Title
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Publication Date
2012

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

Los Angeles

Exploring the Neural Architecture of Cultural Imitative Learning

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Neuroscience

by

Elizabeth Reynolds Losin

2012

ABSTRACT OF THE DISSERTATION

Exploring the Neural Architecture of Cultural Imitative Learning

By

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Doctor of Philosophy in Neuroscience

University of California, Los Angeles, 2012

Professor Mirella Dapretto, Chair

Imitation is a key mechanism by which people learn from others and is a fundamental component of cultural acquisition. Importantly, people do not imitate everyone in their social environment to the same degree. Instead, people preferentially imitate certain individuals including those who are similar to them or have high social status. These imitative biases are thought to automatically direct attention to individuals most likely to exhibit self-relevant or high quality behaviors, thus increasing the efficiency of cultural learning. Though much is known about the neural mechanisms underlying imitation, the neural mechanisms underlying imitative biases are largely unknown. In this dissertation, I began to address this knowledge gap by using fMRI to measure neural activity while people imitated individuals differing in self-similarity and social status. I focus on gender and race, two factors that can index a person's self-similarity and social status and that are known to influence the likelihood of imitation.

In chapter 1, I proposed a tentative model of the neural mechanisms underlying imitative cultural learning. In chapter 2, I tested this model in relation to gender imitative biases. I found

that the brain's reward system was more active during imitation of own-gender compared to other-gender models, suggesting a neural mechanism underlying the preferential imitation of own-gender models. In chapters 3 and 4, I tested this model in terms of imitative biases related to race. I found that both European Americans and African Americans exhibited more activity in visual regions and lateral fronto-parietal regions when imitating African American models compared to either European American or Chinese American models. Regardless of their own race, participants also rated African Americans as having lower social status than either European or Chinese Americans, suggesting that social status rather than self-similarity drives neural responses to race during imitation.

Taken together, these studies demonstrate that the neural systems that support imitation are modulated by the gender and race of the person being imitated. These data also suggest that both self-similarity and social status influence neural responses to race during imitation, highlighting neural mechanisms that may underlie similarity and status biases in cultural imitative learning.

The dissertation of Elizabeth Reynolds Losin is approved.

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2012

DEDICATION

I dedicate my dissertation to my loving and patient husband who has helped me through every stage of the dissertation process from conception to publication. His rigorous and creative scientific input along with his enthusiasm for my research and my success have made an invaluable contribution to both the research itself and my enjoyment of carrying it out. I also dedicate this dissertation to my mother whose contribution to this work started well before I was in graduate school and continued through providing input on this document. She encouraged my early interest in science, and pursuit of an academic career and has provided both moral and intellectual support in each step of my education since.

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Chapter 6: Conclusion

None

ACKNOWLEDGMENTS

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PUBLICATIONS

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Losin, E. A. R., Iacoboni, M., Martin, A., Cross, K.A., Dapretto, M. (2011) Race modulates neural activity during imitation. *NeuroImage*. doi:10.1016/j.neuroimage.2011.10.074.

Losin, E. A. R., Dapretto, M., Iacoboni, M. (2010). Culture and neuroscience: Additive or synergistic. *Social Cognitive and Affective Neuroscience*. doi:10.1093/scan/nsp058.

Losin, E. A. R., Dapretto, M., Iacoboni, M. (2009). Culture in the mind's mirror: How anthropology and neuroscience can inform a model of the neural substrate for cultural imitative learning. *Progress in Brain Research*. 178:175-90.

Losin, E. A. R., Rivera, S. M., O'Hare E. D., Sowell, E. R., Pinter, J. D. (2009) Abnormal fMRI activation pattern during story listening in individuals with Down syndrome. *American Journal of Intellectual and Developmental Disability.* 114(5):369-80.

Losin, E. A. R., Russell J. L., Freeman H., Meguerditchian A., Hopkins W. D. (2008) Left Hemisphere Specialization for Oro-Facial Movements of Learned Vocal Signals by Captive Chimpanzees. *PLoS ONE* 3(6): e2529. doi:10.1371/journal.pone.0002529

Hopkins, W. D., Russell, J. L., Freeman, H., **Reynolds, E. A.,** Griffis, C., Leavens, D. A. (2006). Lateralized Scratching in Chimpanzees (Pan troglodytes): Evidence of a Functional Asymmetry During Arousal. *Emotion*. 6(4): 553-9.

Hopkins, W. D., Russell, J., Freeman, H., Buehler, N., **Reynolds, E**., Schapiro, S. (2005). The Distribution and Development of Handedness for Manual Gestures in Captive Chimpanzees (*Pan troglodytes*). *Psychological Science*. 16(6): 487-493.

ABSTRACTS

Losin, E. A. R., Iacoboni, M., Dapretto, M. Race modulates functional connectivity during imitation. Poster to be given at the Organization of Human Brain Mapping meeting (2012) Bejing, China.

Losin, E. A. R., Iacoboni, M., Dapretto, M. Race-related amygdala activity exhibits an ingroup bias during passive face viewing. Talk given at the Social and Affective Neuroscience meeting (2012) in New York, NY.

Losin, E. A. R., Iacoboni, M., Dapretto, M. Action alters perception: how imitation alters the neural encoding of race. Talk given at the Society for Neuroscience meeting (2011) in Washington, D.C.

Losin, E. A. R., Iacoboni, M., Dapretto, M. Neural mechanisms of cultural learning: imitative biases for gender and race. Talk given at the University of Michigan Center for Culture, Mind, and Brain conference (2011) in Ann Arbor, MI.

Losin, E. A. R., Iacoboni, M., Dapretto, M. Race modulates the neural underpinnings of imitation but self-similarity alone cannot explain differential activity. Poster presented at the Cognitive Neuroscience Society meeting (2011) in San Francisco, CA.

Losin, E. A. R., Iacoboni, M., Martin, A., Dapretto, M. Own-gender imitation activates the brain's reward circuitry. Poster presented at the Society for Neuroscience meeting (2010) in San Diego, CA.

Losin, E. A. R., Iacoboni, M., Martin, A., Dapretto, M. Answering the 'other' question in cultural neuroscience: Theory and data on how culture gets into the brain. Talk given at the Social and Affective Neuroscience meeting (2010) in Chicago, IL.

Losin, E. A. R., Iacoboni, M., Nguyen, K., Morton, D., Dapretto, M. Racial attitudes influence the functional neuroanatomy of cultural imitative learning. Poster presented at the Organization of Human Brain Mapping meeting (2010) in Barcelona, Spain.

Losin, E. A. R., Iacoboni, M., Dapretto, M. Exploring the neural architecture of the similarity bias in cultural imitative learning. Poster presented at Cognitive Neuroscience Society meeting (2010) in Montreal, Canada.

Losin, E. A. R., Dapretto, M., Iacoboni, M. A novel paradigm for investigating the neural architecture of cultural imitative learning. Poster presented at the Primate Mind Workshop (2009) in Erice, Sicily.

Reynolds, E. A., Rivera, S. M., O'Hare, E. D., Sowell, E. R., Pinter, J. D. Deficient temporal lobe activity during passive story listening in individuals with Down syndrome. Poster presented at the Society for Neuroscience meeting (2007) in San Diego, CA.

Reynolds, E. A., Pinter, J. D., Koldewyn, K., Le, L., Backer, K., Tang, M., Rivera, S. M. Deficient intraperietal sulcus activity during number comparison in individuals with Down syndrome. Poster presented at the Cognitive Neuroscience Society meeting (2007) in New York, NY.

Rivera, S., Henry, M., Crone, E., **Reynolds, E.**, Herrera, A., Chen, I., van der Maas, H. Langer, J. Neural basis of protracted developmental changes in proportional reasoning. Poster presented at the Cognitive Neuroscience Society meeting (2006) in San Francisco, California.

Reynolds, E.A., Freeman, H, Russell, J. L., Hopkins, W.D. Oro-facial Asymmetry of voluntary and involuntary vocal signals in chimpanzees (*Pan troglodytes*). Poster presented at the American Society of Primatologists meeting (2005) in Portland, OR.

Freeman, H., Russell, J. L., Shonka, S., **Reynolds, E.**, Hopkins, W. D. Self-Recognition in chimpanzees (*Pan troglodytes*) using a small, LCD screen. Poster presented at the American Society of Primatologists meeting (2005) in Portland, OR.

Russell, J.L., Freeman, H., **Reynolds, E.**, Hopkins, W.D. Lateralized Scratching in Chimpanzees (*Pan troglodytes*). Poster presented at the American Society of Primatologists meeting (2005) in Portland, OR.

CHAPTER 1

Introduction to the dissertation

Imitation is one of the primary ways by which humans acquire culture (Tomasello, Kruger, & Ratner, 1993). Imitation enables efficient learning through copying a model as opposed to costly individual learning strategies such as trial and error (Zentall, 2006). The presence of imitative biases is thought to increase the efficiency of cultural learning via imitation (Henrich & McElreath, 2003). Theoretical models and empirical data from anthropology and psychology suggest that people preferentially imitate certain types of information and certain individuals including those who are perceived to be self-similar (Bandura, 1977; Henrich & McElreath, 2003) or high in status (prestigious or successful) (Chudek, Heller, Birch, & Henrich, 2012; Henrich & Gil-White, 2001). Two factors that can suggest a person's self-similarity and status are gender (Blau & Kahn, 2000; Eagly, 1983; Rudman & Goodwin, 2004) and race (Freeman, Penner, Saperstein, Scheutz, & Ambady, 2011; Karunanayake & Nauta, 2004; Penner & Saperstein, 2008) and both factors have been found to influence imitation. Despite this behavioral evidence, prior to the current studies, investigations of the neural underpinnings of imitation had not considered the influence of the gender or race of the person being imitated (for a review see Caspers, Zilles, Laird, & Eickhoff, 2010). Likewise, studies of neural responses to a person's gender or race had not investigated these processes during active social behaviors such as imitation (for a review see Ito & Bartholow, 2009). In this dissertation, I used functional MRI (fMRI) to investigate how the gender and race of a model influence neural activity during imitation and action observation to provide insight into the neural mechanisms underlying cultural acquisition. These studies also address critical gaps in the current understanding of neural mechanisms underlying imitation as well as gender and race processing.

Cultural learning

Cultural learning is a form of social learning characterized by high fidelity information transfer – both within and between generations – that results in cumulative cultural evolution

(Tomasello, 1999; Tomasello et al., 1993). Cultural knowledge, beliefs, norms, behaviors and practices are all acquired and transmitted in this manner. Imitation is the most prevalent and ontogenetically early means of cultural learning (Tomasello et al., 1993), and was therefore chosen as the focus of this dissertation.

Imitative Biases

Cultural learning theories suggest that humans have several cognitive mechanisms that enhance the efficiency of cultural learning by facilitating the acquisition of the most useful behaviors, beliefs and knowledge from the social environment (Henrich & McElreath, 2003). One of these mechanisms is the existence of imitative biases. People preferentially imitate certain behaviors (content biases), the most common behaviors (frequency-based context biases), and certain individuals (model-based context biases) (Boyd & Richerson, 1985; Henrich & McElreath, 2003). Such imitative biases are thought to have evolved because they automatically direct attention to the highest quality and most self-relevant behaviors and the individuals most likely to exhibit those behaviors, thus increasing the efficiency with which those behaviors are learned and ultimately increasing the fitness of the imitator. In this dissertation, I focused on model-based imitative biases. Cultural learning theories posit that people preferentially imitate self-similar (Bandura, 1977; Henrich & McElreath, 2003) and high status (Chudek et al., 2012; Henrich & Gil-White, 2001) models and there is ample behavioral evidence that both self-similarity and social status influence real-world imitative behavior.

Early evidence for preferential imitation of self-similar models came from a series of laboratory studies conducted by Alfred Bandura and his colleagues (Bandura, 1965; Bandura, Ross, & Ross, 1961; Bandura, Ross, & Ross, 1963). In these studies, children observed different models performing behaviors such as interacting with a life-size doll (Bobo doll) or selecting from an array of toys. Children were then given the opportunity to interact with these objects themselves while the similarity of their behaviors to those of the different models was

measured. Based on these studies, Bandura proposed his Social Learning Theory (SLT), which emphasizes the importance of model self-similarity in biasing social learning (Bandura, 1977). Bandura suggested that model self-similarity influences social learning because observers identify more with self-similar models, thus making it easier for them to relate modeled actions to their own (Bandura, 1977). More recent studies have continued to demonstrate a preference for self-similar models. For instance, Stack (1987) found that the rate of imitative suicide following the suicide of a celebrity was higher than expected by chance among those matched to the celebrity in age, gender and nationality. Similarly, Vescio and colleagues (2005) found that middle school children most often reported having role models of their own gender, their own national heritage and who played the same sports as they did.

Evidence of preferential imitation of high status individuals (both in terms of prestige and success) has also been found through controlled laboratory experiments. For example, in iterative betting (Rosenbaum & Tucker, 1962) and investment experiments (Kroll & Levy, 1992), participants were found to imitate the investment choices of the most successful players even when this strategy was not optimal for winning the game. Similar instances of success-biased imitation have been documented in a number of other studies (Chalmers, Horne, & Rosenbaum, 1963; Greenfeld & Kuznicki, 1975; Mausner, 1954; Mausner & Bloch, 1957). Preferential imitation of prestigious models has also been demonstrated. For example, Bauer and colleagues (1983) found that college undergraduates more readily imitated the strategy used by a professionally dressed model who held a Ph.D. than an immature-looking model who did not yet have a bachelor's degree. Similar prestige-biased imitation has been repeatedly demonstrated (Bandura & Kupers, 1964; Harvey & Rutherford, 1960; Lefkowitz, Blake, & Mouton, 1955).

Gender and race as proxies for self-similarity and social status

In contrast to the laboratory setting, during real-world imitative learning, detailed knowledge about self-similarity (e.g., shared beliefs and goals) and social status (e.g., financial success or job prestige) is often not available to learners. For this reason, phenotypic characteristics such as gender and race are sometimes used as proxies for this information (Boyd & Richerson, 1987; Henrich & Gil-White, 2001). This is because tight psychological associations exist between gender and race and both self-similarity (Blau & Kahn, 2000; Eagly, 1983; Rudman & Goodwin, 2004) and social status (Freeman et al., 2011; Karunanayake & Nauta, 2004; Penner & Saperstein, 2008). Accordingly, both gender and race have been found to influence the likelihood of imitation. Therefore, in the present studies we focused on the influence of gender and race on neural mechanisms of imitation.

Imitative preferences related to gender have been found primarily for own-gender models. In a series of foundational studies, Bandura and colleagues found that a diverse set of behaviors, ranging from aggression to color preference, were more readily transmitted via imitation of own-gender than other-gender models (Bandura et al., 1961; Bussey & Bandura, 1984). Following Bandura's findings, preferences for own-gender models have been documented for models such as parents (Basow & Howe, 1980), teachers (Gilbert, Gallessich, & Evans, 1983), peers (Perloff, 1982; Slaby & Frey, 1975) and even strangers, like musicians (Killian, 1990) and celebrities (Stack, 1987), thus suggesting that own-gender imitative biases are pervasive during development and continue to guide imitation in adulthood. Bandura's early studies and others also demonstrated that a preference for own-gender imitation is present in children before gender identity is fully formed, suggesting that own-gender imitation is not only an effect, but also a cause of gender identity development (Bussey & Bandura, 1984).

In contrast to gender biases which appear to primarily relate to self-similarity, imitative biases related to race have been found both for own-race (self-similar) models and models from

racial groups perceived to be higher in social status. These preferences 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 to 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, Sobol & Copermann, 1972; Neely, Hechel & Leichtman, 1973). Adults have also been found to exhibit such race-biased preferences. For instance, adults practice health-promoting behaviors such as self–screenings more often when someone of their own race models the behaviors (Haas & Sullivan, 1991). Adults have also been found to model their educational and career choices after own-race role models (Karunanayake & Nauta, 2004; King & Multon, 1996; Zirkel, 2002). Thus, like imitative biases related to gender, imitative biases related to race are pervasive and appear to guide learning into adulthood.

Neural mechanisms of imitation

Although no prior studies had investigated the influence of the gender and race of a model on the neural underpinnings of imitation, much is already known about the neural mechanisms subserving imitation. The ideomotor framework of imitation suggests that there is a common neural substrate for action perception and action execution (Prinz, 2005). Mirror neurons, first discovered in macaque monkeys using depth electrode recordings, display these perception-action coupling properties (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). A subset of neurons in the monkey's premotor cortex (area F5) (Gallese et al., 1996) and inferior parietal lobe (area PF) (Fogassi et al., 2005) fire both when the monkey performs a goal-directed action and when it sees a human or conspecific perform the same or a related action (Gallese et al., 1996). Convergent evidence from a variety of imaging modalities, including fMRI (e.g., Iacoboni et al., 1999), EEG (e.g., Muthukumaraswamy, Johnson, & McNair, 2004), positron emission tomography (PET) (e.g., Grafton, Arbib, Fadiga, & Rizzolatti, 1996), transcranial magnetic

stimulation (TMS) (e.g., Patuzzo, Fiaschi, & Manganotti, 2003), and most recently, single unit

recordings (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010) suggests that a mirror neuron

system (MNS) with similar properties exists in the human brain. The putative human MNS

consists of the posterior inferior frontal gyrus (piFG), neighboring ventral premotor cortex (the

human homologue of monkey F5), and the rostral inferior parietal lobule (riPL) (Rizzolatti &

Craighero, 2004). Indeed, a recent meta-analyses of 35 human imitation studies (Caspers et al.,

2010) identified an extended bilateral network important for imitation that includes the canonical

MNS (the pars opercularis in the inferior frontal gyrus, premotor cortex and adjacent superior

frontal gyrus, and inferior parietal lobule) and additional sensorimotor and visual regions

including the supplementary motor area, primary somatosensory cortex, and visual area V5.

