Race modulates neural activity during imitation

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ABSTRACT

Imitation plays a central role in the acquisition of culture. People preferentially imitate others who are self-similar, prestigious or successful. Because race can indicate a person's self-similarity or status, race influences whom people imitate. Prior studies of the neural underpinnings of imitation have not considered the effects of race. Here we measured neural activity with fMRI while European American participants imitated meaningless gestures performed by actors of their own race, and two racial outgroups, African American, and Chinese American. Participants also passively observed the actions of these actors and their portraits. Frontal, parietal and occipital areas were differentially activated while participants imitated actors of different races. More activity was present when imitating African Americans than the other racial groups, perhaps reflecting participants' reported lack of experience with and negative attitudes towards this group, or the group's lower perceived social status. This pattern of neural activity was not found when participants passively observed the gestures of the actors or simply looked at their faces. Instead, during face-viewing neural responses were overall greater for own-race individuals, consistent with prior race perception studies not involving imitation. Our findings represent a first step in elucidating neural mechanisms involved in cultural learning, a process that influences almost every aspect of our lives but has thus far received little neuroscientific study.

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Introduction

One important way people acquire culture is through imitation of others who are self-similar, or whom they perceive to be prestigious or successful (Boyd and Richerson, 1987). Because another person's race can indicate their self-similarity or status, race can influence whom people imitate (Van den Berghe, 1987). Preferences for own-race and higher-status-race models have been found for a variety of social behaviors and at many different ages. Soon after birth, infants have been found to prefer own-race faces and respond more receptively to own-race strangers (Feinman, 1980; Kelly et al., 2005). Children have been found to prefer toys and household objects chosen by or representing higher-status-race (European American) individuals (Clark and Clark, 1947; Liebert et al., 1972; Neely et al., 1973). Adults have also been found to exhibit such race-biased preferences. For instance, adults practice health-promoting behaviors such as self-screenings more when someone of their own race models the behaviors (Haas and Sullivan, 1991). Adults have also been found to model their educational and career choices after own-race role models (Karunanayake and Nauta, 2004; King and Multon, 1996; Zirkel,

2002). Here we investigate the neural mechanisms of race-biased imitation in order to provide insight into the neural mechanisms of cultural acquisition (Losin et al., 2009), a process that shapes almost every aspect of our lives (Losin et al., 2010).

We had three main aims. First, we aimed to investigate whether activity within neural systems previously associated with imitation is modulated by the race of the person being imitated. Second, we set out to determine whether imitation-related neural activity only differs between racial ingroup and outgroup members or instead exhibits race-specific effects. Third, we sought to ascertain whether race-related neural activity during imitation differs from race-related neural activity during perceptual tasks not requiring imitation.

With regard to the first aim, previous neuroimaging studies of imitation have not considered the influence of the model's race (Buccino et al., 2004; Frey and Gerry, 2006; Grèzes et al., 2003; Iacoboni et al., 1999; Koski et al., 2002; Tanaka et al., 2001; Vogt et al., 2007). A recent meta-analyses of 35 of these imitation studies (Caspers et al., 2010) identified an extended bilateral network important for imitation including the inferior frontal gyrus (pars opercularis), premotor cortex and adjacent superior frontal gyrus, supplementary motor area, primary somatosensory cortex, inferior parietal lobule, and visual area V5 (henceforth referred to collectively). In order to directly study the influence of race on the neural underpinnings of imitation, we have included an imitation condition that depicts actors of different races from the waist up (unlike prior studies, which typically

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depicted an isolated effector, such as a hand). Given the role of race in guiding imitative behavior, we expected that neural systems previously associated with imitation (Caspers et al., 2010), would show race effects in the imitation condition of our study.

With regard to the second aim, previous cognitive neuroscience studies on race have focused on comparing members of the participant's own race (most often white) to one other race (most often black) (Eberhardt, 2005; Ito and Bartholow, 2009). Such studies have drawn distinctions between ingroup and outgroup to frame the interpretation of the empirical data. When only two races are compared, however, it is unclear whether race effects are similar across all racial outgroups or are instead related to factors specific to individual racial groups. Here, we included models of three different races, the participant's own race (European American) and two racial outgroups (African American and Chinese American). We chose these two outgroups both because they represent the two most populous racial minorities in the United States (Humes et al., 2011) and because they differ in a number of other factors for which race is a proxy (e.g., perceived social status). White Americans typically report more positive attitudes about Asians than African Americans both in general (Link and Oldendick, 1996) and as social partners including neighbors (Bobo and Zubrinsky, 1996; Weaver, 2008) and spouses (Weaver, 2008). African Americans are also consistently viewed as having a lower social status than East Asians among U.S. minority groups (Fiske et al., 1999, 2002). Given these differences between the racial outgroups, we expected that neural systems previously associated with imitation (Caspers et al., 2010) would differentiate between all three races and that neural responses to African Americans might differ more from responses to European Americans than would neural responses to Chinese American individuals.

With regard to the third aim, previous studies have investigated race effects in the brain mainly using two types of tasks: action observation without imitation or simply looking at the faces of own-race and other-race individuals. Action observation studies have included observing the hand actions (Désy and Théoret, 2007) and hand gestures of own-race and other-race individuals (Liew et al., 2010; Molnar-Szakacs et al., 2007). Overall, studies of action observation have demonstrated that regions including the primary motor cortex, inferior parietal lobule and insula differentiate between actors of different races, although both increased (Molnar-Szakacs et al., 2007; Liew et al., 2010) and decreased (Désy and Théoret, 2007) responses have been reported for own-race compared to other-race actors.

Studies employing face-viewing tasks make up the majority of the existing literature on the neural correlates of race (Eberhardt, 2005; Ito and Bartholow, 2009). By varying the way in which faces were presented and the task participants performed, these studies have addressed a number of cognitive processes related to race including face processing, racial categorization, stereotyping and prejudice. Based on this body of work, Ito and Bartholow (2009) have highlighted a number of brain areas involved in race perception. These include the fusiform gyrus (typically showing greater activity when processing own-race faces, e.g. Golby et al., 2001), the posterior cingulate (usually more strongly activated during retrieval of information about own-race individuals, e.g., Iidaka et al., 2008), the amygdala (showing greater activity for other-race, e.g., Lieberman et al., 2005, as well as own-race, e.g., Chiao et al., 2008, individuals during arousal of affect and evaluation) and the anterior cingulate, dorsolateral prefrontal, and ventrolateral prefrontal cortex (all typically more active when inhibiting stereotypes or prejudice against other-race individuals, e.g., Cunningham et al., 2004).

Here we have included both an action observation and a face-viewing task to determine whether race effects during imitation differ from race effects during these previously studied perceptual tasks. Given that people tend to imitate others of their own race or those from a racial group perceived to be high in social status, we expected lower levels of activation when participants imitated own-

race models within imitation-related regions (Caspers et al., 2010), since familiarity is often associated with reduced brain activity during imitation (Buccino et al., 2004; Vogt et al., 2007). Previous perceptual tasks, on the other hand, have often reported greater levels of activation associated with own-race individuals (fusiform gyrus, posterior cingulate, Ito and Bartholow, 2009; inferior parietal lobule and insula, Liew et al., 2010; motor cortex, Molnar-Szakacs et al., 2007). Thus, we expected that imitation would modulate race effects previously observed in perceptual tasks.

