairwise *t*-tests (one-tailed) between the same racial group in the two studies revealed that the decreased accuracy during imitation of the black and white models relative to the Asians models seen in the Non-Political Study was eliminated in the Political Study due to participants being significantly more accurate at imitating black imitative models in the Political compared to the Non-Political Study ($t(120.075) = 1.79$, $p = 0.038$), with a similar trend for the white imitative models ($t(108.86) = 1.533$, $p = 0.064$; Fig. 4b). Overall, we found that imitation accuracy was high in both the Political and Non-Political studies (>94 % of signs receiving the highest accuracy rating), and did not differ between studies (see Table 1 for group means and between-study comparisons), suggesting that the accuracy differences related to the imitative models' race were not driven by overall differences in imitation accuracy between the studies.

Finally, we wanted to test whether the imitative models's race was represented differentially in the brain during imitation when information on the imitative models' political ideologies was known, in the Political Study, compared to when it was not in the Non-Political Study. As reported previously (Losin et al. 2013, 2011), in the Non-Political Study we found greater activity when participants imitated black imitative models compared to either white or Asian imitative models within brain regions previously associated with imitation (Caspers et al. 2010) including inferior frontal gyrus, pars opercularis, inferior parietal lobule, pre-supplementary motor area, and primary and secondary visual regions (Fig. 4c; Table S2). For the same racial contrasts in the present study, we only saw these differences in primary and secondary visual regions (Fig. 4c; Table S2). A direct comparison revealed that these racial differences were indeed significantly reduced in the Political Study within a subset of brain regions including primary sensory and motor cortices (Fig. 4c; Table S2). These findings suggest that the influence of the model's race on brain regions previously associated with imitation seen in the Non-political study likely stemmed from the sociocultural rather than the physical aspects of race. In contrast, activity in visual regions related to the imitative model's race was similar in both studies, suggesting that this activity may instead relate to the physical aspects of the imitative model's race, such as skin color and facial features, which were identical in both studies.

Discussion

In the present study, we demonstrated that knowledge of an imitative model's political ideology can influence imitation accuracy. This effect was mediated by changes in feelings of similarity to the models and by activity changes in brain regions associated with imitation (e.g., IFGpo) as well as imitation control and mentalizing (e.g., dmPFC). Furthermore, knowledge of the imitative model's political ideology decreased the influence of the model's race on imitation accuracy, the reported feelings of similarity to the model, and neural activity in imitation-related brain regions.

These findings extend our previous work (Losin et al. 2011, 2012, 2013) by showing that a sociocultural category devoid of any physical correlates is sufficient to influence imitation accuracy and its underlying psychological and neural mediators. In terms of the psychological mechanisms subserving imitative biases, these results suggest that abstract sociocultural knowledge about imitative models may play an important role in imitation, even though many aspects of imitation are perceptual-motor in nature. This interpretation is consistent with the ethnic marker hypothesis of culture-gene coevolutionary theory (Boyd and Richerson 1987), which suggests that physical features of imitative models serve only as proxies for the sociocultural information (e.g. self-similarity) relevant to cultural learning.

In terms of the neural mechanisms underlying imitative biases, this is the first study to implicate the mPFC in representing the model's characteristics during imitation. This may be due to the abstract nature of political ideology, given the involvement of the mPFC in mentalizing about the abstract characteristics of the self and others (Frith and Frith 2012). In light of prior evidence that the mPFC (and ACC) plays a role in imitation control (Cross et al. 2013), the presence of mPFC activity may also be due to the fact that this is the first study in which we have linked brain activity associated with the imitative model's characteristics to the control of imitation (i.e., imitation accuracy). Taken together, our neuroimaging findings indicate that brain regions associated with imitation (e.g., the IFGpo) as well as those associated with imitation control and mentalizing (e.g., the dmPFC) can represent model characteristics relevant to cultural learning during imitation. To the extent that activity within these brain regions mediated the link between the model's self-similarity and imitation accuracy, our results also provide a plausible neural mechanism underlying imitative biases related to self-similarity.

The present results underscore the important role of the model's self-similarity in imitation, whereas data from two of our previous studies (Losin et al. 2013, 2011) suggested that social status associations with different racial groups mattered more than self-similarity. While these findings may seem discordant, the more prominent role played by self-similalrity in the current study likely reflects the fact that the model's political ideology—information that was not provided in our prior studies—was made highly salient in the current study. Perhaps more importantly, in the prior studies self-similarity was based on the physical correlates of race whereas in the current study, the feelings of self-similarity rested upon shared political ideology, information more diagnostic of sociocultural similarity.

Interestingly, the neural mediators of the relationship between the model's political ideology and imitation accuracy, including the dmPFC and IFGpo, showed the strongest activity when imitation accuracy and model self-similarity were lowest (i.e., when the political ideologies of the model and imitator were incongruent). This result is consistent with our prior finding of greater activity in imitation-associated brain regions and lower accuracy when people imitated individuals from a racial group they associated with lower levels of social status (Losin et al. 2013). These neuroimaging findings suggests that increased activity within these neural regions may be required when engaging in tasks incongruent with cultural learning biases towards self-similar individuals. Studies in the cultural neuroscience literature on visual processing have similarly demonstrated increased activity when engaging in culturally-atypical, as compared to culturally-typical, tasks (Hedden et al. 2008).

Finally, our finding that knowledge of the model's political ideology reduces the influence of the model's race suggests that others' sociocultural characteristics influence imitative biases more so than their physical attributes. This finding is in line with prior reports in the social neuroscience literature. For example, Van Bavel et al. (2008) found that assigning participants to novel mixed-race teams eliminated typical own-race preferences and the typically observed increase in amygdala activity when viewing racial outgroup members. The present results extend this work by suggesting that well-documented imitative biases related to race (e.g., Clark and Clark 1947; Karunanayake and Nauta 2004) may be altered by exposure to additional sociocultural information about the models (e.g., their political ideology).

This study has some limitations that may influence the interpretation of its findings. First, given the present design, it was not possible to disentangle neural activity related to imitating less self-similar models from activity associated with imitation errors. However, because there was a much stronger association between the model's political ideology and brain activity than between the model's political ideology and imitation accuracy, we believe that that our neuroimaging findings are unlikely to be primarily driven by imitation errors. Second, this study employed a relatively small sample of white liberal participants. A growing literature in political psychology and neuroscience suggests that both psychological (Hibbing et al. 2014) and neural differences (Amodio et al. 2007; Kanai et al. 2011) may exist between liberals and conservatives. Thus, it is unclear if the present results would generalize to conservative individuals. Similarly, given the increased importance of racial identity amongst racial minorities (Sellers et al. 1998), it is unclear how knowledge of the model's political ideology would have influenced the effects of the model's race in individuals belonging to a racial minority group.

In summary, our findings suggest that the sociocultural characteristics of imitative models are likely to be more influential during cultural learning than their physical characteristics and also provide a plausible neural mechanism underlying imitative biases related to self-similarity during cultural learning.

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