Neural mechanisms of imitation: Self-similarity

There is also some evidence that MNS may be sensitive to model self-similarity during

action observation (though this question had not previously been addressed during imitation).

Several studies have demonstrated that the human MNS responds more intensely to the

observation of human conspecifics compared to other animals (Buccino et al., 2004) or robots

(Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Tai, Scherfler, Brooks, Sawamoto, & Castiello,

2004). There is also evidence that the MNS is modulated by model characteristics relevant to

the present study – ethnicity and gender. For example, two studies (Liew, Han, & Aziz-Zadeh,

2010; Molnar-Szakacs, Wu, Robles, & Iacoboni, 2007) found evidence of greater MNS activity

while participants observed an ethnic in-group member versus an ethnic out-group member

performing hand gestures. However, two other studies found more activity in the MNS when

individuals viewed ethnic outgroup members (Désy & Théoret, 2007) or gender outgroup

members (Cheng, Tzeng, Decety, Imada, & Hsieh, 2006). These discrepant findings suggest

that while the MNS may be sensitive to the gender and ethnicity of a model, the direction of the

effect remains to be further clarified. Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni (2005)

more directly tested the influence of self-similarity on the MNS by morphing the faces of

subjects with the faces of familiar others and demonstrated that both the right frontal and

parietal components of the MNS are activated more when viewing morphs containing a greater

proportion of the self-face than familiar-other-face. Furthermore, Uddin, Molnar-Szakacs,

Zaidel, & Iacoboni (2006) later found that disruption of this area using TMS impaired self-face

from other-face discrimination.

Neural encoding of race and gender

Though no prior research has measured the influence of the gender and race of a model

during imitation, a number of studies have investigated differential neural responses to men and

women as well as to individuals from different racial groups. The findings of this work are

informative with regard to the neural systems that may also encode a model's race and gender

during imitation. The majority of the existing literature on the neural correlates of race employs

face-viewing tasks (Eberhardt, 2005; Ito & Bartholow, 2009). By varying the way in which faces

are presented and the task participants are asked to perform, 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 & Bartholow (2009) have highlighted

a number of brain areas involved in race perception. These include the fusiform gyri (typically

showing greater activity when processing own-race faces; e.g., Golby, Gabrieli, Chiao, &

Eberhardt, 2001), the posterior cingulate (usually more strongly activated during retrieval of

information about own-race individuals; e.g., Iidaka, Nogawa, Kansaku, & Sadato, 2008), the

amygdala (showing greater activity during arousal of affect and evaluation for other-race

individuals, e.g., Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005, as well as own-

race individuals, e.g., Chiao et al., 2008) and the anterior cingulate, dorsolateral prefrontal

cortex, and ventrolateral prefrontal cortex (all typically more active when inhibiting stereotypes or prejudice against other-race individuals; e.g., Cunningham et al., 2004). Neural responses to gender have been less well characterized but studies addressing this question have used similar face-viewing paradigms. Overall, this work suggests that gender is encoded in similar visual regions to those showing race effects, including the fusiform gyrus and inferior occipital cortex (Kranz & Ishai, 2006; Wiese, Kloth, Güllmar, Reichenbach, & Schweinberger, 2011).

To summarize, cultural learning theories suggest that the cognitive mechanisms that result in preferential imitation of self-similar and high status models are an important component of efficient cultural learning (Boyd & Richerson, 1985; Henrich & McElreath, 2003). Behavioral data suggest that one way in which these imitative biases manifest themselves is in preferential imitation based on gender (Bandura et al., 1961; Basow & Howe, 1980; Bussey & Bandura, 1984; Gilbert et al., 1983; Killian, 1990; Mesoudi, 2009; Perloff, 1982; Slaby & Frey, 1975) and race (Clark & Clark, 1947; Feinman, 1980; Haas & Sullivan, 1991; Karunanayake & Nauta, 2004; Kelly et al., 2005; King & Multon, 1996; Liebert, Sobol, & Copemann, 1972; Neely, Hechel, & Leichtman, 1973; Zirkel, 2002). The goal of the suite of studies comprising this dissertation was therefore to use fMRI to examine neural responses to the gender and race of a model during imitation in order to gain insight into the neural mechanisms that may underlie imitative biases important for cultural learning.

As a first step in addressing these questions, in Chapter 2 I reviewed the relevant behavioral and cognitive neuroscience literature and, on this basis, formulated a model of the neural systems that may interact to support imitative biases in cultural learning. I next created a novel fMRI paradigm in which participants imitated and observed male and female models from three different racial groups (European American, African American and Chinese American) performing novel meaningless hand gestures. In Chapter 3, I used this paradigm with a sample of European American participants to explore which neural systems are modulated by the

gender of the person being imitated. In Chapter 4, I relied upon the same paradigm to explore which neural systems are modulated by the race of the model during imitation in European Americans. Finally, in Chapter 5, I compared race-related results observed in the European American sample to those obtained in a sample of African American participants in order to disentangle race effects related to self-similarity from those related to social status.

REFERENCES

Bandura, A. (1965). Influence of models' reinforcement contingencies on the acquisition of imitative

responses. *Journal of Personality and Social Psychology*, *1*(6), 589-595.

Bandura, A. (1977). *Social learning theory*. New Jersey: Prentice-Hall.

Bandura, A., & Kupers, C. J. (1964). Transmission of patterns of self-reinforcement through modeling.

The Journal of Abnormal and Social Psychology, *69*(1), 1-9.

Bandura, A., Ross, D., & Ross, S. A. (1961). Transmission of aggression through imitation of

aggressive models. *Journal of Abnormal and Social Psychology*, *63*(3), 575-82.

Bandura, A., Ross, D., & Ross, S. A. (1963). Imitation of film-mediated aggressive models. *Journal of

Abnormal and Social Psychology*, *66*(1), 3-11.

Basow, S. A., & Howe, K. G. (1980). Role-Model influence: Effects of sex and sex-role attitude in

college students. *Psychology of Women Quarterly*, *4*(4), 558-572.

Bauer, G. P., Schlottmann, R. S., Bates, J. V., & Masters, M. A. (1983). Effect of state and trait anxiety

and prestige of model on imitation. *Psychological Reports*, *52*(2), 375-382.

Blau, F. D., & Kahn, L. M. (2000). Gender differences in pay. *The Journal of Economic Perspectives*,

14(4), 75-99.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. University of Chicago Press.

Boyd, R., & Richerson, P. J. (1987). The evolution of ethnic markers. *Cultural Anthropology*, *2*, 65-79.

Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., & Rizzolatti, G. (2004). Neural

circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron*,

42(2), 323-34.

Bussey, K., & Bandura, A. (1984). Influence of gender constancy and social power on sex-linked

    modeling. *Journal of Personality and Social Psychology*, *47*(6), 1292-302.

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation

    and imitation in the human brain. *NeuroImage*, *50*(3), 1148-67.

    doi:10.1016/j.neuroimage.2009.12.112

Chalmers, D. K., Horne, W. C., & Rosenbaum, M. E. (1963). Social agreement and the learning of

    matching behavior. *The Journal of Abnormal and Social Psychology*, *66*(6), 556.

Cheng, Y. W., Tzeng, O. J. L., Decety, J., Imada, T., & Hsieh, J. C. (2006). Gender differences in the

    human mirror system: A magnetoencephalography study. *Neuroreport*, *17*(11), 1115.

Chiao, J. Y., Iidaka, T., Gordon, H. L., Nogawa, J., Bar, M., Aminoff, E., Sadato, N., & Ambady, N.

    (2008). Cultural specificity in amygdala response to fear faces. *Journal of Cognitive*

    Neuroscience, *20*(12), 2167-2174.

Chudek, M., Heller, S., Birch, S., & Henrich, J. (2012). Prestige-biased cultural learning: Bystander's

    differential attention to potential models influences children's learning. *Evolution and Human*

    Behavior, *33*(1), 46-56. doi:10.1016/j.evolhumbehav.2011.05.005

Clark, K. B., & Clark, M. P. (1947). Racial identification and preference in Negro children. *Readings in*

    Social Psychology, 169-178.

Cunningham, W. A., Johnson, M. K., Raye, C. L., Chris Gatenby, J., Gore, J. C., & Banaji, M. R. (2004).

    Separable neural components in the processing of Black and White faces. *Psychological*

    Science, *15*(12), 806-13. doi:10.1111/j.0956-7976.2004.00760.x

Désy, M. C., & Théoret, H. (2007). Modulation of motor cortex excitability by physical similarity with an

    observed hand action. *PLoS ONE*, *2*(10): e971. doi: 10.1371/journal.pone.0000971.

Eagly, A. H. (1983). Gender and social influence: A social psychological analysis. *American Psychologist*, *38*(9), 971-981.

Eberhardt, J. L. (2005). Imaging race. *The American Psychologist*, *60*(2), 181-90. doi:10.1037/0003-066X.60.2.181

Feinman, S. (1980). Infant response to race, size, proximity, and movement of strangers. *Infant Behavior and Development*, *3*, 187-204.

Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*(5722), 662-667.

Freeman, J. B., Penner, A. M., Saperstein, A., Scheutz, M., & Ambady, N. (2011). Looking the part: Social status cues shape race perception. *PLoS ONE*, *6*(9), e25107. doi:10.1371/journal.pone.0025107

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain : A Journal of Neurology*, *119*(2), 593.

Gazzola, V., Rizzolatti, G., Wicker, B., & Keysers, C. (2007). The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. *NeuroImage*, *35*(4), 1674-84. doi:10.1016/j.neuroimage.2007.02.003

Gilbert, L. A., Gallessich, J. M., & Evans, S. L. (1983). Sex of faculty role model and students' self-perceptions of competency. *Sex Roles*, *9*(5), 597-607.

Golby, A. J., Gabrieli, J. D. E., Chiao, J. Y., & Eberhardt, J. L. (2001). Differential responses in the fusiform region to same-race and other-race faces. *Nature Neuroscience*, *4*(8), 845.

Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. *Experimental Brain Research*, *112*(1), 103-111.

Greenfeld, N., & Kuznicki, J. T. (1975). Implied competence, task complexity, and imitative behavior. *The Journal of Social Psychology*, *95*(2), 251-261.

Haas, N. S., & Sullivan, H. (1991). Use of ethnically matched role models in career materials for Hispanic students. *Contemporary Educational Psychology*, *16*(3), 272-278.

Harvey, O. J., & Rutherford, J. (1960). Status in the informal group: Influence and influencibility at differing age levels. *Child Development*, *31*(2), 377-385.

Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige - freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, *22*(3), 165-196.

Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology*, *12*(3), 123-135. doi:10.1002/evan.10110

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*(5449), 2526-8.

Iidaka, T., Nogawa, J., Kansaku, K., & Sadato, N. (2008). Neural correlates involved in processing happy affect on same race faces. *Journal of Psychophysiology*, *22*(2), 91-99.

Ito, T. A., & Bartholow, B. D. (2009). The neural correlates of race. *Trends in Cognitive Sciences*, *13*(12), 524-31. doi:10.1016/j.tics.2009.10.002

Karunanayake, D., & Nauta, M. M. (2004). The relationship between race and students' identified career role models and perceived role model influence. *The Career Development Quarterly, 52*(3), 225-234.

Kelly, D. J., Quinn, P. C., Slater, A. M., Lee, K., Gibson, A., Smith, M., Ge, L., Pascalis, O. (2005).

    Three-month-olds, but not newborns, prefer own-race faces. *Developmental Science*, *8*(6), F31-

    6. doi:10.1111/j.1467-7687.2005.0434a.x

Killian, J. N. (1990). Effect of model characteristics on musical preference of junior high students.

    Journal of Research in Music Education, *38*(2), 115-123.

King, M. M., & Multon, K. D. (1996). The effects of television role models on the career aspirations of

    African American junior high school students. *Journal of Career Development*, *23*(2), 111-125.

Kranz, F., & Ishai, A. (2006). Face perception is modulated by sexual preference. *Current Biology: CB*,

    16(1), 63-8. doi:10.1016/j.cub.2005.10.070

Kroll, Y., & Levy, H. (1992). Further tests of the separation theorem and the capital asset pricing model.

    The American Economic Review, *82*(3), 664-670.

Lefkowitz, M., Blake, R. R., & Mouton, J. S. (1955). Status factors in pedestrian violation of traffic

    signals. *The Journal of Abnormal and Social Psychology*, *51*(3), 704-706.

Lieberman, M. D., Hariri, A., Jarcho, J. M., Eisenberger, N. I., & Bookheimer, S. Y. (2005). An fMRI

    investigation of race-related amygdala activity in African-American and Caucasian-American

    individuals. *Nature Neuroscience*, *8*(6), 720-722. doi:10.1038/nn1465

Liebert, R. M., Sobol, M. P., & Copemann, C. D. (1972). Effects of vicarious consequences and race of

    model upon imitative performance by Black children. *Developmental Psychology*, *6*(3), 453 -

    456. doi: 10.1037/h0020251

Liew, S. L., Han, S., & Aziz-Zadeh, L. (2010). Familiarity modulates mirror neuron and mentalizing

    regions during intention understanding. *Human Brain Mapping.* doi:10.1002/hbm.21164

Mausner, B. (1954). The effect of one partner's success in a relevant task on the interaction of observer

    pairs. *The Journal of Abnormal and Social Psychology*, *49*(4p1), 557-560.

Mausner, B., & Bloch, B. L. (1957). A study of the additivity of variables affecting social interaction. *The*

    Journal of Abnormal and Social Psychology, *54*(2), 250.

Mesoudi, A. (2009). The cultural dynamics of copycat suicide. *PLoS ONE, 4*(9), e7252.

    doi:10.1371/journal.pone.0007252

Molnar-Szakacs, I., Wu, A. D., Robles, F. J., & Iacoboni, M. (2007). Do you see what I mean?

    Corticospinal excitability during observation of culture-specific gestures. *PLoS ONE, 2*(7), e626.

    doi:10.1371/journal.pone.0000626

Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-Neuron responses in

    humans during execution and observation of actions. *Current Biology, 20(8), 750-756.*

    doi:10.1016/j.cub.2010.02.045

Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during

    observation of an object-directed grasp. *Cognitive Brain Research*, *19*(2), 195-201.

Neely, J. J., Hechel, R. V., & Leichtman, H. M. (1973). The effect of race of model and response

    consequences to the model on imitation in children. *Journal of Social Psychology*, *89*, 225-231.

Patuzzo, S., Fiaschi, A., & Manganotti, P. (2003). Modulation of motor cortex excitability in the left

    hemisphere during action observation: A single-and paired-pulse transcranial magnetic

    stimulation study of self-and non-self-action observation. *Neuropsychologia*, *41*(9), 1272-1278.

Penner, A. M., & Saperstein, A. (2008). How social status shapes race. *Proceedings of the National*

    Academy of Sciences, *105*(50), 19628-19630.

Perloff, R. M. (1982). Gender constancy and same-sex imitation: A developmental study. *The Journal of Psychology*, *111*(1), 81-86.

Prinz, W. (2005). An ideomotor approach to imitation. In *Perspectives on imitation: From neuroscience to social science* (pp. 141-56). Cambridge, MA: MIT Press.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169-192. doi:10.1146/annurev.neuro.27.070203.144230

Rosenbaum, M. E., & Tucker, I. F. (1962). The competence of the model and the learning of imitation and non-imitation. *Journal of Experimental Psychology*, *63*(2), 183-190.

Rudman, L. A., & Goodwin, S. A. (2004). Gender differences in automatic in-group bias: Why do women like women more than men like men? *Journal of Personality and Social Psychology*, *87*(4), 494-509.

Slaby, R. G., & Frey, K. S. (1975). Development of gender constancy and selective attention to same-sex models. *Child Development*, *46*(4), 849-856.

Stack, S. (1987). Celebrities and suicide: A taxonomy and analysis, 1948-1983. *American Sociological Review*, *52*(3), 401-412.

Tai, Y. F., Scherfler, C., Brooks, D. J., Sawamoto, N., & Castiello, U. (2004). The human premotor cortex is 'mirror' only for biological actions. *Current Biology*, *14*(2), 117-120.

Tomasello, M. (1999). The human adaptation for culture. *Annual Review of Anthropology*, *28*, 509-529.

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *The Behavioral and Brain Sciences*, *16*(3), 495-511.

Uddin, L. Q., Kaplan, J. T., Molnar-Szakacs, I., Zaidel, E., & Iacoboni, M. (2005). Self-face recognition

   activates a frontoparietal "mirror" network in the right hemisphere: An event-related fMRI study.