In summary, our overarching goal was to begin to shed light on the neural processes that may underlie race-biased imitative learning during cultural acquisition. To do so, in the present study we examined neural activity with fMRI while European American participants imitated, as well as observed, actors of three different races performing novel meaningless hand gestures (participants also viewed portraits of these same actors).

Methods

Participants

Participants were 20 (10 male), right-handed, European American individuals, age 18–26 years old (M = 22.92, SD = 2.09). They were recruited through the Volunteers section on Craigslist (8/20 were students). Participants reported using no medication or drugs (other than oral contraceptives), as well as 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. Written informed consent was obtained from all participants.

Actor hand sign imitation fMRI paradigm

Stimuli were color, waist-up videos of 12 actors (6 male), of 3 different ethnicities [European American (EA), African American (AA) and Han Chinese American (CH)]. Though actors were recruited from these specific ethnic groups in order to minimize phenotypic variation, group differences will be discussed in terms of 'race' because this is the construct most likely perceived by participants based on visual information alone. Actors performed 16 bimanual, symmetrical hand signs derived from New Zealand Sign Language and described as meaningless to both actors and participants. Actor and stimulus appearance was standardized (e.g. neutral expression, white t-shirt, consistent lighting, position and background). Stimuli were presented in the following four conditions: 1) imitate gesture in which participants imitated the actors performing the hand signs during the video presentation, indicated by a green border, 2) observe gesture in which participants passively observed the actors performing hand signs, indicated by a red border, 3) view portrait, in which participants passively viewed still portraits of each actor, also indicated by a red border, and 4) baseline, in which participants fixated on a black cross in the center of a white screen (Fig. 1a).

Four stimuli of the same condition and portraying the same actor were presented in a block (Fig. 1b). For example, during a block of the imitate gesture condition, a participant would imitate the same actor performing four different hand signs. Each stimulus within a block was presented for 2.5 s and separated from the next stimulus by a 0.5-second fixation cross. All blocks were preceded by an instruction screen that was either green with the word "imitate" or red with the word "observe." Stimulus blocks were divided into four balanced runs such that each actor, each hand sign, and each condition were seen an equal number of times in each run. The order of blocks was pseudorandomized within a run, ensuring less than two actors of the same gender in a row, no two actors of the same race in a row, and no two of the same hand sign in a row. Five 22.5-second rest blocks were evenly spaced throughout each run. This run configuration resulted in one block
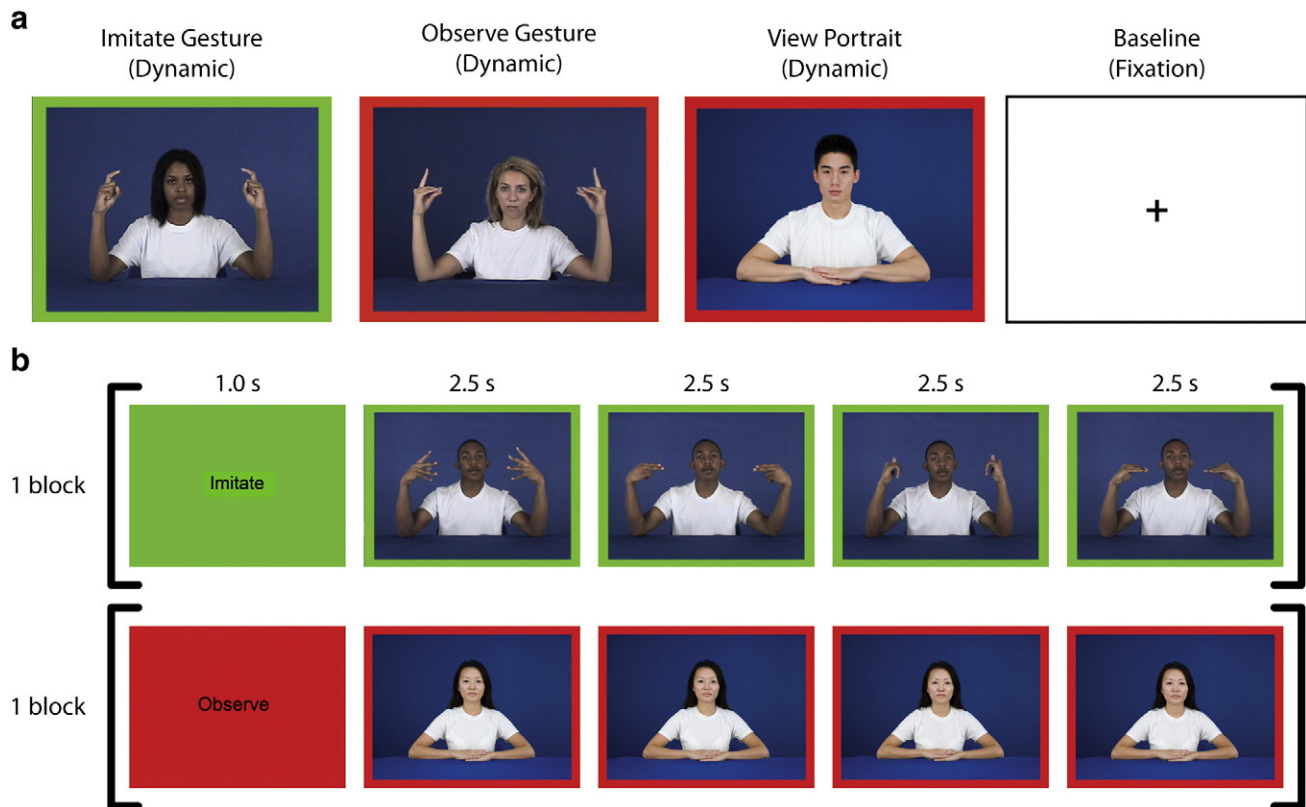
Fig. 1. Experimental stimuli and task design. (a) Example stimuli from 4 experimental conditions (green border = imitation, red border = observation). (b) Examples of block structure from the imitate gesture (first row) and view portrait (second row) conditions.

(4 stimuli) of each condition (imitate gesture, observe gesture and view portrait) per actor, per run for a total run time of 13:45. Over the course of the experiment, each participant saw 64 stimuli (16 blocks) portraying actors from each of the three racial groups in each of the three conditions. A different pseudorandomized stimulus order was created for each participant. Total task time was 55 min. The fMRI task was implemented and presented in the scanner using Presentation® software (Neurobehavioral Systems, Inc., Albany, CA) and viewed in the scanner on magnet-compatible goggles (Resonance Technologies, Inc.).