   NeuroImage, *25*(3), 926-35. doi:10.1016/j.neuroimage.2004.12.018

Uddin, L. Q., Molnar-Szakacs, I., Zaidel, E., & Iacoboni, M. (2006). RTMS to the right inferior parietal

   lobule disrupts self-other discrimination. *Social Cognitive and Affective Neuroscience*, *1*(1), 65-

   71. doi:10.1093/scan/nsl003

Vescio, J., Wilde, K., & Crosswhite, J. J. (2005). Profiling sport role models to enhance initiatives for

   adolescent girls in physical education and sport. *European Physical Education Review*, *11*(2),

   153-170. doi:10.1177/1356336X05052894

Wiese, H., Kloth, N., Güllmar, D., Reichenbach, J. R., & Schweinberger, S. R. (2011). Perceiving age

   and gender in unfamiliar faces: An fMRI study on face categorization. *Brain and Cognition,*

   78(2), 163-168.

Zentall, T. R. (2006). Imitation: Definitions, evidence, and mechanisms. *Animal Cognition*, *9*(4), 335-53.

   doi:10.1007/s10071-006-0039-2

Zirkel, S. (2002). Is there a place for me? Role models and academic identity among White students

   and students of color. *The Teachers College Record*, *104*(2), 357-376.

CHAPTER 2

Culture in the mind's mirror: how anthropology and neuroscience can inform a model of the

neural substrate for cultural imitative learning

CHAPTER 12

Culture in the mind's mirror: how anthropology and neuroscience can inform a model of the neural substrate for cultural imitative learning

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Abstract: Cultural neuroscience, the study of how cultural experience shapes the brain, is an emerging subdiscipline in the neurosciences. Yet, a foundational question to the study of culture and the brain remains neglected by neuroscientific inquiry: "How does cultural information get into the brain in the first place?" Fortunately, the tools needed to explore the neural architecture of cultural learning — anthropological theories and cognitive neuroscience methodologies — already exist; they are merely separated by disciplinary boundaries. Here we review anthropological theories of cultural learning derived from fieldwork and modeling; since cultural learning theory suggests that sophisticated imitation abilities are at the core of human cultural learning, we focus our review on cultural imitative learning. Accordingly we proceed to discuss the neural underpinnings of imitation and other mechanisms important for cultural learning: learning biases, mental state attribution, and reinforcement learning. Using cultural neuroscience theory and cognitive neuroscience research as our guides, we then propose a preliminary model of the neural architecture of cultural learning. Finally, we discuss future studies needed to test this model and fully explore and explain the neural underpinnings of cultural imitative learning.

Introduction

The emerging subfield of cultural neuroscience is based on the concept that cultural experience shapes the human brain, an idea that is increasingly

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accepted and studied in neuroscience. Yet a more basic question remains unaddressed in the realm of neuroscience: "How did the cultural information get into the brain in the first place?" In this paper we review literature from both anthropology and cognitive neuroscience that may help to elucidate the neural architecture of enculturation.

Before we can design effective studies to investigate how differential cultural experience shapes the human brain, we must have a better

understanding of the neurocognitive mechanisms of cultural learning. Fortunately, the conceptual and methodological tools needed to conduct effective neuroscientific investigations of cultural learning already exist; anthropology provides a number of complementary theories of cultural learning, while cognitive neuroscience provides the methods and technologies needed to discover the neural architecture that likely underlies cultural learning. Boundaries between these disciplines, however, have until recently prevented their union.

Anthropological theories of cultural learning are based on fieldwork, computational modeling, and laboratory experiments. These theories converge on several cognitive mechanisms suggested to be fundamental to human cultural learning. The prevailing view is that the core of human cultural learning is sophisticated imitative learning (Higgs, 2000; Hurley and Chater, 2005; Kannetzky, 2007; Meltzoff and Prinz, 2002; Sommerville and Decety, 2006; Tomasello et al., 1993b) which is augmented by forms of learning biases (Henrich and McElreath, 2003), mental state attribution (Tomasello et al., 1993a), and reinforcement learning (Castro and Toro, 2004).

Fortunately, cognitive neuroscience studies have already provided us a great deal of knowledge about the neural architecture of imitation, learning biases, mental state attribution, and reinforcement learning in vivo through the use of neuroimaging techniques such as functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). Thus, by using anthropological cultural learning theory to guide future neuroimaging investigations of imitation, we can better understand the neurocognitive architecture of cultural learning. This can, in turn, inform our study of how differing cultural experience shapes other neurocognitive systems and of the neurocognitive machinery of cultural learning itself.

This review is organized into three sections. The first section treats theoretical and behavioral accounts of cultural learning, with a focus on imitative learning. The second section describes neural systems that may underlie the cognitive components of cultural imitative learning. In the third section, we propose a preliminary model

of the neural architecture of cultural imitative learning and suggest future studies needed to test this model.

Section I: cultural learning and imitation — theory and behavior

Cultural learning

In the following discussion of cultural learning theory we will briefly define cultural learning and highlight aspects of human cultural learning that differ from the cultural capacities of other animals. We utilize this comparative perspective to focus our discussion of cultural learning on aspects of human cognition that may be most informative for elucidating the neural underpinnings of the sophistication of human cultural capacities.

The first step in discussing cultural learning is defining culture itself. Bates and Plog (1990, p. 7) define culture as "the system of shared beliefs, values, customs, behaviours, and artifacts that the members of society use to cope with their world and with one another, and that are transmitted from generation to generation through learning". This definition highlights a critical point: culture is not merely the sum of cultural products: beliefs, behaviors, and artifacts; instead culture is created through the transmission and modification of these products within and between generations: cultural learning. Thus, by studying cultural learning and its neural basis, we will not only be studying the way in which culture is transmitted, we will also be studying a critical component of culture itself.

Tomasello et al. (1993a) describe cultural learning as a form of social learning in which perspective-taking plays a critical role in both the transmission of information and the resulting cognitive product. In other words, during cultural learning, information in addition to modeled behaviors, such as the inferred intentions and emotional states of the model, are encoded and retained along with the behavior in order to give that behavior contextual meaning. Tomasello et al. (1993a) propose that cultural learning includes imitative learning, instructed learning,

and collaborative learning — these types of learning emerge in successive stages of development. Cultural learning is distinguished from other forms of learning by its social nature and the niche it occupies within the learning environment. Modeling work by McElreath (2004) demonstrates that cultural learning is favored when individual learning is costly and inaccurate. Boyd and Richerson (1985) suggest that human social learning abilities were evolutionarily favored as a strategy for learning information relevant to rapidly changing environmental conditions.

Culture and cultural transmission are most fully developed in humans; however, great apes, especially chimpanzees, also have basic cultural capacities. A number of studies in both captive and wild chimpanzees have documented rich behavioral traditions specific to particular groups (Boesch, 2003; McGrew, 1992; Wrangham et al., 1994). Additionally, several recent experimental studies in groups of captive chimpanzees have demonstrated faithful transmission of food retrieval techniques (Whiten et al., 2007), as well as arbitrary actions (Bonnie et al., 2007) taught to a few group members throughout the group and, in the case of Whiten et al. (2007), between groups that had only visual contact. These experiments demonstrate with a new level of empirical certainty that chimpanzee groups can not only maintain unique cultural repertories, but also that — as in humans — a prominent means of chimpanzee cultural transmission is imitative learning.

The notion of chimpanzee culture and chimpanzee imitative cultural learning raises the question, "What explains the formidable differences between human and chimpanzee culture?" The answers may lie in the accuracy and complexity of human imitation abilities, compared to those of chimpanzees, and in the other cognitive mechanisms that augment human imitation, such as learning biases, mental state attribution, and reinforcement learning. The unique combination, and degree of sophistication, of these cognitive abilities enable humans to encode inferred intentions, emotions, and reward values along with learned behaviors. This contextual information allows individuals to modify culturally learned

behaviors. In turn, the continual modification of culturally learned behavior leads to the summing of cognitive resources within and between generations and the creation of distinct and rich cultures that are constantly evolving (Henrich and McElreath, 2003; Tomasello, 1999; Tomasello et al., 1993a). We will structure our discussion of cultural learning around the suite of cognitive mechanisms that distinguish human from nonhuman cultural capacities as the neural underpinnings of these abilities may be most informative in revealing the neural architecture of human cultural learning.

Imitation and imitative learning

Imitation learning is at the core of cultural learning; therefore, cultural imitative learning will be the focus of our review. In the following section we will provide a broad overview of imitative learning including its definition, theoretical accounts of the mechanisms of imitation, and behavioral accounts of imitation learning at different stages of development.

Although the meaning of the word "imitation" seems intuitive, the precise definition of imitation and imitative learning has been the subject of much debate (Chalmeau and Gallo, 1993). The imitation controversy is due in part to the question of whether there are any uniquely human abilities (Miklósi, 1999). Additionally, there are a number of mimetic but nonimitative processes, such as contagion and observational conditioning, that can result in the appearance or behavior of one individual resembling that of another (Zentall, 2006). Two mimetic processes closely related to but distinct from imitation are stimulus enhancement, in which an individual's attention is drawn toward a particular *object*, and goal emulation, where an individual learns the *goal* of an action but may accomplish that goal by other means (Whiten, 2000). True imitation is distinguished by the faithful copying of the *means* by which a goal is achieved (Whiten, 2000; Zentall, 2006). Tomasello et al. (1993a) argues that true imitation requires recognizing the intentional structure of the modeled behavior. Intention recognition is especially important during a

special type of imitation termed opaque imitation (Piaget, 1962) [also called blind or cross-modal imitation (Moore, 2004)], which involves imitation with a body part to which the imitator does not have direct visual access, such as the face.

There is also some debate over the neurocognitive mechanism of imitation. Iacoboni (2009) states that the two psychological theories of imitation mechanisms that best fit neurophysiological data are the ideomotor framework and the associated sequence-learning model. The ideomotor framework postulates that imitation is achieved through a shared neural representation system for observation and execution (Prinz, 2005). In the associative sequence-learning model, rather than a single neural substrate linking observation and execution, experience-based Hebbian learning (the strengthening of neural connections due to repeated coincident neural firing) links separate neural systems for observation and execution (Heyes, 2005).

In addition to theoretical accounts of the mechanisms of imitative behavior, extensive behavioral studies of imitation have been conducted from the neonatal period through adulthood. There is considerable evidence that the basic neurocognitive machinery of imitation is hard-wired. For example, Meltzoff and Moore (1977, 1983, 1989) found imitation of facial and manual gestures such as protruding the tongue in infants only hours old; this finding has since been replicated in 13 independent laboratories (Meltzoff and Decety, 2003). In addition to innate imitation mechanisms, which results in the basic forms of imitation seen in infants, elements of the human socio-cultural environment, such as joint attention and turn-taking, promote the rapid development of more sophisticated imitative abilities (Kumashiro et al., 2003). The imitation-promoting effects of the human socio-cultural environment are strikingly illustrated by Tomasello et al.'s (1993b) finding that children and enculturated chimpanzees perform similarly on an imitation task and outperform non-enculturated chimpanzees.

Human imitative abilities reach a high level very early in life. Infants as young as 12 months are sensitive to the rationality of modeled actions (Schwier et al., 2006), and at 18 months, they have been found to imitate object-directed real and pretend actions (Rakoczy et al., 2005), as well as imitate the goal of incomplete actions (Meltzoff, 1995). Because of the early emergence of imitative abilities, imitation makes up a large portion of social interaction during early development (Masur, 2006) and is the likely means by which many important types of cultural information, such as language and behavioral norms, are learned (Arbib, 2005).

An ongoing debate is whether the motor system is engaged during action observation, as suggested by the ideomotor framework, or whether connections between observation and action only happen during reenactment of the behavior (Iacoboni, 2009; Vogt and Thomaschke, 2007). A number of studies suggest that, in the domains of imitative learning of sequences, timing, and task dynamics, pure observation has an equivalent effect to motor practice on later behavioral performance. However, for configural postures and inter-limb coordination the data are less clear and motor practice may result in superior behavioral performance (for a review see Vogt and Thomaschke, 2007). It is important to note that even in cases when observational and motor practice appear equivalent, nether strategy results in a carbon copy of the imitated action. Rather, observational practice results in elements of the imitator's own behavioral repertoire being activated and built upon (Greer et al., 2006; Iacoboni, 2009; Vogt and Thomaschke, 2007).

Reinforcement is another critical element of imitation learning as it guides both the likelihood and direction of learning. Both internal and external reinforcement of the imitator influence the likelihood and direction of imitative learning (Greer et al., 2006). Reward and punishment of the model (vicarious reinforcement) has also been found to influence imitation (Bandura, 1971). Finally, motivation at the time of observation (e.g., whether the imitator is hungry or sated while observing a food retrieval task) can also affect the probability of later imitation (Dorrance and Zentall, 2001).

Greer et al. (2006) distinguished between performance of modeled behaviors already in the imitator's repertoire and imitative learning

of novel behaviors. In particular, they suggest that learning of novel behaviors and performance of previously learned behaviors can be differentially affected by reinforcement. An imitation learning study by Bandura (1965) illustrates these differential effects of reward on learning and performance. Bandura showed subjects modeled behavior that was either vicariously rewarded or punished. Following behavioral modeling, subjects were directly provided incentives for imitation. These incentives resulted in the production of learned but previously unimitated behaviors, suggesting that vicarious reinforcement influenced the imitation but not the learning of modeled behaviors (Bandura, 1965).

In summary, imitative learning consists of many components including imitation of timing, configural postures, sequences, and reinforcement sensitivity. Action observation likely activates the motor system, which facilitates imitative learning. Sophisticated imitation abilities are clearly key to human cultural learning especially early in life, but they are likely not the whole story. Comparative studies of primate cognition, modeling studies, and human ethnographic work have identified several other cognitive mechanisms that augment our imitative abilities during cultural learning and have likely been instrumental in the dramatic explosion of cultural capacities in *Homo sapiens*. In the following section we will discuss three of these hallmarks of human cultural learning: learning biases, mental state attribution, and flexible reinforcement learning.

Learning biases

Cultural learning is not indiscriminate; rather it is biased toward certain contexts and content, which likely results in the more efficient acquisition of knowledge, beliefs, and practices (Henrich and McElreath, 2003). Context biases result in the information held by certain individuals (model-based bias) or the highest frequency information (frequency-based bias) being favored (Henrich and McElreath, 2003). Henrich and Boyd (1998) argue that the cognitive mechanisms supporting these learning biases were likely shaped by natural selection.

A number of empirical laboratory studies conducted by Bandura and his colleagues (Bandura et al., 1961, 1963) suggest that high model-observer similarity favorably biases social learning. Based on these studies, Bandura proposed his Social Learning Theory (SLT) which describes the conditions governing the occurrence of social learning. SLT emphasizes the importance of model-observer similarity in biasing social learning because, Bandura suggested, model-observer similarity increases the observer's identification with the model making it easier for the observer to relate modeled actions to his or her own (Bandura, 1977). More recent studies in fields ranging from sports psychology (Vescio et al., 2005) to health behaviors (Larsen et al., 2009; Perry et al., 1979) have continued to emphasize the importance of the similarity bias in cultural learning.

Both empirical and theoretical studies have suggested that another important model-based bias exists for high prestige individuals (Henrich and Gil-White, 2001). More broadly, Coussi-Korbel and Fragaszy (1995) stress the general importance of social dynamics such as egalitarianism and social dominance hierarchies in shaping model-biased cultural transmission. Laboratory experiments using the closed group method, in which information is circulated through a fixed group of individuals, have also found similarity and prestige biases and revealed an additional model-based biases for learning from successful individuals (Mesoudi and Whiten, 2008).

Content biases result in certain types of information being learned preferentially. Laboratory experiments using the transmission chain method, in which information transfer fidelity is measured among a group of people, have substantiated theoretical accounts of content biases. These studies have shown that counterintuitive information, gender stereotypes, social situations, and situations involving hierarchical relationships transmit with high fidelity (Mesoudi and Whiten, 2008).

Mental state attribution (a.k.a. Theory of mind)

Many cultural learning theorists argue that a unique human adaptation for culture is our sophisticated mental state attribution abilities

(Boyd, 2008; Tomasello, 1999; Tomasello et al., 1993a). During mental state attribution individuals develop ideas about the mental states of others and distinguish these mental states from their own. The ability to infer and subsequently encode the mental states of behavioral models during learning allows humans to modify cultural objects with their original purpose in mind. Iterative modification of cultural objects in turn creates a "ratchet effect" which allows for the summing of cognitive resources within and between generations (Tomasello, 1999).

Basic mental state attribution abilities emerge early in life and rapidly develop as the abilities for coordinated perspective-taking (intersubjectivity) and integrated perspective-taking (reflective intersubjectivity) come online (Tomasello et al., 1993a). Around the first birthday, human infants already recognize that other individuals have intentions as evidenced by their gaze-following and attention-sharing abilities (Tomasello et al., 1993a). Gergely et al. (2002) convincingly illustrate the intention understanding of 14-month olds by showing that they will only imitate a novel behavioral strategy when that strategy appears to be the most rational means to achieve a goal. By around 4 years of age, children recognize others as mental agents with thoughts different from their own (Perner et al., 1987). The ability of children to distinguish between their own thoughts and the thoughts of others is often explored using false belief tasks in which children have to predict the behavior of another individual based on that individual's false belief (Frith and Frith, 2003). The final developmental milestone of mental state attribution abilities occurs by 5 or 6 years of age when children are able to think about others reflecting on the beliefs of third parties (Sullivan, 1994). Mental state attribution abilities continue to improve into adulthood, with increasing social experience, and continue to constitute key elements of cultural learning.