Prior to scanning, each participant completed two training tasks: a hand sign familiarization task during which participants imitated each sign in slow motion and then at full speed, and a task structure familiarization during which participants performed one block of each task condition (the actors and hand signs used during the task structure familiarization were different from those seen in scanner). During these training tasks, participants performed the imitation condition with their hands in their laps and under a table to mimic scanner conditions.

fMRI data acquisition

Data were collected using a 3 T Siemens Trio whole-body MRI scanner at the UCLA Ahmanson-Lovelace Brain Mapping Center. The following scans were performed on each participant: 1) Four functional echo-planar imaging (EPI) scans ($3 \times 3 \times 4$ mm voxels, TR: 2250 ms, TE: 28 ms, slices: 34, flip angle: 90°, FoV read: 192 mm, echo spacing: 47 ms, bandwidth: 2442 Hz/Px, time: 13:45); 2) a co-planar high resolution T2-weighted structural scan ($1.5 \times 1.5 \times 4$ mm voxels, TR: 5000 ms, TE: 34 ms, slices: 34, flip angle: 90°, FOV Read: 192 mm, echo spacing: .89 ms, bandwidth: 1302 Hz/Px, time: 1:30); 3) a high resolution T1-weighted magnetization-prepared rapid gradient echo (MPRAGE) structural scan ($1 \times 1 \times 1$ mm voxels, TR:

1900 ms, TE: 2.26 ms, Flip angle: 90°, Tl: 900 ms, FoV Read: 250 mm, echo spacing 6.9 ms, bandwidth: 200 hz/px, time: 6:50).

Behavioral measures

Behavioral measures of the participants' explicit and implicit racial attitudes and racial experience were collected post-scan and used to facilitate the interpretation of the fMRI data. Participants' explicit attitudes about the three racial groups were measured using a feeling thermometer (Judd et al., 1995) from 0° (very cold feelings) to 100° (very warm feelings,). Feeling thermometers have been demonstrated to be reliable measures of people's attitudes with an analysis of 17 feeling thermometer measures yielding an average reliability of $\rho = .8$, SD = .1 (Alwin, 1997).

Participant's implicit racial attitudes were measured using an Implicit Association Test (IAT; Greenwald et al., 1998). During the IAT, positive and negative words (e.g., love and hate) were associated with EA and AA or EA and CH faces. The difference between the average matching speed for the (positive/white + negative/black) pairings and the (positive/black + negative/white) pairings results in the IAT score, which was used as a measure of implicit racial bias. IAT scores are reported as D scores (difference between pairing response latencies divided by combined standard deviation) using the improved scoring algorithm described in Greenwald et al. (2003). Positive values reflect a pro-white bias and negative values reflect a pro-other-race bias (either AA or CH). The IAT has also been found to be a reliable measure, especially among implicit measures, with internal consistency estimates (split-half correlations or alphas) for IAT measures ranging from .7 to .9 (Greenwald and Nosek, 2001; Schmukle and Egloff, 2004).

Participants' experience with members of the three racial groups was measured using an in-house questionnaire based on Intergroup Contact Theory (Pettigrew, 1998). In the racial experience measure,

participants reported the races of their 5 closest friends. Participants also indicated how many people (none, a few, many, most, or all) of the three racial groups are or have been part of different social groups in their lives (e.g., romantic partners, neighbors, classmates and co-workers). Numerical values were assigned to participant responses and summed across friends and social groups to create a composite score of experience with each racial group. We calculated reliability measures (Cornbach's alpha) for this measure of racial experience with each of the stimuli racial groups: European Americans (.64), Chinese American (.63) and African Americans (.58). To explore whether the somewhat low reliability of this measure related to its potential multidimensionality, we created subscales for close relationships (friends and romantic partners) and more distant relationships (neighbors, classmates, teachers, coworkers, and other activities) for each racial group. We found that reliability was not consistently better for these subscales compared to the total measure (higher for some of the subscales than for the total measure but lower for others). Additionally, use of the subscales instead of the total experience measure did not alter the significance of the relationship between racial experience and the fMRI data, therefore we do not discuss these racial experience subscales further. Explicit racial attitudes and experience measures were compared between the three racial groups using a repeated measures ANOVA in SPSS with post-hoc pairwise comparisons using Šidák correction for multiple comparisons.

To quantify participants' task compliance and imitation accuracy, participants were visually monitored through the control room window during scanning to ensure no movement occurred during the observation-only blocks. Additionally, for 16/19 participants, hand sign imitation accuracy was assessed by watching the participants' hands through the control room window. Each sign was assigned a rating of 2, performed sign correctly; 1, performed sign but with errors; or 0, did not perform sign. Imitation accuracy was high. An average of 94.8% (SD = 6.83) of signs received the highest accuracy rating (the range for individual subjects was 82.6%–99.7%), suggesting participants were able to accurately perform the hand sign imitation task.

MRI data analysis

Structural and functional MRI data analyses were performed using FSL (FMRIB's Software Library: http://www.fmrib.ox.ac.uk/fsl/), AFNI (Cox, 1996) and ART (Ardekani et al., 1995). We have used several software packages in order to optimize our data processing stream to perform as accurately and reliably as possible. Preprocessing included skull-stripping (AFNI), realignment (mean image, FSL), high-pass filtering (100 ms, FSL) and spatial smoothing (6 mm, FSL). Functional data were registered to the in-plane high resolution scan (3-parameter affine) and, in turn, to the T1 MPRAGE (7-parameter affine). Finally, registration of the MPRAGE to MNI space (FSL's MNI Avg152, T1 $2 \times 2 \times 2$ mm) was carried out with FSL (12-parameter affine) and refined using ART (non-linear transformation). Statistical analyses were performed in FSL. First-level analyses included voxel pre-whitening, double-gamma hemodynamic response function (HRF) convolution, temporal filtering, and temporal derivative inclusion. For each subject, the four runs were averaged using a fixed-effects analysis. A mixed-effects analysis (i.e. random and fixed effects) was then used to average across all subjects (FLAME $1 + 2$). All group results were thresholded at z > 2.3 corrected for multiple comparisons using cluster-based Gaussian random field theory controlling familywise error across the whole-brain at p = 0.05.

To examine differences in neural activity for actors belonging to distinct racial groups, regressors for each racial group (EA, AA, CH), in each condition (imitate gesture, observe gesture, view portrait), were entered into a general linear model at the first-level of analysis (single subject, single run). Block instructions ("observe" or "imitate") were also entered into the model as nuisance regressors. All possible

pairwise racial contrasts were estimated (e.g., imitate gesture EA > imitate gesture AA) and each racial group was also compared to the fixation baseline for each condition. In order to determine whether any race effects found in the imitate gesture condition reflected processes unique to imitation, interaction contrasts were also estimated by subtracting each pairwise racial contrast for the observe gesture or view portrait condition from the same contrast for the imitate gesture condition (e.g., imitate gesture $_{AA > EA}$ > observe gesture $_{AA > EA}$).

Several data quality control measures were implemented prior to data analysis. In addition to standard realignment for motion correction, we also removed the effects of volumes exhibiting an unusual amount of residual intensity change, i.e. artifacts due to sudden movements during volume acquisition. We did so by using a modified version of the fsl_motion_outliers script which calculated the root mean square error of each voxel's time-series and created nuisance regressors for volumes where the volume-average root mean square error was greater than 0.2 SD (which approximated the threshold for visually identifying motion artifacts). We excluded any runs from which more than 25 volumes were removed (4 runs out of 80). We also removed one male participant and the fourth (last) run from two other participants due to hardware failures during data collection. These quality control measures resulted in a total of 19 participants (10 female) and 70 runs being utilized in the statistical analyses. Within these runs, an average of 5.3 volumes (SD = 6.4) out of 362 (approximately 1.5%) were removed due to motion artifacts per run.

Results and discussion

Race effects during imitation

In order to determine which neural systems are modulated by the model's race during imitation, we first compared imitation of own-race actors to imitation of actors from the two racial outgroups (EA > CH, CH > EA, EA > AA, AA > EA). Two of these comparisons yielded significant results. First, we found increased activity during imitation of EA actors compared to CH actors (EA > CH) within the visual system including the primary and extrastriate cortices (V1–V5) and the occipital fusiform gyrus (Fig. 2a, Table 1). This result is consistent with previous studies that have found enhanced activity in the fusiform gyrus and other extrastriate regions during own-race face viewing (Golby et al., 2001; Iidaka et al., 2008; Lee et al., 2008; Lieberman et al., 2005). Second, we found increased activity during imitation of AA actors compared to EA actors (AA > EA) within extrastriate regions, the fusiform gyrus and fronto-parietal imitation-related regions including the inferior frontal gyrus, premotor and primary motor cortices, primary somatosensory cortex, inferior and superior parietal lobules and the pre-supplementary motor area (Fig. 2b, Table 1). This finding suggests that activity within neural systems found to underlie imitation in studies where race was not a factor is modulated by the race of the actor being imitated. Notably, this finding of more activity during imitation of African Americans, a racial outgroup, is the opposite of what was found in the previous comparison with the CH group, and previous action observation (Liew et al., 2010; Molnar-Szakacs et al., 2007) and face viewing studies (Ito and Bartholow, 2009), all of which found more activity associated with racial ingroup members in visual and fronto-parietal regions.

Specificity of race effects (ingroup vs. outgroup or individual racial groups?)

Based on these comparisons between the imitation of own-race and other-race individuals, it is already clear that neural regions previously found to exhibit different levels of activity based on the model's race during face viewing (fusiform) and action observation (primary motor cortex, inferior parietal lobule) are also modulated by the model's race during imitation. These comparisons also suggest
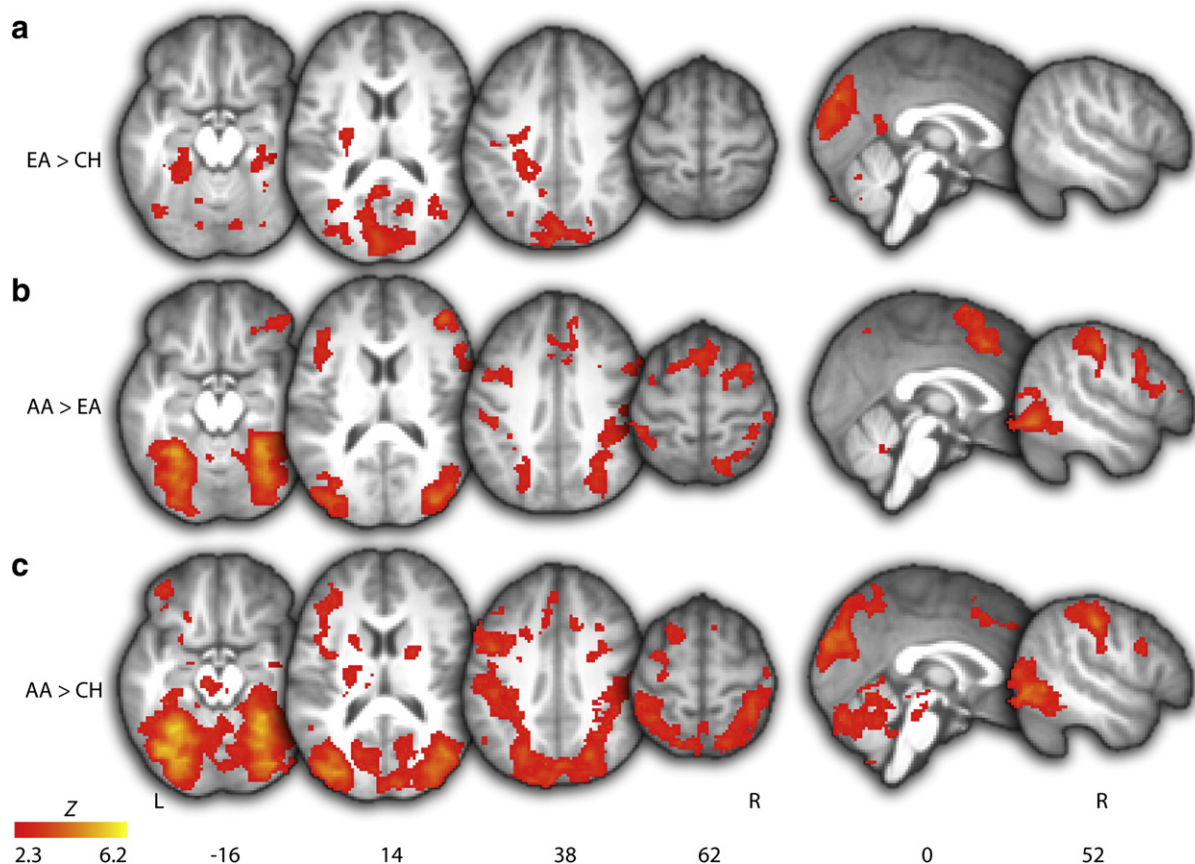
Fig. 2. Neural regions differentiating between imitation of individuals from three different racial groups, European American (EA; own-race) and two racial outgroups: Chinese American (CH) and African American (AA). (a–c) Whole-brain racial comparisons yielding significant differences from all possible pairwise racial comparisons. Functional activity is thresholded at Z>2.3 with whole-brain correction for multiple comparisons applied at the cluster level (p<.05), and overlaid on a group average (n=19) T1 weighted structural scan. Values under brains represent the MNI coordinate of the axial (z) or sagittal slice (x). L=left and R=right sides of the brain.

that race-related neural modulation during imitation cannot be explained by the ingroup/outgroup distinction and may instead be related to factors specific to each racial group because comparisons between own-race imitation and imitation of each of the two racial outgroups yielded different results. To test for race-specificity directly, we next compared imitation of the two outgroup races (AA>CH, CH>AA). One of these contrasts yielded significant results. We found increased activity during imitation of AA actors compared to CH actors in extrastriate visual regions including the fusiform gyrus and fronto-parietal regions related to imitation including premotor and primary motor cortices, primary somatosensory cortex and inferior and superior parietal lobules (Fig. 2c, Table 1). Thus, activity within visual and imitation-related regions differs between racial outgroups. This result suggests that activity within these neural systems is modulated by race-specific information during imitation rather than merely whether the model is a member of the imitator's racial ingroup or not.