Reward

Reward is another critical component of many types of learning including imitative learning, as described above, and cultural learning in general.

Schultz (2006) defines the purpose of reward to be threefold: (1) induction of learning, (2) approach behavior for the reward itself, and (3) positive feelings associated with the reward and rewarded behavior. Rewards can be primary reinforcers (unlearned and culturally invariant), such as food and pleasant smells or secondary reinforcers (classically or instrumentally conditioned and culturally specific), such as money and attractive cars (Walter et al., 2005). Social stimuli such as smiling faces and cooperative behaviors are also powerful primary reinforcers (Walter et al., 2005).

Tomasello et al. (2005) suggest that the social situations inherent in cultural learning are powerful primary reinforcers and that the intrinsic reward value of cultural learning is a keystone of human cultural evolution. This means that the first time an individual engages in cultural learning, the experience is rewarding and thus the likelihood of learning and future learning is increased. While cultural learning in general may be rewarding, Castro and Toro (2004) suggest that the preferential learning of particular cultural information is dependent on the development of parental ability to approve or disapprove of offspring behavior. The child's sensitivity to both reward and punishment allows for preferential learning of correct, rewarded, behaviors over incorrect, punished ones. Castro and Toro (2004) suggest that this reward- and punishment-guided learning is a necessary addition to mental state attribution abilities in order for the ratchet effect to occur.

These three characteristics of human culture: learning biases, mental state attribution, and flexible reinforcement learning, when combined with humans' sophisticated imitative learning abilities, provide promising starting places for investigations into the neural architecture of human cultural transmission. The neural systems that subserve these functions are likely to play important roles in human cultural transmission.

Section II: candidate neural mechanisms of imitative cultural learning

A number of cognitive neuroscience studies have already identified neural systems underlying some

of the key components of cultural imitative learning described above. In this section we review primate and specifically human cognitive neuroscience studies that investigate neural mechanisms associated with imitation and imitative learning, and model-based learning biases. We also briefly discuss how these neural mechanisms may implement mental state attribution and how they can potentially interact with neural systems processing reward.

The human mirror system, imitation, and imitative learning

Imitation learning is at the core of cultural learning and imitation learning processes have been well characterized behaviorally. Major cognitive neuroscience discoveries over the last decade have also given us a great deal of information about the neural mechanisms of imitation behavior. Recall that the ideomotor framework of imitation suggests that there is a common neural substrate for perception and action (Prinz, 2005). The mirror neuron system (MNS), first discovered in macaque monkeys using depth electrode recordings, has these perception-action coupling properties (Gallese et al., 1996). Neurons in the monkey's premotor cortex (area F5) (Gallese et al., 1996) and inferior parietal lobe (area PF) (Fogassi et al., 2005) fire both when the monkey performs a goal-directed action and when it sees a human or conspecific perform the same or a related action (Gallese et al., 1996).

Convergent evidence from a variety of imaging modalities, including fMRI, EEG, positron emission tomography (PET), transcranial magnetic stimulation (TMS), and most recently, single unit recordings (Mukamel et al., 2007) has suggested the presence of an MNS in humans (for a review see Iacoboni and Mazziotta, 2007). Putative human mirror neuron areas are present in the frontal lobe [posterior inferior frontal gyrus (piFG) and ventral premotor cortex (the human homologue of monkey F5)], and in the parietal lobe [rostral inferior parietal lobule (riPL)] (Rizzolatti and Craighero, 2004). Human studies have demonstrated brain responses compatible with mirror neuron activity while viewing and imitating object-oriented hand and foot actions (Buccino et al., 2001, 2004b), and hearing the sounds associated with these actions (Gazzola et al., 2006; Kaplan and Iacoboni, 2007). Additionally, the human MNS is also activated by viewing and imitating intransitive actions such as gestures (Iacoboni et al., 1999; Koski et al., 2003), mouth actions (Buccino et al., 2001), and facial expressions (Carr et al., 2003; Pfeifer et al., 2008).

Because mirror neurons provide a neural mechanism for pairing action observation and action execution, it has been hypothesized that the MNS is a key component of the neural substrate underlying imitation and imitative learning (Iacoboni, 2005; Iacoboni et al., 1999; Rizzolatti and Craighero, 2004). Iacoboni (2005) suggests, based on human neuroimaging and TMS data, that the core neural circuitry involved in human imitation consists of frontal and parietal MNS components as well as the superior temporal sulcus (STS). In this model, the STS gives rise to a higher-order visual description of the observed action, which is then fed into the MNS where the action's goal (piFG) and the motor plan to achieve the action (riPL) are coded. Finally, the predicted motor plan is fed back into the STS, where a comparison is made between the visual description of the action and the predicted sensory consequences of the imitative motor plan. It is at this point in the action-observation neural circuitry — when the observed and simulated motor plans are compared — that imitation accuracy and model-based cultural learning biases might be especially important. Presumably, the motor plans of self and other will be more similar in those cases where imitation accuracy and model-observer physical similarity is higher, though future studies will be needed to empirically test this hypothesis.

Iacoboni (2005) also proposes a model of the circuitry involved in imitative learning in which the aforementioned core circuitry communicates with the dorsolateral prefrontal cortex and motor preparation areas including the mesial frontal, dorsal premotor, and superior parietal regions. Though few neuroimaging studies of imitative learning have been conducted, the extant studies support the involvement of the MNS in imitation learning in general and support the imitative

learning model proposed by Iacoboni (2005) in particular. In an fMRI study of observational learning of guitar chords by non-guitarists, Buccino et al. (2004b) found that the MNS and the above motor preparation areas were active. In a subsequent fMRI study, Frey and Gerry (2006) found more MNS activity when subjects observed complex hand action sequences with the intention to learn them and reproduce them later than when the same actions were viewed passively. Thus, the MNS is likely a key player in imitative learning of novel actions, a critical component of cultural learning.

The MNS and experience — could culture shape the MNS?

In addition to connecting executed and observed action, several studies discussed below indicate that activity of the MNS and interconnected regions is influenced by motor practice both in the short term (hours) and in the long term (years). Thus, the MNS may not only play a role in the acquisition of culturally mediated behaviors, but the MNS itself may be shaped by the presence of culturally mediated behaviors in one's motor repertoire.

Behavioral studies have demonstrated that action execution can be affected by previous experience observing related actions. For instance, Gillmeister et al. (2008) found that action imitation was facilitated by previous observation of task-irrelevant actions with the same effector; this priming effect was decreased by incongruent practice (observe foot and imitate with hand). Research using TMS has demonstrated that the behavioral effects of observational practice described above are directly mediated by the motor system. Stefan et al. (2008) had subjects practice thumb movements in the opposite direction of their baseline TMS-evoked thumb movements. The authors found that simultaneous movement execution and observation altered the direction of TMS-evoked thumb movements more than physical practice alone. Most intriguingly, Catmur et al. (2007) used an incongruent training strategy similar to Gillmeister et al. (2008) to create a "counter mirror" effect. After incongruent

practice, observing the movements of one finger increased motor evoked potentials (MEPs) resulting from TMS in the finger paired during practice, rather than the same finger.

fMRI studies demonstrate that the behavioral and TMS-evoked practice effects described above are likely related to changes in MNS activity. Vogt et al. (2007) found increased activity in a number of brain regions (including putative mirror neuron areas) during observation of practiced versus nonpracticed guitar chords. On a longer timescale, Cross et al. (2006) demonstrate practice-related increases in MNS activity over the course of five fMRI scans at weekly intervals while subjects learned a novel dance sequence. Finally, Calvo-Merino et al. (2005) demonstrate that practice-related changes in MNS activity extend to real-world expertise built over many years. The authors find greater MNS activity when experienced dancers observe their own style of dance rather than a comparable but unfamiliar style. Collectively, these data suggest that daily experiences and those that extend over a lifetime, such as the practices of one's culture, have the potential to influence MNS function.

The MNS and model-based biases

In addition to playing a key role in human imitation, the MNS may represent the neural substrate of the similarity cultural learning bias, at least for the visuomotor aspects of similarity. Several studies have demonstrated that the MNS responds more intensely to the observation of conspecifics. For example, Buccino et al. (2004a) found that activity in the putative human MNS is modulated by model-observer similarity for the observation of biting actions of humans (greatest activity), monkeys (intermediate activity), and dogs (least activity). These species-dependent differences in MNS responses were even more pronounced for communicative actions (no measurable response for the dog barking action). This finding suggests that differences in physical appearance alone cannot explain these differential responses.

The MNS is also preferentially responsive to human biological motion. For example, Press et al.

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(2006) compared subjects simultaneously observing and imitating human hands, human hands disguised to look like robotic hands, and actual robotic hands. The authors found that human hand observation, regardless of the hand's appearance, had a greater facilitatory effect on action performance than did robotic hand observation, even when the robotic and human hand were matched on size, color, and brightness (Press et al., 2006). Thus, human-like motion preferentially activates the MNS even when the effector is robotic. Gazzola et al. (2007) found MNS activity while subjects observed a robotic hand performing in a human-like fashion (by performing a variety of actions); however, neither Gazzola et al. (2007) nor Tai et al. (2004) found MNS activity when subjects viewed a robotic hand that was performing the same action repeatedly, which is less typical of human behavior. Intriguingly, Press et al. (2007) found that practice simultaneously observing and imitating a robotic hand abolished the human-biased action facilitation found pre-training, suggesting that human-biased activity in the MNS is, at least in part, the result of experience. Biological-motion related activity in the MNS extends to motion of the entire body. Ulloa and Pineda (2007) and Saygin et al. (2004) both found that the MNS responds to human actions represented by point-light walkers (moving groups of white dots representing the joints of a human) but not to the same stimuli when other dots were added to obscure motion the human form.

Current data suggest that the human MNS is also sensitive to more subtle aspects of model-observer physical similarity, such as ethnicity and gender, which may be more relevant cultural learning. For example, Molnar-Szakacs et al. (2007) found greater corticospinal excitability (a proxy for MNS activity, measured with TMS) in European American observers while they observed an ethnic in-group member versus an ethnic out-group member performing hand gestures, suggesting a positive relationship between MNS activity and model-observer similarity. In contrast, two other studies found more activity in the MNS when individuals viewed ethnic (Désy and Théoret, 2007) or gender (Cheng et al., 2006) out-group members, suggesting a negative relationship between MNS activity and model-observer similarity. Taken together, these data suggest that the MNS is sensitive to the visual similarity between model and observer at the level of species-typical appearance and biological motion, and in more culturally relevant domains such as gender and ethnicity. However, because of the variety of conclusions reached by these studies, and the potential role of experience in shaping MNS activity, the relationship between the degree of model-observer similarity and MNS activity remains unclear.

Neural mechanisms for mental state attribution

The cultural learning theories previously discussed (Tomasello et al., 1993a, 1999; Henrich and McElreath, 2003) propose that the ability to think about the intentions and mental states of others is critical for understanding the goal of observed actions. Intention understanding is thus vital for efficient and flexible imitative learning. After the discovery of mirror neurons, Gallese and Goldman (1998) proposed that the properties of these cells supported a simulation model of mental state attribution (simulation theory). Simulation theory assumes that we understand the intentions of others via a process of simulation, as if we were the other person. During simulation, the observation of another individual activates a similar suite of neural areas to when the observer performed the behavior himself "creat[ing] in the observer a state that resembles the target" (Gallese and Goldman, 1998). Indeed, subsequent studies in both monkeys (Fogassi et al., 2005) and humans (Iacoboni et al., 2005) suggested that mirror neurons are able to code the intention of an action, not simply the action itself. In Iacoboni et al. (2005) subjects were shown a hand picking up a cup, in one of two different contexts, a table set for tea, or the same table at the end of the meal. Despite the hand action being identical in both conditions, putative MNS regions demonstrated different levels of activity when the actions were viewed in the two different contexts. Thus, mirror neurons may implement not only imitation but also the function of mental state attribution in cultural learning.

Another model of mental state attribution assumes that we understand others' mental states by using an inferential process (Gopnik and Schulz, 2004). We observe the behavior of other people and then relate it to a set of folk psychology laws. By doing so, we can make theories about the mental states of other people as scientists make theories about the natural phenomena they study. From a functional standpoint, this inferential route to intention understanding does not map well onto the properties of mirror neurons. Indeed, a set of tasks typically used to study mental state attribution (the false belief task, the comparison of social interaction story listening to physical interaction story listening, and the comparison of viewing moving geometric shapes that depict social interactions to viewing randomly moving geometric shapes), consistently activate a set of neural regions that are not typically considered part of MNS: the dorsomedial prefrontal cortex (dmPFC), the posterior STS (pSTS), and the temporal pole (see Gallagher and Frith, 2003; Frith and Frith, 2003 for reviews). Activity in the pSTS area, however, is largely indistinguishable from the STS activations observed in imitation tasks (Iacoboni, 2005).

A number of individuals have proposed that the MNS and the above suite of brain areas (dmPFC, pSTS, and temporal poles) represent complementary neural systems underlying mental state attribution (Keysers and Gazzola, 2006, 2007; Pineda and Hecht, 2008; Uddin et al., 2007). For example, Keysers and Gazzola (2007) suggest the MNS provides a "pre-reflective" description of intention based on the visual description of a model's actions while cortical midline structures such as the dmFPC provide a "reflective" description of intentions based social introspection. Keysers and Gazzola (2007) suggest the inferential route to intention understanding may be especially important under circumstances when model-observer similarity is low or modeled behaviors were not previously present in the observer's repertoire, as is commonly the case during cultural learning. However, the interpretation of the activity in dmPFC in mentalizing tasks is rather difficult, due to the peculiar activation profile of this brain region (i.e., cognitive tasks result in signal decreases, rather than the typical signal increases, as compared to baseline activity; Iacoboni et al., 2004). Thus, it is at present unclear whether there is a distinct network for mental state attribution that relies on inferential mechanisms and that is anatomically located outside the MNS.

The reward system, sharing intentions, and imitation accuracy

The neural mechanisms of reward learning have been well mapped in animals ranging in complexity from *Aplysia* slugs (Hawkins et al., 1983) to rats (for a review see Schultz, 2006). Neural systems related to reward have been investigated in humans through the use of neuroimaging (for a review see O'Doherty, 2004). As is the case for the MNS, the current belief is that there is a putative reward system in the human brain encompassing brain systems homologues to the neural systems processing reward in animals. Three neural structures that are believed important in human reward processing are the ventral striatum, the nucleus accumbens, and the orbitofrontal cortex (OfC) (Hollerman et al., 2000; McClure et al., 2004; O'Doherty, 2004; Walter et al., 2005).

Reinforcement learning theory suggests reward is used to bias action selection and accordingly reward circuitry is often active during motor task performance (McClure et al., 2004). Significantly for the study of cultural learning, components of the reward network are also active during imitation. Activity in the lateral OfC was one of the main effects observed in the Chaminade et al. (2002) study of deferred imitation of Lego® assembly and a study by Williams et al. (2007) involving finger movement imitation. The lateral OfC activity in both of these studies was interpreted to reflect the uncertainty involved in producing the appropriate action as well as error monitoring between executed and observed actions, both functions suggested by Elliott, Dolan, and Frith (2000) to be reward-related. Lee et al. (2006) also found OfC activity during facial mimicry, perhaps related to the intrinsic reward value of viewing human faces (Walter et al., 2005).

In addition to the previous studies of generalized imitation, OfC activity has also been reported in studies comparing imitation or observation of actions with differing levels of familiarity to the subject. Jackson et al. (2006) report more OfC activity when subjects imitate models from a first person perspective than from a third person perspective. The authors attribute this activity to the increased similarity between imitation and observation in the first person perspective. Similarly, Calvo-Merino et al. (2005) find more OfC activity when dancers watch their own compared to an unfamiliar style. Elliott et al. (2000) suggest that the selection of stimuli on the basis of familiarity is related to the reward-related value of these stimuli. A more parsimonious explanation of these findings may simply invoke the role of OfC in inhibitory control (Elliott et al., 2000; Roberts and Wallis, 2000). For instance, dancers may have a stronger tendency to imitate, and therefore stronger need for motor inhibition, while watching the style of dance they typically practice. Future studies will have to disentangle the alternative hypotheses of reward processing and inhibitory control regarding the involvement of OfC in imitation.

Reward is also a central component of robotic models of human imitation, further highlighting the importance of reward in imitative learning. Mataric (1994) incorporate both vicarious reward and direct reward for conformity into their imitative learning algorithms used to drive social learning robots. Similarly, Atkeson and Schaal (1997) develop a robotic control strategy for single trial learning in which a reward function is learned from a demonstration and the behavior itself is acquired through trial and error learning.

Taken together, the neuroimaging studies discussed in this section highlight neural systems that play important roles in the cognitive mechanisms suggested by both theoretical and empirical work to be hallmarks of human cultural learning.