Task-dependency of race effects (similar to perceptual studies or unique to imitation?)

We next sought to determine whether neural race effects during imitation were different from those observed in prior studies using action observation and face-viewing tasks as suggested by the increased activity found for imitation of members of a racial outgroup (AA) compared to imitation of individuals from the participants' ingroup (EA). To do so, we examined several Race×Task interaction contrasts to identify regions in which racial modulation of neural activity during imitation may differ from racial modulation of activity during gesture observation and

portrait viewing (e.g., imitate gesture $_{AA>EA}$>observe gesture $_{AA>EA}$ and imitate gesture $_{AA>EA}$>view portrait $_{AA>EA}$). Similar contrasts were performed for each pairwise race combination, yielding two interaction analyses for each combination of races: Race×Task (imitate gesture, observe gesture) and Race×Task (imitate gesture, view portrait). Results from these interaction contrasts indicate regions in which racial modulation was different for imitation compared to *either* gesture observation *or* portrait viewing. To determine which neural regions differentiated between races in a way that was unique to imitation (where gesture imitation was different from *both* gesture observation and portrait viewing) we investigated the overlap of the two interaction analyses for each racial pair. Because interaction contrasts between imitation and the other two tasks were intended to provide further information about neural activity during imitation, we only considered interactions falling within a post-threshold mask from the imitation condition for a given racial comparison. Out of all possible pairwise comparisons involving race, significant interactions were only found for the three racial comparisons exhibiting main effects during imitation (EA>CH, AA>EA, AA>CH). In order to visualize the source of these interactions, we plotted average parameter estimates from the conditions contributing to each interaction compared to baseline.

For the (AA>EA) racial comparison, we found a significant Race×Task interaction when imitation was compared to gesture observation as well as when imitation was compared to portrait viewing. There was considerable overlap between these two interactions within visual regions including the fusiform gyrus and imitation-related regions including the primary motor cortex, primary somatosensory cortex, and inferior and superior parietal lobules (Fig. 3b, Table 2). This overlap suggests that neural regions differentiating

Table 1

Anatomical regions differentiating between races during gesture imitation.

Anatomical regions	x	y	z	Z
Imitate gesture EA>CH				
L postcentral gyrus	−22	−34	48	3.96
R precuneus	14	−58	26	3.21
R posterior temporal fusiform cortex	30	−34	−22	3.33
L cuneal cortex	−2	−86	32	4.44
R lingual gyrus	18	−72	−2	4.04
L lingual gyrus	−18	−62	−6	3.63
L inferior lateral occipital cortex	−48	−74	−12	3.43
R superior lateral occipital cortex	34	−86	30	3.29
L thalamus	−18	−24	0	3.30
R cerebellum	14	−80	−42	3.52
L cerebellum	−36	−48	−42	3.49
Imitate gesture AA>EA				
L paracingulate gyrus (Pre-sma)	−6	18	46	4.20
R frontal pole	42	42	14	4.02
L precentral gyrus	−40	2	32	3.85
R superior frontal gyrus	22	2	70	3.54
R precentral gyrus	52	10	26	3.40
L middle frontal gyrus	−46	32	22	3.39
R superior frontal gyrus	−26	4	66	3.00
R superior parietal lobule	28	−56	50	4.09
R postcentral gyrus	54	−20	44	3.99
L postcentral gyrus	−48	−34	54	3.70
R middle temporal gyrus, temporooccipital part	56	−56	−4	3.31
L inferior temporal gyrus, temporooccipital part	−44	−46	−14	3.23
L occipital fusiform gyrus	−28	−72	−10	5.29
R occipital fusiform gyrus	30	−72	−8	5.10
L superior lateral occipital cortex	−30	−78	20	4.20
R superior lateral occipital cortex	36	−72	24	3.72
L cerebellum	−16	−52	−46	3.24
Imitate gesture AA>CH				
L precentral gyrus	−44	2	34	4.17
R precentral gyrus/superior frontal gyrus	24	−4	44	3.88
L superior frontal gyrus	−20	14	56	3.67
L middle frontal gyrus	−48	36	20	3.42
L frontal pole	−28	52	0	3.27
R middle frontal gyrus	38	24	46	3.23
R Insula	42	0	2	3.39
R postcentral gyrus	54	−20	44	4.43
L superior parietal lobule	−24	−54	52	4.27
R superior parietal lobule	38	−50	42	3.43
R precuneus	10	−62	22	2.74
L hippocampus	−18	−34	−6	3.92
R temporal occipital fusiform cortex	42	−40	−22	3.69
L inferior temporal gyrus, temporooccipital part	−44	−46	−16	3.25
L middle temporal gyrus, temporooccipital part	−58	−56	10	2.66
L occipital fusiform gyrus	−30	−74	−10	6.26
R occipital fusiform gyrus	32	−66	−10	5.68
L superior lateral occipital cortex	−32	−74	20	5.02
L occipital pole	−2	−90	34	4.47
R superior lateral occipital cortex	36	−82	16	4.34
L caudate	−16	16	6	3.57
R thalamus	20	−30	8	3.32
L cerebellum	−16	−52	−46	3.99
R cerebellum	2	−80	−26	3.67

Note: Local maxima were the highest Z values within activated regions falling at least 15 mm apart. Anatomical regions for each maximum were assigned using the Harvard–Oxford Cortical and Subcortical probabilistic atlases. Only the first maximum within each anatomical region on each side of the brain is listed. Maxima are grouped by lobe in the following order: frontal, parietal, temporal, occipital, subcortical, cerebellum.

between AA and EA individuals during imitation do so in a way that is unique to imitation and not driven by observing gestures or looking at faces of AA compared to EA individuals. Parameter estimates from the overlapping region reveal that more activity was present in visual and imitation-related regions during imitation of AA actors than during imitation of EA actors. In contrast, a similar amount of activity was present in these regions during observation of gestures performed by actors of both races. Strikingly, more activity was

actually present for viewing the portraits of EA actors compared to AA actors, the opposite of what was found during imitation. In fact, a number of neural regions including visual (fusiform gyrus, inferior lateral occipital cortex) and fronto-parietal regions (inferior frontal gyrus, premotor and primary motor cortices, parietal operculum) also exhibited more activity in response to EA compared to AA actors in contrasts examining racial effects only during the portrait viewing condition (view portrait EA > view Portrait AA; Figure S1b). Thus, the previously reported effect of enhanced activity when participants view the faces of own-race individuals compared to those of another race is also present in our data. The act of imitation, however, appears to reverse the relative activity levels for EA and AA individuals, resulting in more activity during imitation of AA actors.

For the (AA > CH) racial comparison we again found a Race × Task interaction when imitation was compared to gesture observation as well as when imitation was compared to portrait viewing. This effect is similar to the comparison of AA and EA actors, and again there was considerable overlap between these interactions within visual regions including the fusiform gyrus and lateral occipital cortex and imitation-related regions including inferior frontal gyrus, premotor and primary motor cortices, primary somatosensory cortex and superior parietal lobule (Fig. 3c, Table 2). This overlap suggests that neural regions differentiating between AA and CH individuals do so in a way that is unique to imitation. Parameter estimates also revealed similar effects to those described for the comparisons between EA and AA actors: activity was higher for *imitation* of AA actors compared to CH actors, similar for *observation* of AA and CH actors, and lower for *viewing portraits* of AA compared to CH actors. Once again, several neural regions (medial prefrontal cortex, caudate) also exhibited more neural activity in response to CH compared to AA actors when only the portrait viewing condition was examined (view portrait CH > view portrait AA; Fig. S1c, Table S1).

Finally, for the (EA > CH) racial comparison, we found a Race × Task interaction when imitation was compared to gesture observation but not when imitation was compared to portrait viewing (Fig. 3a, Table 2). Parameter estimates revealed that more activity was present within primary and early extrastriate visual regions for EA compared to CH actors during imitation, whereas a similar amount of activity was present for these two groups during passive gesture observation. Although there was no Race × Task interaction when imitation was compared to portrait viewing for this racial comparison, for completeness we have plotted parameter estimates for portrait viewing from the regions exhibiting the Race × Task (gesture imitation > gesture observation) interaction. During portrait viewing, as during gesture imitation and observation, there was more activity for EA actors than for CH actors. Again, similar to the previous two racial comparisons, the difference between activity for EA and CH actors reflected in the parameter estimates from the portrait viewing condition, was also significant within visual (fusiform gyrus and lateral occipital cortex) and frontal regions (inferior frontal gyrus) in a contrast examining racial effects only during the portrait viewing condition (view portrait EA > view portrait CH; Fig. S1a, Table S1). This is consistent with our finding of more activity during EA compared to AA portrait viewing and prior reports of more activity in visual regions during own-race compared to other-race face viewing (e.g., (Golby et al., 2001; Lieberman et al., 2005)). In contrast to the previous two comparisons with the AA group, the Race × Task interaction results for the comparison between EA and CH actors suggest that similar racial modulation of neural activity may be occurring during imitation as during the previously investigated perceptual tasks of face viewing and action observation for this racial comparison.

Overall, these Race × Task interactions reveal two important features of the data. First, for contrasts between AA actors and the other two racial groups, there is a great deal of overlap (Fig. 3, green areas) between both Race × Task interactions (comparing imitation to gesture observation and to portrait viewing). This suggests
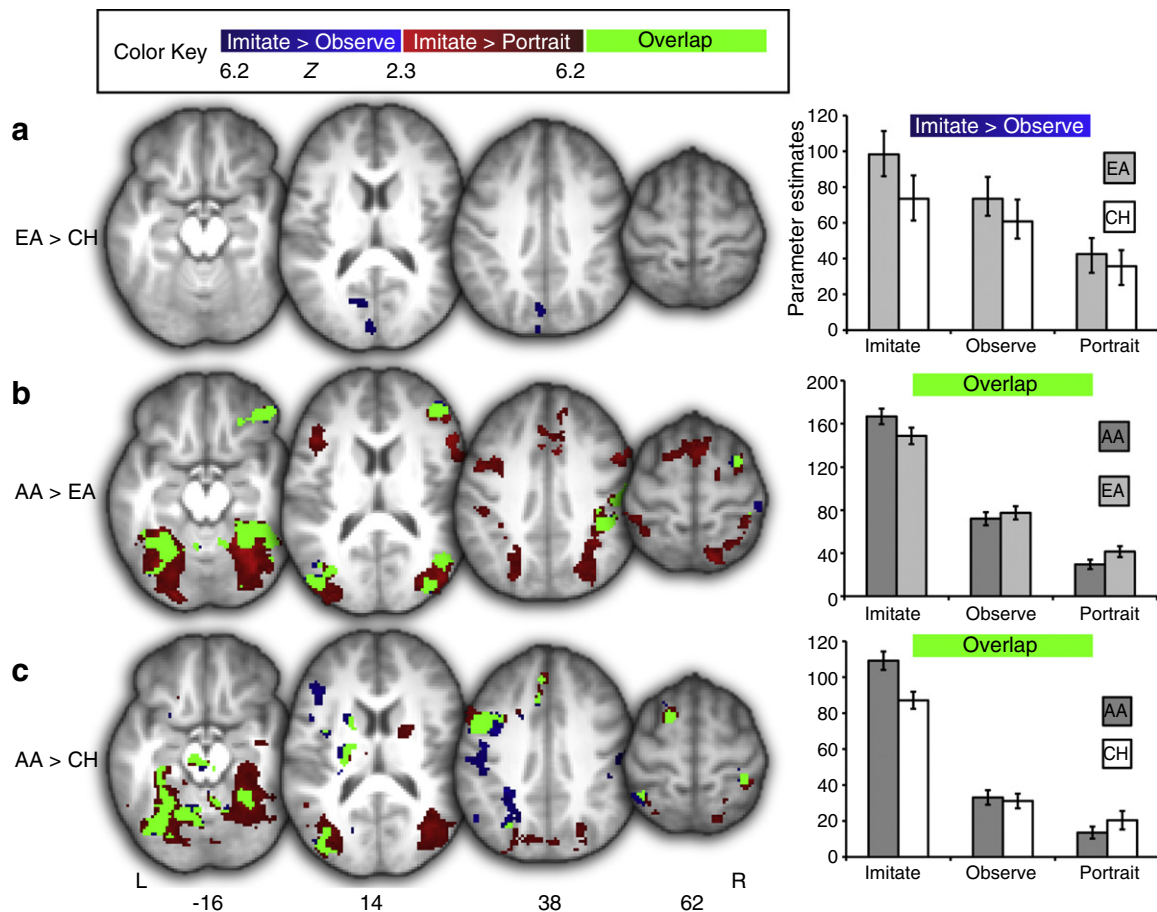
Fig. 3. Neural regions exhibiting Race × Task interactions. (a–c) All pairwsie racial comparisons between European American (EA), Chinese American(CH), African American (AA) actors exhibiting differences between imitation and non-imitation conditions. (Left) Whole-brain Race × Task interaction effects are displayed for the (imitate gesture > observe gesture; blue) and (imitate gesture > view portrait; red) comparisons and their overlap (green) which can be interpreted as activity that is unique to imitation. Results are thresholded at Z > 2.3 with whole-brain correction for multiple comparisons applied at the cluster level (p < .05). Values under brains represent the MNI coordinate of the axial (z) slice. (Right) Bar graphs of average parameter estimates from the conditions contributing to each interaction compared to baseline. Parameter estimates were averaged across the entire region of overlap for (AA > EA) and (AA > CH) comparisons (green) and the (imitate gesture > observe gesture) cluster for the (EA > CH) comparison (no other effects were significant). Parameter estimates for comparisons with the AA group reveal larger racial differences during gesture imitation than during gesture observation and a reversal of racial differences during imitation, during portrait viewing.

that many of the neural regions underlying imitation including the premotor and primary motor cortices, and inferior and superior parietal lobules differentiate between these racial groups in a way that is unique to imitation rather than being driven by other aspects of the imitation condition that are shared by one or both of the other conditions such as observing individuals of different races performing gestures or simply looking at their faces. Second, parameter estimates revealed that while more activity is present within visual and imitation-related regions during imitation of AA individuals compared to EA and CH individuals, more activity was present in the same regions while viewing portraits of EA and CH individuals compared to AA individuals. Parameter estimates also reveal more activity during EA portrait viewing than during CH portrait viewing within visual regions including the fusiform gyrus. Thus, although we replicate previously reported higher activity in response to own-race individuals within the fusiform gyrus during portrait viewing, during imitation the race of the model modulates neural activity in a substantially different way.