Section III: a model of the neural architecture of cultural imitative learning and future directions

We propose a tentative neural architecture of cultural imitative learning that has the MNS and associated imitative learning areas as its core. In our model, the reward network may support the motivation to imitate and reinforcement sensitivity important for cultural learning. MNS regions likely support mental state attribution through motor simulation (Koski et al., 2003). Under certain circumstances, medial prefrontal areas, typically considered "mentalizing" areas in the imaging literature (Frith and Frith, 2003; Gallagher and Frith, 2003), may also contribute to mental state attribution through an inferential route. Though tentative, the proposed cultural imitative learning circuitry generates testable hypotheses that future studies of cultural imitative learning can explore.

Future neuroscientific studies of imitative learning embedded in ecologically valid cultural contexts are needed to truly elucidate how the previously described neural systems (including those sub serving mental state attribution and reward processes) may function during real-world cultural imitative learning. In the remaining sections, we will discuss some future studies that will be required to further characterize the neural architecture of cultural imitative learning.

Future directions: the human mirror system and imitation

Though many neuroimaging studies of action execution, observation, and imitation have been conducted, relatively few studies of imitative learning of novel actions or action combinations exist to date (Buccino et al., 2004b; Frey and Gerry, 2006). Additionally, stimuli in existing imitation studies typically consist of photographs or videos of an isolated effector of a single individual performing simple movements against a blank backdrop. Though this type of reduction makes interpretation more straightforward, future studies investigating the role of imitation in cultural learning will need to employ more ecologically valid stimuli. By including the face, in addition to the acting effector, in action stimuli, important social information portrayed by the face can be utilized in action understanding. Facial information may change the way in which the action itself is processed and/or interpreted.

Action stimuli with increased complexity, such as action sequences rather than single actions, and increased social relevance, such as communicative actions directed toward others will more closely approximate the natural conditions in which cultural learning occurs. Finally, embedding imitation paradigms in a social context, such as imitative learning of the communicative gestures will also be useful in engaging neurocognitive mechanisms involved in cultural imitative learning.

Future directions: the MNS and model-based biases

The sensitivity of the MNS to aspects of model-observer similarity, such as ethnicity and gender, suggested by several studies (Cheng et al., 2006; Désy and Théoret, 2007; Molnar-Szakacs et al., 2007), may underlie the well-documented cultural learning biases for self-similar individuals (Bandura, 1977; Henrich and McElreath, 2003; Mesoudi and Whiten, 2008). These studies have examined model-observer similarity only in the context of action observation. No studies to date have addressed model-observer similarity during imitation or imitative learning. Furthermore, whether there is a positive or negative correlation between model-observer similarity and MNS activity in terms of ethnicity and gender remains unclear from present studies.

Other socially salient physical characteristics such as age, socioeconomic status (as reflected in physical appearance), as well as action quality and model-observer familiarity should also be considered in the context of neurobehavioral investigations of cultural learning. A final point concerns the relationship between the physical and nonphysical elements of social characteristics such as gender, ethnicity, and age. In order to determine which aspects of similarity — physical/ bottom-up or social/top-down — influence brain activity during imitation, it will be necessary to design studies in which the physical appearance of observed models and social information can be disassociated.

Future directions: the MNS, mental state attributions, and the reward system

It is clear that mental state attribution abilities are of central importance for cultural imitative learning. However, the question of whether mental state attribution is achieved via simulation mechanisms supported by the MNS, "mentalizing" mechanisms supported by neural regions including the dmPFC, or some integration of these two remains unanswered. The use of tasks that differentiate between simulative and inferential mechanisms during imitation will be useful in identifying the neural substrates of mental state attribution during cultural imitative learning.

The human reward system is critical for learning and is some times active during action observation and imitation. Cultural learning theory suggests that reward is important for the motivation to learn imitatively, for sharing intentions, as well as for learning behaviors accurately. A next step in elucidating the role of reward circuitry in human imitative learning will be to investigate the neural basis of imitation and imitative learning of directly and vicariously rewarded actions. Comparison of tasks when motivation to imitate differs, such as virtual food retrieval tasks in hungry and sated subjects as in Dorrance and Zentall (2001), will be useful for determining the role of motivation in the neural basis of cultural imitative learning.

Conclusion

Cultural learning theory suggests that imitation, mental state attribution, and reinforcement learning are key cognitive mechanisms underlying human cultural learning. Cognitive neuroscience studies provide insight into the neural systems associated with these functions. Thus, anthropology and cognitive neuroscience provide the neuroscientific study of cultural learning a head start. However, many studies of imitation learning in cultural contexts that will engage mental state attribution and reinforcement learning will be

needed to fully explore and explain the neural architecture of cultural imitative learning.

Acknowledgments

References

Arbib, M. A. (2005). From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *The Behavioral and Brain Sciences*, *28*(2), 105–167.

Atkeson, C. G., & Schaal, S. (1997). Learning tasks from a single demonstration. *Proceedings of the 1997 IEEE International Conference on Robotics and Automation*, 1706–1712.

Bandura, A. (1965). Influence of models' reinforcement contingencies on the acquisition of imitative responses. *Journal of Personality and Social Psychology*, *1*(6), 589–595.

Bandura, A. (1971). Vicarious and self-reinforcement processes. In R. Glaser (Ed.), *The nature of reinforcement* (pp. 228–278). New York: Academic Press.

Bandura, A. (1977). *Social learning theory*. NJ: Prentice-Hall.

Bandura, A., Ross, D., & Ross, S. A. (1961). Transmission of aggression through imitation of aggressive models. *Journal of Abnormal and Social Psychology*, *63*(3), 575–582.

Bandura, A., Ross, D., & Ross, S. A. (1963). Imitation of film-mediated aggressive models. *Journal of Abnormal and Social Psychology*, *66*(1), 3–11.

Bates, D. G., & Plog, F. (1990). *Cultural anthropology*. New York, NY: McGraw-Hill.

Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology*, *12*(2), 82–91.

Bonnie, K. E., Horner, V., Whiten, A., & de Waal, F. B. M. (2007). Spread of arbitrary conventions among chimpanzees: A controlled experiment. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 367–372.

Boyd, J. H. (2008). Have we found the Holy Grail? Theory of mind as a unifying construct. *Journal of Religion and Health*, *47*(3), 366–385.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. University of Chicago Press.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*(2), 400–404.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al. (2004a). Neural circuits involved in the recognition of actions performed by nonconspecifics:

An fMRI study. *Journal of Cognitive Neuroscience*, *16*(1), 114–126.

Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., et al. (2004b). Neural circuits underlying imitation learning of hand actions an event-related fMRI study. *Neuron*, *42*(2), 323–334.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, *15*(8), 1243–1249.

Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences*, *100*(9), 5497–5502.

Castro, L., & Toro, M. A. (2004). The evolution of culture: From primate social learning to human culture. *Proceedings of the National Academy of Sciences*, *101*(27), 10235–10240.

Catmur, C., Walsh, V., & Heyes, C. (2007). Sensorimotor learning configures the human mirror system. *Current Biology*, *17*(17), 1527–1531.

Chalmeau, R., & Gallo, A. (1993). Social transmission among nonhuman-primates. *Annals of Psychology*, *93*(3), 427–439.

Chaminade, T., Meltzoff, A. N., & Decety, J. (2002). Does the end justify the means? A PET exploration of the mechanisms involved in human imitation. *NeuroImage*, *15*, 318–328.

Cheng, Y. W., Tzeng, O. J., Decety, J., Imada, T., & Hsieh, J. C. (2006). Gender differences in the human mirror system: A magnetoencephalography study. *Neuroreport*, *17*(11), 1115–1119.

Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*, 1441–1453.

Cross, E. S., Hamilton, A. F. C., & Grafton, S. T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *NeuroImage*, *31*(3), 1257–1267.

Désy, M. C., & Théoret, H. (2007). Modulation of motor cortex excitability by physical similarity with an observed hand action. *PLos ONE*, *2*(10).

Dorrance, B. R., & Zentall, T. R. (2001). Imitative learning in Japanese quail (*Coturnix japonica*) depends on the motivational state of the observer quail at the time of observation. *Journal of Comparative Psychology (Washington, DC: 1983)*, *115*(1), 62–67.

Elliott, R., Dolan, R. J., & Frith, C. D. (2000). Dissociable functions in the medial and lateral orbitofrontal cortex: Evidence from human neuroimaging studies. *Cerebral Cortex*, *10*(3), 308–317.

Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*(5722), 662–667.

Frey, S. H., & Gerry, V. E. (2006). Modulation of neural activity during observational learning of actions and their sequential orders. *Journal of Neuroscience*, *26*(51), 13194–13201.

Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the*

Royal Society of London. Series B, Biological Sciences, *358*(1431), 459–473.

Gallagher, H. L., & Frith, C. D. (2003). Functional imaging of 'theory of mind'. *Trends in Cognitive Sciences*, *7*(2), 77–83.

Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, *2*(12), 493–501.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain: A Journal of Neurology*, *119*(2), 593.

Gazzola, V., Aziz-Zadeh, L., & Keysers, C. (2006). Empathy and the somatotopic auditory mirror system in humans. *Current Biology*, *16*(18), 1824–1829.

Gazzola, V., Rizzolatti, G., Wicker, B., & Keysers, C. (2007). The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. *NeuroImage*, *35*(4), 1674–1684.

Gergely, G., Bekkering, H., & Király, I. (2002). Developmental psychology: Rational imitation in preverbal infants. *Nature*, *415*, 755–755.

Gillmeister, H., Catmur, C., Liepelt, R., Brass, M., & Heyes, C. (2008). Experience-based priming of body parts: A study of action imitation. *Brain Research*, *1217*, 157–170.

Gopnik, A., & Schulz, L. (2004). Mechanisms of theory formation in young children. *Trends in Cognitive Sciences*, *8*(8), 371–377.

Greer, R. D., Dudek-Singer, J., & Gautreaux, G. (2006). Observational learning. *International Journal of Psychology*, *41*(6), 486–499.

Hawkins, R. D., Abrams, T. W., Carew, T. J., & Kandel, E. R. (1983). A cellular mechanism of classical conditioning in aplysia: Activity-dependent amplification of presynaptic facilitation. *Science*, *219*(4583), 400–405.

Henrich, J., & Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior*, *19*(4), 215–241.

Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige-freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, *22*(3), 165–196.

Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology*, *12*(3), 123–135.

Heyes, C. (2005). Imitation by association. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From neuroscience to social science* (pp. 157–176). Cambridge, MA: MIT Press.

Higgs, P. G. (2000). The mimetic transition: A simulation study of the evolution of learning by imitation. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1450), 1355–1361.

Hollerman, J. R., Tremblay, L., & Schultz, W. (2000). Involvement of basal ganglia and orbitofrontal cortex in goal-directed behavior. *Progress in Brain Research*, *126*, 193–215.

Hurley, S., & Chater, N. (2005). *Perspectives on imitation: From cognitive neuroscience to social science.* Cambridge: Cambridge University Press.

Iacoboni, M. (2005). Neural mechanisms of imitation. *Current Opinion in Neurobiology*, *15*(6), 632–637.

Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology*, *60*, 653–670.

Iacoboni, M., Lieberman, M. D., Knowlton, B. J., Molnar-Szakacs, I., Moritz, M., Throop, C. J., et al. (2004). Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *NeuroImage*, *21*(3), 1167–1173.

Iacoboni, M., & Mazziotta, J. C. (2007). Mirror neuron system: Basic findings and clinical applications. *Annals of Neurology*, *62*(3), 213–218.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLos Biology*, *3*(3), e79.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*(5449), 2526–2528.

Jackson, P. L., Meltzoff, A. N., & Decety, J. (2006). Neural circuits involved in imitation and perspective-taking. *NeuroImage*, *31*(1), 429–439.

Kannetzky, F. (2007). What makes cultural heredity unique? On action-types, intentionality and cooperation in imitation. *Mind & Language*, *22*(5), 592–623.

Kaplan, J. T., & Iacoboni, M. (2007). Multimodal action representation in human left ventral premotor cortex. *Cognitive Processing*, *8*(2), 103–113.

Keysers, C., & Gazzola, V. (2006). Towards a unifying neural theory of social cognition. *Understanding Emotions*, 379.

Keysers, C., & Gazzola, V. (2007). Integrating simulation and theory of mind: From self to social cognition. *Trends in Cognitive Sciences*, *11*(5), 194–196.

Koski, L., Iacoboni, M., Dubeau, M. C., Woods, R. P., & Mazziotta, J. C. (2003). Modulation of cortical activity during different imitative behaviors. *Journal of Neurophysiology*, *89*(1), 460–471.

Kumashiro, M., Ishibashi, H., Uchiyama, Y., Itakura, S., Murata, A., & Iriki, A. (2003). Natural imitation induced by joint attention in Japanese monkeys. *International Journal of Psychophysiology*, *50*(1–2), 81–99.

Larsen, H., Engels, R. C., Granic, I., & Overbeek, G. (2009). An experimental study on imitation of alcohol consumption in same-sex dyads. *Alcohol and Alcoholism*, *44*(3), 250–255.

Lee, T. W., Josephs, O., Dolan, R. J., & Critchley, H. D. (2006). Imitating expressions: Emotion-specific neural substrates in facial mimicry. *Social Cognitive and Affective Neuroscience*, *1*(2), 122–135.

Masur, E. F. (2006). Vocal and action imitation by infants and toddlers during dyadic interactions. In S. J. Rogers & J. H. G. Williams (Eds.), *Imitation and the social mind: Autism and typical development*. New York: The Guilford Press.

Mataric, M. J. (1994). Learning motor skills by imitation. In *Proceedings of the AAAI Spring Symposium Toward Physical Interaction and Manipulation*, Stanford University.

McClure, S. M., York, M. K., & Montague, P. R. (2004). The neural substrates of reward processing in humans: The modern role of fMRI. *The Neuroscientist*, *10*(3), 260–268.

McElreath, R. (2004). Social learning and the maintenance of cultural variation: An evolutionary model and data from east Africa. *American Anthropologist*, *106*(2), 308–321.

McGrew, W. C. (1992). *Chimpanzee material culture: Implications for human evolution*. Cambridge: Cambridge University Press.

Meltzoff, A. N. (1995). Understanding the intentions of others: Re-enactment of intended acts by 18-month-old children. *Developmental Psychology*, *31*, 5.

Meltzoff, A. N., & Decety, J. (2003). What imitation tells us about social cognition: A rapprochement between developmental psychology and cognitive neuroscience. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *358*(1431), 491–500.

Meltzoff, A. N., & Moore, M. K. (1977). Imitation of facial and manual gestures by human neonates. *Science*, *198*(4312), 75–78.

Meltzoff, A. N., & Moore, M. K. (1983). Newborn infants imitate adult facial gestures. *Child Development*, *54*(3), 702–709.

Meltzoff, A. N., & Moore, M. K. (1989). Imitation in newborn infants: Exploring the range of gestures imitated and the underlying mechanisms. *Developmental Psychology*, *25*(6), 954–962.

Meltzoff, A. N., & Prinz, W. (2002). *The imitative mind: Development, evolution and brain bases*. Cambridge: Cambridge University Press.

Mesoudi, A., & Whiten, A. (2008). The multiple roles of cultural transmission experiments in understanding human cultural evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1509), 3489–3501.

Miklósi, A. (1999). The ethological analysis of imitation. *Biological Reviews of the Cambridge Philosophical Society*, *74*(3), 347–374.

Molnar-Szakacs, I., Wu, A. D., Robles, F. J., & Iacoboni, M. (2007). Do you see what I mean? Corticospinal excitability during observation of culture-specific gestures. *PLos ONE*, *2*(7), e626.

Moore, B. R. (2004). The evolution of learning. *Biological Reviews of the Cambridge Philosophical Society*, *79*(2), 301–335.

Mukamel, R., Ekstrom, E., Kaplan, J.T., Iacoboni, M., & Fried, I. (2007). Mirror properties of single cells in human medial frontal cortex. *Program No. 127.4 2007 Abstract Viewer/ Itinerary Planner. San Diego, CA: Society for Neuroscience. Online.*

O'Doherty, J. P. (2004). Reward representations and reward-related learning in the human brain: Insights from neuroimaging. *Current Opinion in Neurobiology*, *14*(6), 769–776.

Perner, J., Leekam, S. R., & Wimmer, H. (1987). Three-year-olds' difficulty with false belief: The case for a conceptual deficit. *British Journal of Developmental Psychology*, *5*(2), 125–137.

Perry, R. P., LeBow, M. D., & Buser, M. M. (1979). An exploration of obese observational learning in modifying selected eating responses of obese children. *International Journal of Obesity*, *3*(3), 193–199.

Pfeifer, J. H., Iacoboni, M., Mazziotta, J. C., & Dapretto, M. (2008). Mirroring others' emotions relates to empathy and interpersonal competence in children. *NeuroImage*, *39*(4), 2076–2085.

Piaget, J. (1962). *Play, dreams and imitation in childhood*. New York: Norton.

Pineda, J. A., & Hecht, E. (2008). Mirroring and mu rhythm involvement in social cognition: Are there dissociable subcomponents of theory of mind? *Biological Psychology*, *80*(3), 306–314.

Press, C., Gillmeister, H., & Heyes, C. (2006). Bottom-up, not top-down, modulation of imitation by human and robotic models. *The European Journal of Neuroscience*, *24*(8), 2415–2419.

Press, C., Gillmeister, H., & Heyes, C. (2007). Sensorimotor experience enhances automatic imitation of robotic action. *Proceedings. Biological Sciences/the Royal Society*, *274* (1625), 2509–2514.

Prinz, W. (2005). An ideomotor approach to imitation. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From neuroscience to social science* (pp. 141–156). Cambridge, MA: MIT Press.

Rakoczy, H., Tomasello, M., & Striano, T. (2005). On tools and toys: How children learn to act on and pretend with 'virgin objects'. *Developmental Science*, *8*(1), 57–73.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192.

Roberts, A. C., & Wallis, J. D. (2000). Inhibitory control and affective processing in the prefrontal cortex: Neuropsychological studies in the common marmoset. *Cerebral Cortex*, *10*(3), 252–262.

Saygin, A. P., Wilson, S. M., Hagler, D. J., Bates, E., & Sereno, M. I. (2004). Point-light biological motion perception activates human premotor cortex. *Journal of Neuroscience*, *24*(27), 6181–6188.

Schultz, W. (2006). Behavioral theories and the neurophysiology of reward. *Annual Review of Psychology*, *57*, 87–115.

Schwier, C., van Maanen, C., Carpenter, M., & Tomasello, M. (2006). Rational imitation in 12-month-old infants. *Infancy*, *10*(3), 303–311.

Sommerville, J. A., & Decety, J. (2006). Weaving the fabric of social interaction: Articulating developmental psychology and cognitive neuroscience in the domain of motor cognition. *Psychonomic Bulletin & Review*, *13*(2), 179–200.

Stefan, K., Classen, J., Celnik, P., & Cohen, L. G. (2008). Concurrent action observation modulates practice-induced motor memory formation. *The European Journal of Neuroscience*, *27*(3), 730–738.

Sullivan, K. (1994). Preschoolers can attribute second-order beliefs. *Developmental Psychology*, *30*(3), 395–402.

Tai, Y. F., Scherfler, C., Brooks, D. J., Sawamoto, N., & Castiello, U. (2004). The human premotor cortex is 'mirror' only for biological actions. *Current Biology*, *14*(2), 117–120.

Tomasello, M. (1999). The human adaptation for culture. *Annual Review of Anthropology*, *28*, 509–529.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *The Behavioral and Brain Sciences*, *28*(5), 675–691.

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993a). Cultural learning. *The Behavioral and Brain Sciences*, *16*(3), 495–511.

Tomasello, M., Savagerumbaugh, S., & Kruger, A. C. (1993b). Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Development*, *64*(6), 1688–1705.

Uddin, L. Q., Iacoboni, M., Lange, C., & Keenan, J. P. (2007). The self and social cognition: The role of cortical midline structures and mirror neurons. *Trends in Cognitive Sciences*, *11*(4), 153–157.

Ulloa, E. R., & Pineda, J. A. (2007). Recognition of point-light biological motion: Mu rhythms and mirror neuron activity. *Behavioural Brain Research*, *183*(2), 188–194.

Vescio, J., Wilde, K., & Crosswhite, J. J. (2005). Profiling sport role models to enhance initiatives for adolescent girls in physical education and sport. *European Physical Education Review*, *11*(2), 153.

Vogt, S., Buccino, G., Wohlschläger, A. M., Canessa, N., Shah, N. J., Zilles, K., et al. (2007). Prefrontal involvement in imitation learning of hand actions: Effects of practice and expertise. *NeuroImage*, *37*(4), 1371–1383.

Vogt, S., & Thomaschke, R. (2007). From visuo-motor interactions to imitation learning: Behavioural and brain imaging studies. *Journal of Sports Sciences*, *25*(5), 497–517.

Walter, H., Abler, B., Ciaramidaro, A., & Erk, S. (2005). Motivating forces of human actions. Neuroimaging reward and social interaction. *Brain Research Bulletin*, *67*(5), 368–381.

Whiten, A. (2000). Primate culture and social learning. *Cognitive Science*, *24*(3), 477–508.

Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J., et al. (2007). Transmission of multiple traditions within and between chimpanzee groups. *Current Biology*, *17*(12), 1038–1043.

Williams, J. H., Whiten, A., Waiter, G. D., Pechey, S., & Perrett, D. I. (2007). Cortical and subcortical mechanisms at the core of imitation. *Social Neuroscience*, *2*(1), 66–78.

Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., & Heltne, P. G. (1994). *Chimpanzee cultures*. Cambridge, MA: Harvard University Press.

Zentall, T. R. (2006). Imitation: Definitions, evidence, and mechanisms. *Animal Cognition*, *9*(4), 335–353.

CHAPTER 3

Own-gender imitation activates the brain's reward circuitry

Own-gender imitation activates the brain's reward circuitry

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Imitation is an important component of human social learning throughout life. Theoretical models and empirical data from anthropology and psychology suggest that people tend to imitate self-similar individuals, and that such imitation biases increase the adaptive value (e.g., self-relevance) of learned information. It is unclear, however, what neural mechanisms underlie people's tendency to imitate those similar to themselves. We focused on the own-gender imitation bias, a pervasive bias thought to be important for gender identity development. While undergoing fMRI, participants imitated own- and other-gender actors performing novel, meaningless hand signs; as control conditions, they also simply observed such actions and viewed still portraits of the same actors. Only the ventral and dorsal striatum, orbitofrontal cortex and amygdala were more active when imitating own-compared to other-gender individuals. A Bayesian analysis of the BrainMap neuroimaging database demonstrated that the striatal region preferentially activated by own-gender imitation is selectively activated by classical reward tasks in the literature. Taken together, these findings reveal a neurobiological mechanism associated with the own-gender imitation bias and demonstrate a novel role of reward-processing neural structures in social behavior.

Keywords: imitation; neuroimaging; reward; gender; cultural learning

INTRODUCTION

Imitation is widespread in humans, emerges early in development and is the means by which many critical skills are learned throughout life (Tomasello *et al.,* 1993). Theoretical models and behavioral data from psychology and anthropology indicate that people tend to imitate certain individuals, including those who are self-similar (Bandura, 1977; Henrich and McElreath, 2003). These 'similarity biases' are thought to increase the adaptive value of learned information by increasing its self-relevance.

One of the best-documented similarity biases is the own-gender bias, which is thought to play a critical role in the acquisition of gender roles and continues to guide learning in adulthood (Bussey and Bandura, 1984). In a series of foundational studies, Bandura and colleagues found that a diverse set of behaviors, ranging from aggression to color preference, were more readily transmitted via imitation of own-gender than other-gender models (Bandura *et al.,* 1961; Bussey and Bandura, 1984). These studies also demonstrated that a preference for own-gender imitation is present in children before gender identity is fully formed, suggesting that own-gender imitation is not only an effect, but also a

cause of gender identity development (Bussey and Bandura, 1984).

Following Bandura's findings, preference for own-gender models has been documented for models such as parents (Basow and Howe, 1980), teachers (Gilbert *et al.,* 1983), peers (Slaby and Frey, 1975; Perloff, 1982) and even strangers, like musicians (Killian, 1990) and celebrities (Mesoudi, 2009). Own-gender imitation biases are thus pervasive, yet neuroimaging studies of human imitation have provided little insight into the neural underpinnings of such model-based imitative learning biases, as they have typically utilized stimuli depicting an isolated, gender-neutral effector (e.g. a hand or foot) performing simple actions (e.g. Iacoboni *et al.,* 1999; Buccino *et al.,* 2004; Frey and Gerry, 2006).

Here, we used fMRI to investigate the neural circuitry underlying the own-gender imitation bias. We addressed two main questions. First, which neural systems encode gender during imitation? Second, are these neural mechanisms imitation-specific and thus more likely related to the own-gender imitative bias? We have previously proposed that neural systems related to imitation, mental state attribution and reinforcement learning might underlie human cultural imitative learning (Losin *et al.,* 2009). Given that imitative biases such as the own-gender bias are a key component of cultural learning, we predicted that one or more of these neural systems would differentially encode own- and other-gender individuals during imitation and do so to a greater degree or exclusively during imitation.

METHODS

Participants

Participants were 20 (10 males), right-handed, European American individuals, 18 to 26 years old (mean = 22.92, s.d. = 2.09). Seventeen participants reported being heterosexual, and three participants reported being homosexual (two males, one female). Participants were recruited through the volunteers section on Craigslist (8/20 were students). Participants had no history of medication or drug use other than oral contraceptives, no heavy use of alcohol and no prior or concurrent diagnosis of any neurological, psychiatric, or developmental disorders according to self-report. The study was approved by the UCLA Institutional Review Board. Written informed consent was obtained from all participants.

fMRI task

Stimuli were color, waist-up videos of 12 actors (six males), of three different ethnicities (European American, African American and Chinese American), performing 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 either outlined with a red border, indicating that the participant should observe passively (observe gesture condition), or a green border, indicating that the participant should imitate the signs during the video presentation (imitate gesture condition). Two control conditions were utilized: (i) portraits of each actor to control for viewing *vs* imitating actors (view portrait condition, also outlined with a red border) and (ii) a fixation cross (baseline) (Figure 1).

Four stimuli from the same condition and portraying the same actor were presented in a block. 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-s 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 of same gender in a row, no two of same ethnicity in a row, and no two of same hand sign in a row. Five 22.5-s rest blocks were evenly spaced throughout each run. This run configuration resulted in one block 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, gestures were each seen an equal number of times as each gesture was performed by each actor once in each condition. Also over the course of the experiment, each participant saw 96 stimuli (24 blocks) portraying own-gender actors and 96 stimuli (24 blocks) portraying other-gender actors in each of the conditions. The stimulus order for each participant was unique. These functional data were acquired over a total of 55 min of scan time. The fMRI task was created and presented in the scanner using Presentation® software (Neurobehavioral Systems, Inc., Albany, CA, USA) and viewed in the scanner on magnet-compatible goggles (Resonance Technologies, Inc.).

Prior to scanning, each subject 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 (task structure familiarization hand signs and actor were not later seen in scanner). During 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 Tesla Siemens Trio whole-body MRI scanner at the UCLA Ahmanson–Lovelace Brain Mapping Center. The following scans were performed on each participant: (i) 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); (ii) 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: 0.89 ms, bandwidth: 1302 Hz/Px, time: 1:30); (iii) 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°, T1: 900 ms,

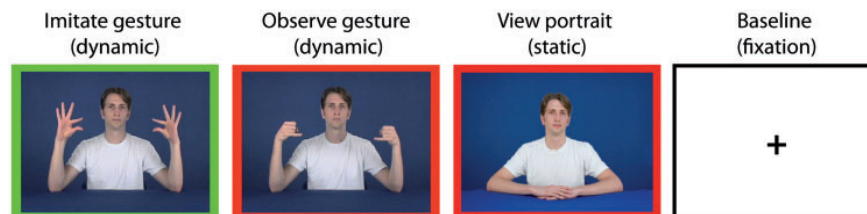

Fig. 1 Example stimuli from four experimental conditions (Imitate gesture stimuli have a green border = participants imitate and observe gesture and view portrait stimuli have red borders = participants observe).

FoV Read: 250 mm, echo spacing 6.9 ms, bandwidth: 200 hz/ px, time: 6:50).

Behavioral measures

To quantify participants' task compliance and imitation accuracy, participants were visually monitored during scanning to ensure that no movement occurred during observation-only blocks. Additionally, for 16 of 19 participants, hand-sign imitation accuracy was assessed by watching 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 with an average of 94.8% (subject range = 82.6%–99.7%) of signs receiving the highest accuracy rating, suggesting participants were able to perform the hand-sign imitation task accurately.

fMRI data analysis

One male participant was not included in the analysis due to a failure of the stimulus randomization script. Additionally, the fourth run was dropped from two participants due to failure of the stimulus presentation computer, and two runs were dropped from each of two participants due to head motion. This resulted in a total of 19 (10 females) participants and 70 runs being utilized in the statistical analyses. Head motion in the remaining data was low, with an average mean relative head motion per run of 0.077 mm, s.d. = 0.004 mm and a an average maximum relative head motion per run of .648 mm, s.d. = 0.074 mm.

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). Preprocessing included skull-stripping (AFNI), realignment (mean image, FSL), highpass 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 2x2x2mm) was carried out with FSL (12-parameter affine) and refined using ART (non-linear transformation). First-level analyses included voxel prewhitening, double-gamma hemodynamic response function (HRF) convolution, temporal filtering, and temporal derivative inclusion.

The following contrasts were entered in the first-level analysis: (own gender > other gender), (other gender > own gender), (own gender > baseline), (other gender > baseline), for each of the imitate gesture, observe gesture and view portrait conditions. Interaction contrasts were also entered, subtracting the above contrasts for the observe gesture or view portrait condition from the equivalent contrasts in the imitate gesture condition {e.g., [(imitate gesture own gender > other gender) > (observe gesture own gender > other gender)]}. Interaction contrasts were intended to reveal whether results found in the imitate gesture condition reflected processes unique to imitation. For each participant,

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 participants (FLAME 1 + 2). All data were thresholded at $Z > 2.3$ and whole-brain cluster corrected for multiple comparisons ($P < 0.05$).

Additional analyses were conducted to explore the robustness of the significant effect observed in the (imitate gesture own gender > other gender) contrast. The consistency of this effect across participants was evaluated by examining whether significant activity for this contrast was present in each individual (fixed effect 4-run average, $P < 0.05$, uncorrected) within the region where significant activity was observed at the group level. An additional group analysis excluding the three homosexual participants was also conducted. Finally, in order to further test whether differential activity for own- and other-gender models was specific to the imitate gesture condition, parameter estimates of activity were extracted for all conditions from an anatomical region of interest (ROI) of the bilateral nucleus accumbens from the Harvard–Oxford probabilistic atlas (Desikan et al., 2006), thresholded at $P = 0.25$ (at least 25% of people have nucleus accumbens tissue in every voxel) and entered into a two gender (own and other) × three condition (imitate gesture, observe gesture and view portrait) repeated measures ANOVA in SPSS.

Bayesian analysis of the BrainMap database

To assess how selectively the region more active for own- than other-gender imitation is activated by reward tasks in the literature, we performed a Bayesian analysis of the BrainMap neuroimaging database, following the methods outlined by Poldrack (2006). We used a 10-mm cuboid ROI around the peak voxel of the cluster more active for own- than other-gender imitation [(14, 14, −8), converted from MNI to Talairach using the BrainMap search tool]. This ROI was fully contained within the active cluster. We searched for all experiments containing activity within this region that did and did not employ reward tasks (denoted by the Paradigm Class code in the database) and also for all experiments without activity in this region that did and did not employ reward tasks (Table 1). We used these frequencies along with a neutral prior estimate of a reward task being used ($P = 0.5$) to calculate a posterior probability and corresponding Bayes factor ($P/1 − P$) for the likelihood a reward task was employed based on the presence of activity within our nucleus accumbens-centered functional ROI. We also calculated the conditional probability of a reward task being used given the activity within the ROI (Table 1, first row).

RESULTS

Comparing imitation of one's own gender to the other gender (imitate gesture own gender > other gender) produced a single cluster of significant activity, centered in bilateral nucleus accumbens and extending into the dorsal

Table 1 Frequency table for searches conducted in BrainMap database reflecting number of experimental comparisons found for each search

	Reward task	Not reward task
Activated	47	37
Not activated	460	8666

Note. Search location was (14, 14, −8) MNI converted to Talairach (12, 13, −3) using icbm2tal through the BrainMap search tool Sleuth v1.2, extending 5 mm in each direction.

Table 2 Peaks of activity for own > other gender during imitation and the interaction between imitation and the other conditions

Anatomical region	X	y	z	Z
Imitate gesture own gender > other gender				
R putamen/nucleus accumbens	14	14	−8	3.83
R orbitofrontal cortex/putamen	18	18	−12	3.76
L nucleus accumbens	−8	14	−8	3.43
R caudate	18	18	2	3.38
R putamen	20	18	−2	3.38
(Imitate gesture own gender > other gender) > (observe gesture own gender > other gender)				
R putamen/nucleus accumbens	16	14	−10	3.96
R orbitofrontal cortex/putamen	18	18	−12	3.78
R caudate	20	16	6	3.26
R pallidum/putamen	16	4	−16	3.19
(Imitate gesture own gender > other gender) > (view portrait own gender > other gender)				
R putamen/caudate	18	18	−10	3.61
R orbitofrontal cortex/insula	28	20	−8	3.59
R insula/orbitofrontal cortex	32	20	−6	3.55
R nucleus accumbens/putamen	14	16	−10	3.54

Note. All clusters present at statistical threshold of $Z > 2.3$, whole-brain corrected for multiple comparions ($P < 0.05$) ($n = 19$). Anatomical regions of peak voxel within cluster assigned using Harvard–Oxford Cortical and Subcortical Probabilistic Structural Atlases. First cluster within each anatomical region listed. Interaction contrasts masked by significant clusters in imitate condition. L and R refer to left and right hemispheres; *x, y* and *z* refer to the MNI coordinates corresponding to the left–right, anterior–posterior and inferior–superior axes, respectively; Z refers to the highest Z score within a cluster.

striatum, orbitofrontal cortex (OFC) and left amygdala (Table 2 and Figure 2a-b). This result held when the three homosexual participants were removed from the analysis and in both males and females when the sexes were analyzed separately. Additionally, 16 of 19 study participants had significant activity within this cluster when imitating own-compared to other-gender individuals, confirming the robustness of the own-gender effect even at the single subject level (two-tailed sign test, $P = .004$). No significant activity was found for the reverse contrast (imitate gesture other gender > own gender). Furthermore, no significant differences were found for the (own gender > other gender) contrast in either the observe gesture or view portrait conditions.