Participants' racial attitudes and experiences

Participants' self-reported racial attitudes and experience levels may help to explain the enhanced neural activity during imitation of AA actors, and the differences in neural activity in response to the two racial outgroups (AA & CH). Participants reported having significantly less experience with African Americans (M = 4.32, SD = 2.08) than either Chinese Americans (M = 7.42, SD = 2.85, p = .005), or European Americans (M = 19.32, SD = 2.85, p < .001). Participants also reported having less experience with Chinese Americans than European Americans (p < .001). Additionally, participants reported significantly less explicitly positive attitudes towards African Americans (M = 73.42, SD = 13.13) than European Americans (M = 83.42, SD = 9.58, p = .001) and had lower implicit positive associations with African Americans than European Americans (mean D = .43).

In contrast, there was only a trend of lower explicit positive attitudes towards Chinese Americans (M = 73.42, SD = 20.55) compared to European American individuals (p = .097). Similarly, while participants also had lower implicit positive associations with Chinese Americans than European Americans (mean D = .19), this difference in implicit attitude was less than half of that observed between African Americans and European Americans. Due to the large variance in explicit attitudes towards the AA group, there was no difference between attitudes towards African Americans and Chinese. Because there was no IAT directly comparing between African Americans and Chinese Americans, no direct implicit attitude comparison is available between the two outgroups; however, comparisons between these groups and participants' ingroup (European Americans) suggest that

Table 2
Anatomical regions exhibiting Race × Task interactions.

Anatomical regions	x	y	z	Z
(Imitate gesture$_{EA>CH}$) > (observe gesture$_{EA>CH}$)				
L cuneal cortex	−6	−78	24	3.38
(Imitate gesture$_{AA>EA}$) > (observe gesture$_{AA>EA}$)				
R frontal pole	42	46	14	3.97
R precentral gyrus	40	4	32	3.32
R postcentral gyrus	48	−24	56	3.69
R superior parietal lobule	36	−52	60	3.03
L temporal occipital fusiform cortex	−30	−60	−14	3.59
R inferior lateral occipital cortex	34	−84	0	3.89
L superior lateral occipital cortex	−30	−80	20	3.58
R superior lateral occipital cortex	44	−62	20	3.41
L cerebellum	−34	−76	−42	3.25
(Imitate gesture$_{AA>EA}$) > (view portrait$_{AA>EA}$)				
Precentral gyrus	46	10	32	4.41
Paracingulate gyrus (Pre-sma)	0	20	46	4.15
L inferior frontal gyrus, pars opercularis	−42	11	18	4.11
R frontal pole	40	40	16	4.00
L middle frontal gyrus	−50	6	44	3.56
R superior frontal gyrus	18	0	68	3.36
R superior parietal lobule	30	−56	54	4.13
R postcentral gyrus	56	−20	48	3.92
L superior parietal lobule	−28	−54	52	3.57
L postcentral gyrus	−50	−26	48	3.42
R temporal occipital fusiform cortex	36	−42	−22	4.10
R posterior superior temporal gyrus	66	−16	0	3.39
R middle temporal gyrus, temporooccipital part	60	−54	10	3.25
L hippocampus	−22	−38	−6	3.21
L occipital fusiform gyrus	−32	−68	−10	5.32
R occipital fusiform gyrus	36	−72	−10	4.80
L superior lateral occipital cortex	−26	−78	26	4.23
R superior lateral occipital cortex	30	−76	30	4.09
R lingual gyrus	12	−54	−8	3.21
L occipital pole	−14	−94	−6	3.18
L thalamus	−10	−12	4	3.24
L cerebellum	−6	−74	−36	3.70
(Imitate gesture$_{AA>CH}$) > (observe gesture$_{AA>CH}$)				
L inferior frontal gyrus, pars triangularis	−48	30	16	3.56
L superior frontal gyrus	−12	0	72	3.00
L paracingulate gyrus	−6	24	46	3.37
L superior parietal lobule	−30	−42	38	3.58
R postcentral gyrus	52	−20	40	3.42
L postcentral gyrus	−60	−22	34	3.19
L hippocampus	−18	−36	−4	3.44
L amygdala	−30	0	−20	2.97
L occipital fusiform gyrus	−36	−70	−10	3.73
L superior lateral occipital cortex	−30	−78	20	3.47
L cerebellum	−26	−70	−44	3.45
R cerebellum	30	−64	−38	3.12
(Imitate gesture$_{AA>CH}$) > (view portrait$_{AA>CH}$)				
L precentral gyrus	−48	6	38	3.81
L superior frontal gyrus	−22	24	52	3.70
R paracingulate gyrus	2	46	−8	3.38
L inferior frontal gyrus, pars triangularis	−56	22	8	3.03
L lateral occipital cortex	−36	−88	30	4.06
L precuneus, posterior cingulate	−2	−48	38	3.89
R postcentral gyrus	40	−38	62	3.49
L superior parietal lobule	−24	−54	66	3.34
L supramarginal gyrus	−50	−48	52	3.33
L angular gyrus	−50	−52	14	3.22
R temporal occipital fusiform cortex	30	−50	−8	4.49
L posterior parahippocampal gyrus	−32	−30	−18	3.83
R hippocampus	26	−22	−20	3.35
L posterior middle temporal gyrus	−66	−26	−12	3.25
R middle temporal gyrus, temporooccipital part	64	−48	−8	2.89
L occipital fusiform gyrus	−28	−70	−10	5.28
R cuneal cortex	6	−86	26	3.65
R superior lateral occipital cortex	28	−70	56	3.05
L cerebellum	−4	−72	−36	3.68
R cerebellum	34	−72	−48	3.41

Note: See Table 1 for notes concerning table organization an assignment of anatomical labels.

implicit positive associations with African Americans are likely lower than those with Chinese Americans. Finally, there was a marginally significant correlation between participants' explicit attitudes about and experience with Chinese Americans ($r = .45$, $p = .06$), but no significant correlations between experience and attitude measures for the other two racial groups.