To determine whether own-gender enhanced activity within reward-related regions was unique to imitation, we next compared the (own gender > other gender) contrast in the imitate gesture condition to both the observe gesture and view portrait conditions [(imitate gesture own gender > other gender) > (observe gesture own gender > other gender)] and [(imitate gesture own gender > other gender) > (view portrait own gender > other gender)]. Since the purpose of these analyses was to determine what activity from the (imitate gesture own gender > other gender) contrast was unique to imitation, interaction contrasts were post-threshold masked by the result of the (imitate gesture own gender > other gender) contrast. There was reliably higher activity in the nucleus accumbens, dorsal striatum, OFC and amygdala for imitating own- compared to other-gender actors, even after activity associated with passively observing the gestures (Figure 2c, red activity) or portraits (Figure 2c, blue activity) of own- compared to other-gender actors was removed. Furthermore, there was considerable overlap between these two analyses (Figure 2c, green activity), suggesting that much of the enhanced activity in response to own- compared to other-gender individuals during imitation was unique to imitation.

We also conducted a more targeted inquiry into whether the own-gender effect seen in the imitate condition was also seen during gesture observation or portrait viewing, by restricting our search to an anatomical nucleus accumbens ROI. We extracted parameter estimates of activity from this cluster for all six conditions (as compared to baseline) and entered these into a two-gender (own and other) × three-condition (imitate gesture, observe gesture and view portrait) repeated measures ANOVA. We found a significant gender × condition interaction [F (2,17) = 4.26, $P = 0.02$], whereby significantly greater activity for own than other gender was observed in the imitate gesture condition [$t(18) = 3.3$, $P = 0.004$] but not in the observe gesture [$t(18) = −0.9$, $P = 0.378$] or view portrait [$t(18) = −0.7$, $P = 0.518$] condition. Furthermore, the (own gender > other gender) contrast in the imitate gesture condition was significantly different from both the observe gesture [$F(1,18) = 7.26$, $P = 0.015$] and view portrait condition [$F(1,18) = 6.69$, $P = 0.019$], but the non-imitative conditions did not differ from one another (Figure 2d). This ROI analysis suggests that the increased activity in the nucleus accumbens when participants imitated individuals of their own gender is indeed specific to the process of imitation, as no effect was found during gesture observation or portrait viewing, even when the search was restricted to an anatomical region where this difference was seen during imitation.

To assess the likelihood that the enhanced activity in the nucleus accumbens and other regions indicated the engagement of reward-related cognitive processes, as opposed to other cognitive functions related to these structures, we conducted a Bayesian analysis of the BrainMap neuroimaging database (Laird *et al.*, 2005). We estimated the degree to which the region found to be more active for own-compared to other-gender imitation is selectively activated by reward tasks within the BrainMap database (Poldrack, 2006). We found that activity within this nucleus accumbens
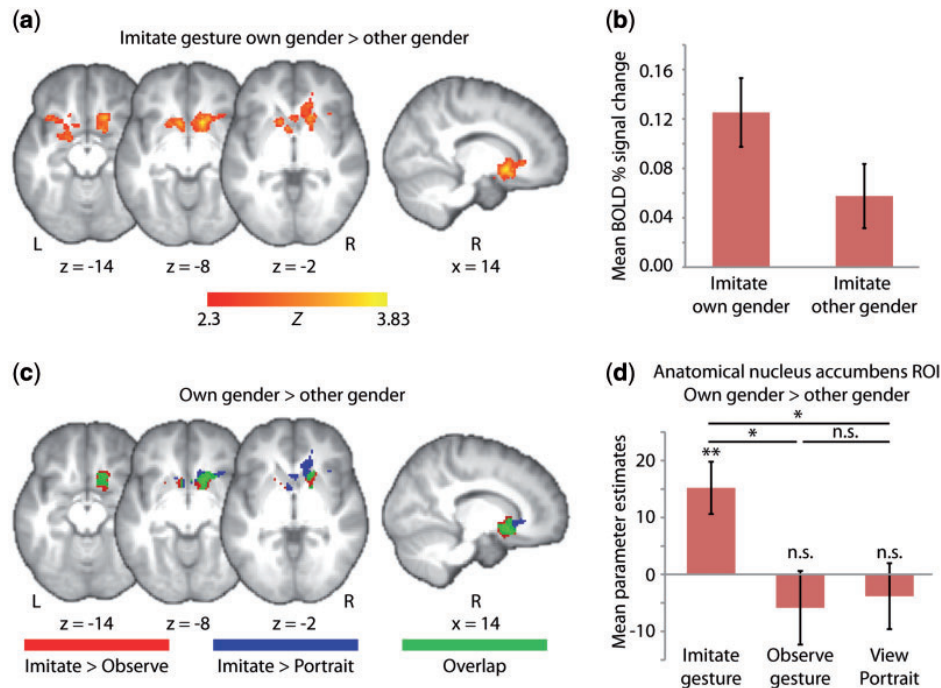
Fig. 2 Results. Functional activity is thresholded at $Z > 2.3$ with whole-brain correction for multiple comparisons at the cluster level ($P < .05$), and overlaid on a group average ($n = 19$) T1-weighted structural scan. (a-b) Whole-brain analysis. (**a**) During imitation of own gender compared to other gender models, significantly more activity was seen in reward-related neural regions, including the bilateral ventral striatum [MNI coordinates: R (14,14,-8), L (-8, 14, -8)], dorsal striatum and left amygdala. Cluster is 1148 voxels, cluster $P = 0.0023$, peak $Z = 3.83$. (**b**) Percent fMRI signal change from baseline averaged across entire cluster of significant activity shown in (a). Error bars are s.e. (**c-d**) Gender x condition interaction. (**c**) Whole-brain interaction effects in regions exhibiting greater activity for own- than other-gender in the imitate gesture condition as compared to the observe gesture condition (red) and the view portrait condition (blue). The overlap between these interaction effects (green) can be interpreted as activity that is unique to imitation. All contrasts are post-threshold masked by significant activity within the (imitate gesture own gender > other gender) contrast; (**d**) mean differences for (own gender - other gender) parameter estimates averaged across a bilateral nucleus accumbens anatomical ROI. Results displayed are from two gender (own and other) × three condition (imitate gesture, observe gesture and view portrait) repeated measures ANOVA. *$P < 0.05$, **$P < 0.01$.

region was associated with a substantial increase in the probability that a reward task was used (i.e. from a neutral prior probability of 0.5–0.96, corresponding to a Bayes factor of 21.8). A Bayes factor of >10 is thought to reflect strong increases in confidence over the prior probability (Jeffreys, 1998). We also calculated the conditional probability of a reward task being used, given the presence of activity within this nucleus accumbens region. This measure provides a different metric of the likelihood that activity within this region is related to reward processing, which unlike the Bayesian calculation does not depend on a specific comparison set. We found that 56% of contrasts eliciting activity within this region involved reward tasks, indicating that activity within this area is more likely to be related to reward than to any other cognitive function. Notably, this metric likely underestimates the conditional probability because a number of contrasts among the 44% not explicitly labeled as reward tasks involved comparison between conditions that may differ in their reward value (e.g. amphetamine > saline; erotic pictures > neutral pictures). Taken together, these analyses suggest that own-gender imitation

is most likely associated with cognitive processes similar to those associated with more traditional reward tasks, such as reward and reinforcement.

DISCUSSION

While preferential imitation of own-gender models has been well documented behaviorally, until now no proximate neural mechanism underlying own-gender imitation was known. Consistent with our prediction, we found that reward-related structures, including the ventral striatum, OFC, dorsal striatum and left amygdala, were more active during own- compared to other-gender imitation. The specificity of the own-gender effect to the imitation condition suggests that this effect is not merely due to low-level perceptual features of the stimuli (e.g. simply looking at own- compared to other-gender individuals) but rather is related to the process of imitation of own-gender models in particular. Furthermore, using a Bayesian analysis, we demonstrated that the region more active for own- than other-gender imitation is most often activated by

reward tasks in the BrainMap database. Taken together, these findings provide a plausible neural mechanism for the pervasive gender similarity bias in imitative learning.

The neural regions observed to be preferentially active during own-gender imitation are part of a dopaminergic neural system that has been associated with processing reward and reinforcement learning in both humans and animals (Haber and Knutson, 2010). Specifically, the OFC, ventral striatum and amygdala have each been implicated in coding the value of current and future rewards. The ventral striatum and amygdala are also sensitive to reward salience. These structures are thought to work in concert with the dorsal striatum (caudate and putamen; also structures preferentially active for own-gender imitation) to guide subsequent action selection (O'Doherty, 2004; Haber and Knutson, 2010). Thus, activity in reward-related circuitry during own-gender imitation may be providing a reinforcement signal that facilitates learning from own-gender models. It has previously been demonstrated that activation of reward-related neural structures including the ventral striatum may be contingent on the interaction between anticipated reward and the need to perform an instrumental response (Bjork and Hommer, 2007). Accordingly, the reinforcement signal in the present study may result from the act of own-gender imitation itself or the interaction between neural activity directly related to imitation with activity related to the salience and self-similarity of own-gender models.

Importantly, these data reveal a similarity between the neural underpinnings of own-gender imitation and those of classical reward tasks, which would not have been apparent from behavior alone. Bayesian analysis of the BrainMap database using the peak of the region found to be more active for own- *vs* other-gender imitation, located in the nucleus accumbens, confirmed that this region is most often activated by reward tasks in the literature. Ariely and Berns (2010) found a similar level of selective activation of the nucleus accumbens by reward tasks in the BrainMap database using an anatomical nucleus accumbens ROI. Such Bayesian calculations are heavily influenced by the nature of the comparison set, but even when we only considered studies that had activation within the nucleus accumbens, reward tasks still constitute the majority. Thus, although inferring cognition from brain activity in many areas of the brain may be complicated due to the large number of functions these brain areas may perform, the ventral striatum appears to be most often active during reward-related tasks, thereby increasing our confidence that own-gender imitation is an intrinsically rewarding process.

Previous theoretical and empirical work on gender identity development suggests *why* own-gender imitation may be rewarding. Social learning theory proposes that acting like own-gender individuals is encouraged by parents, teachers and peers from an early age, thus facilitating gender identity formation (Bandura, 1977). Social-cognitive theory posits that once gender identity has begun to form, own-gender imitation is perpetuated by the confidence derived from perceiving one's self to be similar to a group of same-sex individuals (Kohlberg, 1966). Indeed, both the reception of praise from others (Izuma *et al.*, 2008) and the act of conforming to a group (Klucharev *et al.*, 2009) have been associated with increases in activity within reward-related neural circuitry including the ventral striatum. Future studies are needed to determine how the positive relationship found between own-gender imitation and reward in the present study is related to gender identity development.

The present study represents the first step toward elucidating the neural mechanisms of model-observer similarity biases during imitation, a key element of real-world imitative learning. Our findings provide strong support for the hypothesis that imitation of own-gender models is indeed accompanied by intrinsic reinforcement and may thus facilitate the acquisition of gender norms and gender role behaviors. This finding is in keeping with our recently proposed model of the neural architecture of cultural imitative learning, which posits that reward-related responses play a critical role in reinforcing the learning of culturally transmitted behavior (Losin *et al.*, 2009). Future developmental and cross-cultural studies may help determine the extent to which increased responsiveness in the reward system when imitating individuals of one's own gender may be driven by experiential *vs* biologically determined factors.

REFERENCES

Ardekani, B.A., Braun, M., Hutton, B.F., Kanno, I., Iida, H. (1995). A fully automatic multimodality image resistration algorithm. *Journal of computer assisted tomography*, *19*, 615–23.

Ariely, D., Berns, G.S. (2010). Neuromarketing: the hope and hype of neuroimaging in business. *Nature Reviews Neuroscience*, *11*, 283–292.

Bandura, A. (1977). *Social Learning Theory*. New Jersey: Prentice-Hall.

Bandura, A., Ross, D., Ross, S.A. (1961). Transmission of aggression through imitation of aggressive models. *Journal of Abnormal and Social Psychology*, *63*, 575–82.

Basow, S.A., Howe, K.G. (1980). Role-model influence: effects of sex and sex-role attitude in college students. *Psychology of Women Quarterly*, *4*, 558–72.

Bjork, J.M., Hommer, D.W. (2007). Anticipating instrumentally obtained and passively-received rewards: a factorial fMRI investigation. *Behavioural Brain Research*, *177*, 165–70.

Buccino, G., Vogt, S., Ritzl, A., et al. (2004). Neural circuits underlying imitation learning of hand actions an event-related fMRI atudy. *Neuron*, *42*, 323–34.

Bussey, K., Bandura, A. (1984). Influence of gender constancy and social power on sex-linked modeling. *Journal of Personality and Social Psychology*, *47*, 1292–302.

Cox, R.W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, *29*, 162–73.

Desikan, R.S., Segonne, F., Fischl, B., et al. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *Neuroimage*, 31, 968–80.

Frey, S.H., Gerry, V.E. (2006). Modulation of neural activity during observational learning of actions and their sequential orders. *Journal of Neuroscience*, 26, 13194–201.

Gilbert, L.A., Gallessich, J.M., Evans, S.L. (1983). Sex of faculty role model and students' self-perceptions of competency. *Sex Roles*, 9, 597–607.

Haber, S.N., Knutson, B. (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology*, 35, 4–26.

Henrich, J., McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology*, 12, 123–35.

Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286, 2526–8.

Izuma, K., Saito, D.N., Sadato, N. (2008). Processing of social and monetary rewards in the human striatum. *Neuron*, 58, 284–94.

Jeffreys, S.H. (1998). *Theory of Probability*. USA: Oxford University Press.

Killian, J.N. (1990). Effect of model characteristics on musical preference of junior high students. *Journal of Research in Music Education*, 38, 115–23.

Klucharev, V., Hytönen, K., Rijpkema, M., Smidts, A., Fernández, G. (2009). Reinforcement learning signal predicts social conformity. *Neuron*, 61, 140–51.

Kohlberg, L. (1966). A cognitive-developmental analysis of children's sex-role concepts and attitudes. In: Maccoby, E.E., editor. *The Development of Sex Differences*. Stanford, CA: Stanford University Press, pp. 82–173.

Laird, A.R., Lancaster, J.L., Fox, P.T. (2005). The social evolution of a human brain mapping database. *Neuroinformatics*, 3, 65–77.

Losin, E.A., Dapretto, M., Iacoboni, M. (2009). Culture in the mind's mirror: how anthropology and neuroscience can inform a model of the neural substrate for cultural imitative learning. *Progress Brain Research*, 178, 175–90.

Mesoudi, A. (2009). The cultural dynamics of copycat suicide. *PLoS ONE*, 4, e7252.

O'Doherty, J.P. (2004). Reward representations and reward-related learning in the human brain: insights from neuroimaging. *Current Opinion in Neurobiologia*, 14, 769–76.

Perloff, R.M. (1982). Gender constancy and same-sex imitation: a developmental study. *Journal of Psychology*, 111, 81–6.

Poldrack, R.A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Science*, 10, 59–63.

Slaby, R.G., Frey, K.S. (1975). Development of gender constancy and selective attention to same-sex models. *Child Development*, 46, 849–56.

Tomasello, M., Kruger, A.C., Ratner, H.H. (1993). Cultural Learning. *Behavioural Brain Science*, 16, 495–511.