These self-report and behavioral measures of participants' racial attitudes and experience levels were not significantly correlated with parameter estimates extracted from neural regions differentiating between racial groups during imitation. These measures were also not significantly related to neural activity during imitation when used in whole-brain regression analyses after significant outliers (>2 standard deviations from mean) were removed. The similarity of the outcomes of these measures to the fMRI results (with larger differences between the AA group and either the EA or CH group than between the EA and CH groups) suggests, however, that racial familiarity and attitudes might in part contribute to the observed fMRI findings, albeit indirectly. Future investigations are needed to identify which individual difference factors may directly influence brain activity when imitating other-race individuals.

Conclusions

Race can influence imitative behaviors that are important for cultural acquisition. Although much is already known about neural mechanisms underlying imitation and how the brain responds to looking at people of different races, to our knowledge no studies to date have investigated how the race of a model influences neural activity during imitation. Our study provides data that are relevant to answering this question thereby giving insight into the neural underpinnings of cultural learning processes.

With regard to the first aim of our study, we found that neural systems previously reported to be important for imitation (Caspers et al., 2010), such as fronto-parietal and motor planning systems, are modulated by the race of the person being imitated. Our data cannot speak directly to the origin of this modulation. One possibility is that all of the neural regions modulated by race are actively processing and differentiating models on the basis of race. Alternatively, a single (or several) "race processing" region(s) may modulate activity within the rest of the imitation system. The latter possibility seems more likely because all of the regions modulated by race during imitation are modulated in a similar way (i.e., for each significant racial comparison, all of the regions were more active for one of the two races). What *is* clear from our findings is that a wide range of neural regions is modulated by model race during imitation, rather than this modulation being confined to the early visual regions in which the perceptual information indicative of race originates.

This is an especially significant finding because the neural systems modulated by race, which include the putative mirror neuron system, have been hypothesized to underlie many complex social processes (Iacoboni, 2009; Ramachandran, 2000; Rizzolatti and Craighero, 2004), but many of the studies published thus far have focused on their basic visuomotor properties (Caspers et al., 2010). Evidence that these neural regions are also modulated by key social variables such as race provides empirical support for their hypothesized role in complex social processes such as cultural learning (Losin et al., 2009). More specifically, the current data suggest that characteristics of the actor, and not just the action itself, modulate activity within the putative mirror neuron system and other neural systems supporting imitation thereby suggesting a role for them in shaping race-biased imitative learning.

With regard to the second aim of our study, we found that neural systems underlying imitation are modulated by the race of the model in a race-specific manner. In other words, these neural systems are not only differentially activated by racial ingroup and outgroup members but also by distinct racial outgroups. This is not only a

novel finding regarding neural systems underlying imitation, but also in terms of how neural systems are modulated by target race in general because the designs of most previous studies, which compared actors of only two racial groups (Désy and Théoret, 2007; Ito and Bartholow, 2009; Liew et al., 2010; Molnar-Szakacs et al., 2007), prevented them from making this distinction. This finding further implicates imitation-related neural systems in supporting complex social interactions as it suggests their activity is modulated by social information such as race at a finer level of detail than simply ingroup versus outgroup.

In terms of race-specific neural activity, we found that neural regions important for imitation primarily distinguished between African Americans and the other two racial groups, whereas activity levels in visual regions differed between all three groups. This finding suggests that factors differentiating African Americans from European Americans and Chinese Americans may be driving neural activity in imitation-related regions. Because we did not find a direct relationship between participants' self-reported racial attitudes and experience levels and observed race-related neural activity differences during imitation, we hypothesize that another factor that varies considerably across these racial groups, perceived social status, may help explain observed differences. European Americans are perceived to have a high social status as the racial majority in the United States (Dunham et al., 2008). Importantly, the racial outgroups in our study also differed in perceived social status. Chinese American individuals and East Asians in general, often referred to as a model minority, are typically regarded as having a higher social status than African Americans (Bobo and Zubrinsky, 1996; Fiske et al., 2007; Link and Oldendick, 1996; Weaver, 2008), and by certain metrics have even been regarded as having a similar or even higher status than European Americans (Wong et al., 1998). Thus, it is possible that the greater recruitment of imitation-related neural structures during imitation of African Americans reflects a reduced propensity of participants to imitate these individuals in their daily lives due to the lower status attributed to this minority group, similar to the prestige and success related imitation biases described by Boyd and Richerson (1987).

With regard to the third aim of our study, we found that the magnitude of neural activity associated with the different racial groups within visual and imitation-related regions differed between imitation and previously used perceptual tasks. Not only were neural differences between racial groups heightened during imitation compared to action observation, but neural activity in response to the different racial groups during imitation was actually reversed when compared to tasks in which participants simply looked at faces (Golby et al., 2001; Iidaka et al., 2008; Lee et al., 2008; Lieberman et al., 2005; Molnar-Szakacs et al., 2007). Our replication of the previously-reported enhancement of neural activity in response to own-race individuals when people simply look at others' faces supports the idea that the race-related neural activity we found during imitation is indeed specific to the imitation process rather than merely reflecting general methodological differences between the current study and previous ones. This finding indicates that action may alter the perception of race and its underlying neural processing.

It has been proposed that enhanced visual activity when participants look at the faces of own-race individuals is related to more in-depth visual processing of faces that are more familiar (Golby et al., 2001). In contrast, during imitation, race may function as an indicator of the action's self-relevance given that race can signal the actor's self-similarity or social status. Thus, enhanced activity during imitation of actors from a low status racial outgroup could reflect a neural "cost" associated with imitation of a potentially less self-relevant action. Such a cost could relate to the greater processing resources required to imitate an individual who is more unpredictable due to their dissimilarity to the self or unfamiliarity as a model (due to their lower status). If low perceived self-similarity is driving

increased neural activity when European Americans imitate African Americans, one would predict that African Americans would not exhibit this effect. One would also not expect this effect to diminish with practice, as perceptions of self-similarity related to race presumably remain constant over time. In contrast, if unfamiliarity with imitating those from groups perceived to be low in status is driving increased activity when imitating African Americans, then African and European Americans should exhibit similar neural activity during imitation of African Americans, as individuals from both racial groups have been found to rate African Americans as having lower status (Bobo and Zubrinsky, 1996; Fiske et al., 2007; Link and Oldendick, 1996; Weaver, 2008). In this case, one would predict that enhanced activity during imitation of African Americans would diminish with practice in line with evidence that imitating familiar actions is associated with decreased neural activity compared to imitating more novel actions (Buccino et al., 2004; Vogt et al., 2007).

In conclusion, our findings demonstrate that neural systems underlying imitation show different responses based on the race of the person being imitated. Furthermore, these systems are modulated by the model's race in a way that is race-specific and unique to imitation. Given that race is known to influence imitative learning, these findings highlight some of the neural mechanisms relevant to cultural acquisition, a process that affects nearly every aspect our lives but has been largely unexplored in neuroscience. Future studies are called for to further determine the extent to which the pattern of racial encoding during imitation found in the present study relates to the race of the actors as compared to the race of the participants. Furthermore, future investigations should also examine the behavioral consequences of the race-related neural differences observed here, such as imitation accuracy and quality of learning, to help link these findings to potential applications in educational, physical training, and rehabilitation settings.

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