CHAPTER 4

Race modulates neural activity during imitation
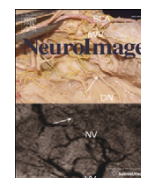
Race modulates neural activity during imitation

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ARTICLE INFO

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
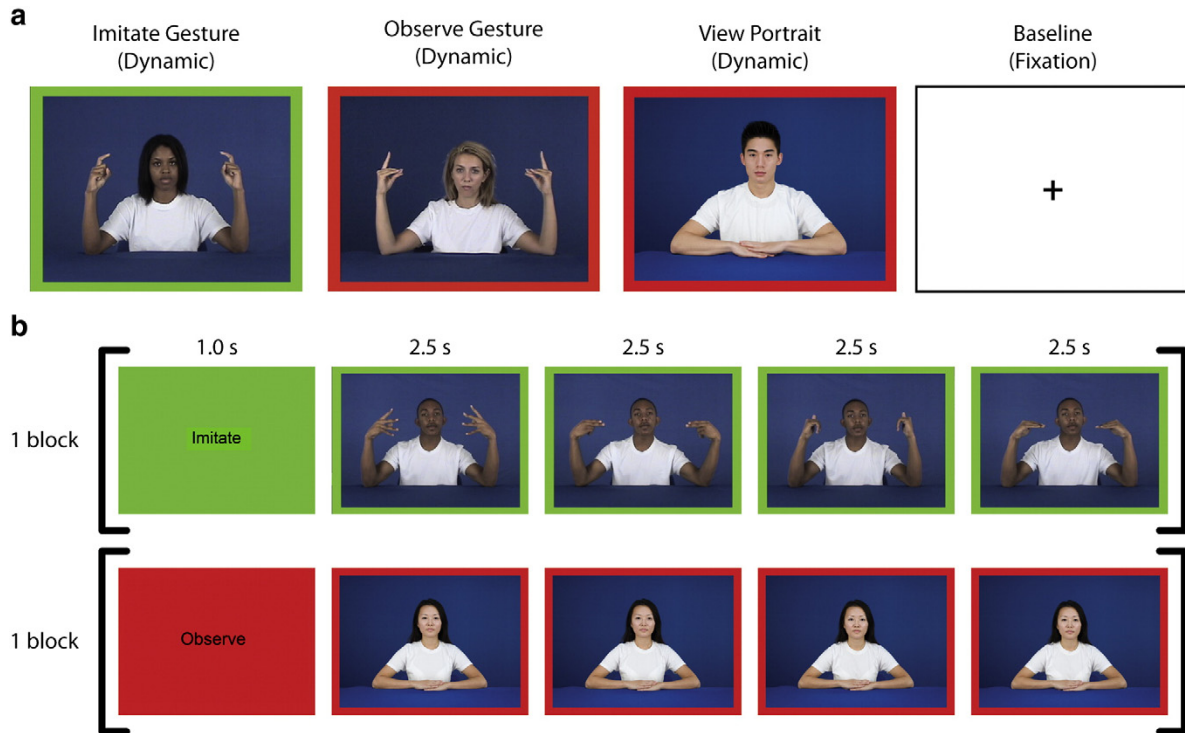
Fig. 1. Experimental stimuli and task design. (a) Example stimuli from 4 experimental conditions (green border = imitation, red border = observation). (b) Examples of block structure from the imitate gesture (first row) and view portrait (second row) conditions.

(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,

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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
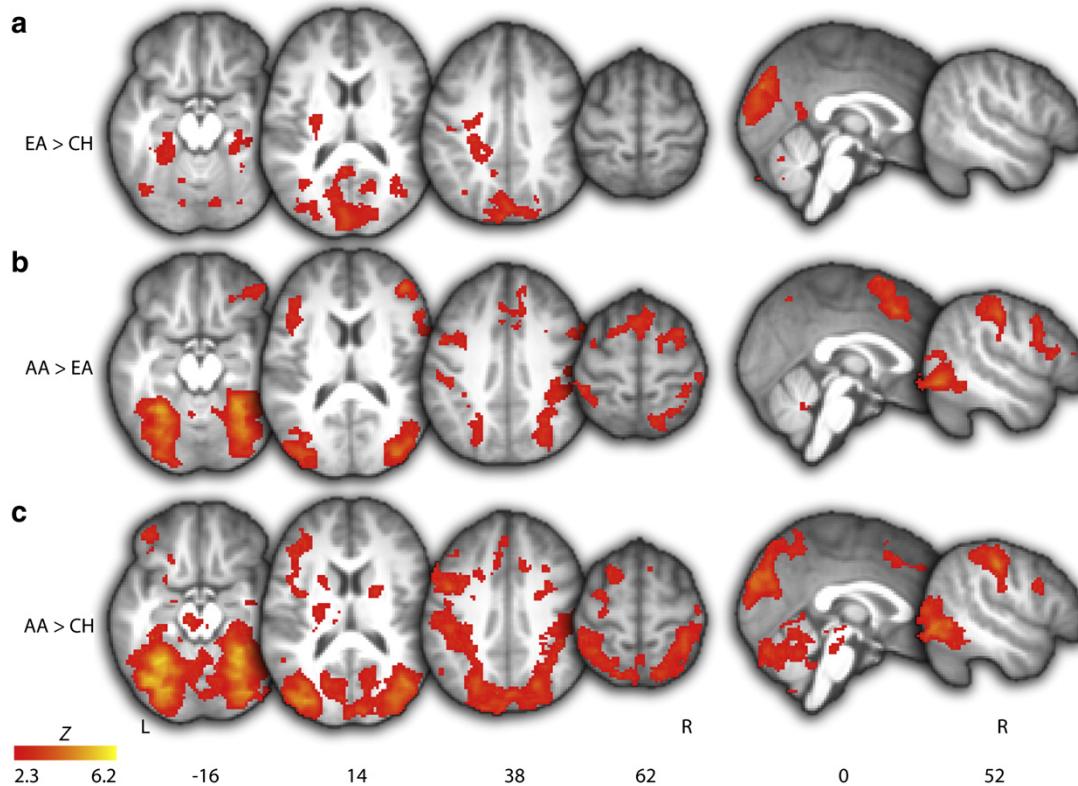
Fig. 2. Neural regions differentiating between imitation of individuals from three different racial groups, European American (EA; own-race) and two racial outgroups: Chinese American (CH) and African American (AA). (a–c) Whole-brain racial comparisons yielding significant differences from all possible 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
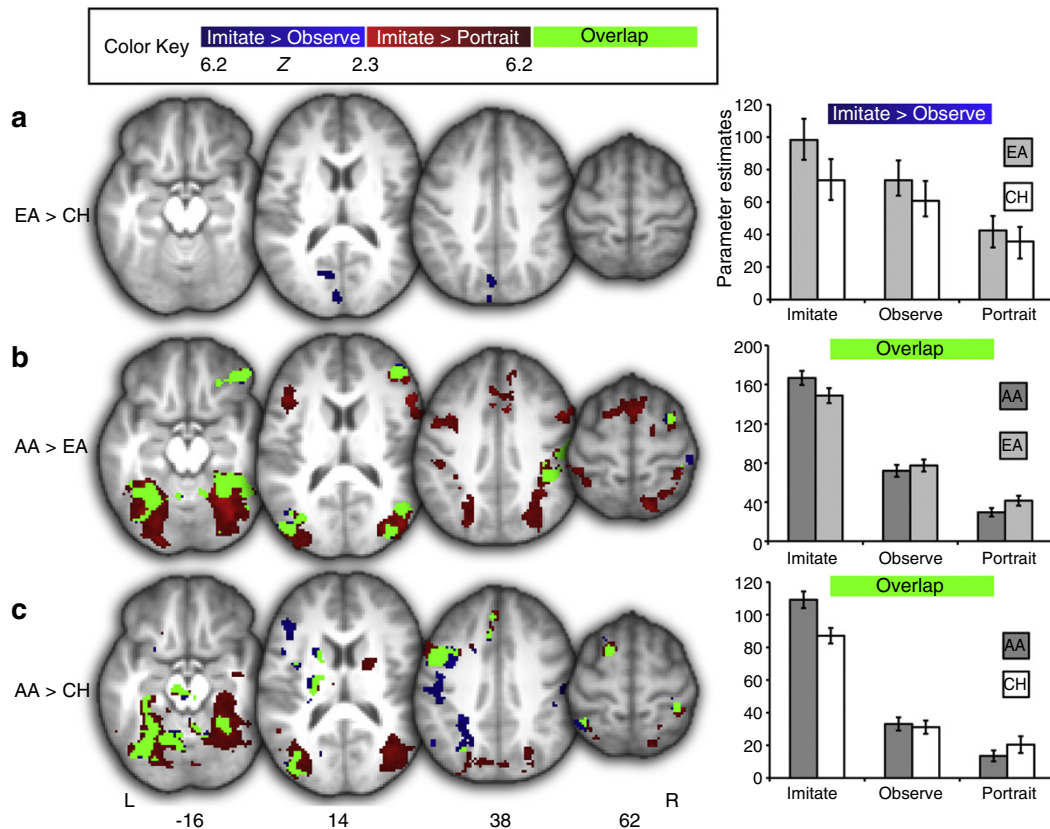
Fig. 3. Neural regions exhibiting Race×Task interactions. (a–c) All pairwsie racial comparisons between European American (EA), Chinese American(CH), African American (AA) actors exhibiting differences between imitation and non-imitation conditions. (Left) Whole-brain Race×Task interaction effects are 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

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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.

Supplementary materials related to this article can be found online at doi:10.1016/j.neuroimage.2011.10.074.

References

Alwin, D.F., 1997. Feeling thermometers versus 7-point scales. Sociol. Meth. Res. 25, 318–340.
Ardekani, B.A., Braun, M., Hutton, B.F., Kanno, I., Iida, H., 1995. A fully automatic multi-modality image registration algorithm. J. Comput. Assist. Tomogr. 19, 615–623.
Bobo, L., Zubrinsky, C.L., 1996. Attitudes on residential integration: perceived status differences, mere in-group preference, or racial prejudice? Soc. Forces 74, 883–909.
Boyd, R., Richerson, P.J., 1987. The evolution of ethnic markers. Cultural Anthropology 65–79.

Buccino, G., Vogt, S., Ritzl, A., Fink, G.R., Zilles, K., Freund, H.J., Rizzolatti, G., 2004. Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. Neuron 42, 323–334.

Caspers, S., Zilles, K., Laird, A.R., Eickhoff, S.B., 2010. ALE meta-analysis of action observation and imitation in the human brain. Neuroimage 50, 1148–1167.

Chiao, J.Y., Iidaka, T., Gordon, H.L., Nogawa, J., Bar, M., Aminoff, E., Sadato, N., Ambady, N., 2008. Cultural specificity in amygdala response to fear faces. J. Cogn. Neurosci. 20, 2167–2174.

Clark, K.B., Clark, M.P., 1947. Racial identification and preference in Negro children. Read. Soc. Psychol. 169–178.

Cunningham, W.A., Johnson, M.K., Raye, C.L., Gatenby, J.C., Gore, J.C., Banaji, M.R., 2004. Separable neural components in the processing of black and white faces. Psychol. Sci. 15, 806–813.

Désy, M.C., Théoret, H., 2007. Modulation of motor cortex excitability by physical similarity with an observed hand action. PLoS ONE 2.

Dunham, Y., Baron, A.S., Banaji, M.R., 2008. The development of implicit intergroup cognition. Trends Cogn. Sci. 12, 248–253.

Eberhardt, J.L., 2005. Imaging race. The American Psychologist 60 (2), 181–190. doi:10.1037/0003-066X.60.2.181.

Feinman, S., 1980. Infant response to race, size, proximity, and movement of strangers. Infant Behav. Dev. 3, 187–204.

Fiske, S.T., Xu, J., Cuddy, A.C., Glick, P., 1999. (Dis) respecting versus (dis) liking: status and interdependence predict ambivalent stereotypes of competence and warmth. J. Soc. Issues 55 (3), 473–489.

Fiske, S.T., Cuddy, A.J.C., Glick, P., Xu, J., 2002. A model of (often mixed) stereotype content: competence and warmth respectively follow from perceived status and competition. J. Pers. Soc. Psychol. 82 (6), 878.

Frey, S.H., Gerry, V.E., 2006. Modulation of neural activity during observational learning of actions and their sequential orders. J. Neurosci. 26, 13194–13201.

Golby, A.J., Gabrieli, J.D.E., Chiao, J.Y., Eberhardt, J.L., 2001. Differential responses in the fusiform region to same-race and other-race faces. Nat. Neurosci. 4, 845.

Greenwald, A.G., McGhee, D.E., Schwartz, J.L.K., et al., 1998. Measuring individual differences in implicit cognition: the implicit association test. J. Pers. Soc. Psychol. 74, 1464–1480.

Greenwald, A.G., Nosek, B.A., 2001. Health of the Implicit Association Test at age 3. Z. Exp. Psychol. 48, 85–93.

Greenwald, A.G., Nosek, B.A., Banaji, M.R., 2003. Understanding and using the Implicit Association Test: I. An improved scoring algorithm. J. Pers. Soc. Psychol. 85, 197–216.

Grèzes, J., Armony, J.L., Rowe, J., Passingham, R.E., 2003. Activations related to "mirror" and "canonical" neurons in the human brain: an fMRI study. Neuroimage 18, 928–937.

Haas, N.S., Sullivan, H., 1991. Use of ethnically matched role models in career materials for Hispanic students. Contemp. Educ. Psychol. 16, 272–278.

Humes, K.R., Jones, N.A., Ramirez, R.R., 2011. Overview of race and Hispanic origin: 2010. Census Briefs 2010, 1–23.

Iacoboni, M., 2009. Imitation, empathy, and mirror neurons. Annu. Rev. Psychol. 60, 653–670.

Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. Science 286, 2526–2528.

Iidaka, T., Nogawa, J., Kansaku, K., Sadato, N., 2008. Neural correlates involved in processing happy affect on same race faces. J. Psychophysiol. 22, 91–99.

Ito, T.A., Bartholow, B.D., 2009. The neural correlates of race. Trends Cogn. Sci. 13, 524–531.

Judd, C.M., Park, B., Ryan, C.S., Brauer, M., Kraus, S., 1995. Stereotypes and ethnocentrism: diverging interethnic perceptions of African American and White American youth. J. Pers. Soc. Psychol. 69, 460-460.

Karunanayake, D., Nauta, M.M., 2004. The relationship between race and students' identified career role models and perceived role model influence. Career Dev. Q.

Kelly, D.J., Quinn, P.C., Slater, A.M., Lee, K., Gibson, A., Smith, M., Ge, L., Pascalis, O., 2005. Three-month-olds, but not newborns, prefer own-race faces. Dev. Sci. 8, F31–F36.

King, M.M., Multon, K.D., 1996. The effects of television role models on the career aspirations of African American junior high school students. J. Career Dev. 23, 111–125.

Koski, L., Wohlschlager, A., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C., Iacoboni, M., 2002. Modulation of motor and premotor activity during imitation of target-directed actions. Cereb. Cortex 12, 847–855.

Lee, K.U., Khang, H.S., Kim, K.T., Kim, Y.J., Kweon, Y.S., Shin, Y.W., Kwon, J.S., Ho, S.H., Garfinkel, S.N., Chae, J.H., 2008. Distinct processing of facial emotion of own-race versus other-race. Neuroreport 19, 1021.

Lieberman, M.D., Hariri, A., Jarcho, J.M., Eisenberger, N.I., Bookheimer, S.Y., 2005. An fMRI investigation of race-related amygdala activity in African-American and Caucasian-American individuals. Nat. Neurosci. 8, 720–722.

Liebert, R.M., Sobol, M.P., Copemann, C.D., 1972. Effects of vicarious consequences and race of model upon imitative performance by Black children. Dev. Psychol. 6, 453–456.

Liew, S.L., Han, S., Aziz-Zadeh, L., 2010. Familiarity modulates mirror neuron and mentalizing regions during intention understanding. Hum Brain Mapp. 32, 1986–1997.

Link, M.W., Oldendick, R.W., 1996. Social construction and white attitudes toward equal opportunity and multiculturalism. J. Polit. 58, 149–168.

Losin, E.A., Dapretto, M., Iacoboni, M., 2009. Culture in the mind's mirror: how anthropology and neuroscience can inform a model of the neural substrate for cultural imitative learning. Prog. Brain Res. 178, 175–190.

Losin, E.A.R., Dapretto, M., Iacoboni, M., 2010. Culture and neuroscience: additive or synergistic? Soc. Cogn. Affect. Neurosci. 5, 148–158.

Molnar-Szakacs, I., Wu, A.D., Robles, F.J., Iacoboni, M., 2007. Do you see what I mean? Corticospinal excitability during observation of culture-specific gestures. PLoS One 2, e626.

Neely, J.J., Hechel, R.V., Leichtman, H.M., 1973. The effect of race of model and response consequences to the model on imitation in children. J. Soc. Psychol. 89, 225–231.

Pettigrew, T.F., 1998. Intergroup contact theory. Annu. Rev. Psychol. 49, 65–85.

Ramachandran, V.S., 2000. Mirror neurons and imitation learning as the driving force behind "the great leap forward" in human evolution. Edge Website article. http://www.edge.org/3rd_culture/ramachandran/ramachandran_p1.html.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.

Schmukle, S.C., Egloff, B., 2004. Does the Implicit Association Test for assessing anxiety measure trait and state variance? Eur. J Pers. 18, 483–494.

Tanaka, S., Inui, T., Iwaki, S., Konishi, J., Nakai, T., 2001. Neural substrates involved in imitating finger configurations: an fMRI study. Neuroreport 12, 1171–1174.

Van den Berghe, P.L.B., 1987. Ethnicity and other bases of sociality. The Ethnic Phenomenon. Elsevere.

Vogt, S., Buccino, G., Wohlschläger, A.M., Canessa, N., Shah, N.J., Zilles, K., Eickhoff, S.B., Freund, H.J., Rizzolatti, G., Fink, G.R., 2007. Prefrontal involvement in imitation learning of hand actions: effects of practice and expertise. Neuroimage 37, 1371–1383.

Weaver, C.N., 2008. Social distance as a measure of prejudice among ethnic groups in the United States. J. Appl. Soc. Psychol. 38, 779–795.

Wong, P., Lai, C.F., Nagasawa, R., Lin, T., 1998. Asian Americans as a model minority: Self-perceptions and perceptions by other racial groups. Sociol. Perspect. 41, 95–118.

Zirkel, S., 2002. Is there a place for me? Role models and academic identity among white students and students of color. Teach. Coll. Rec. 104, 357–376.
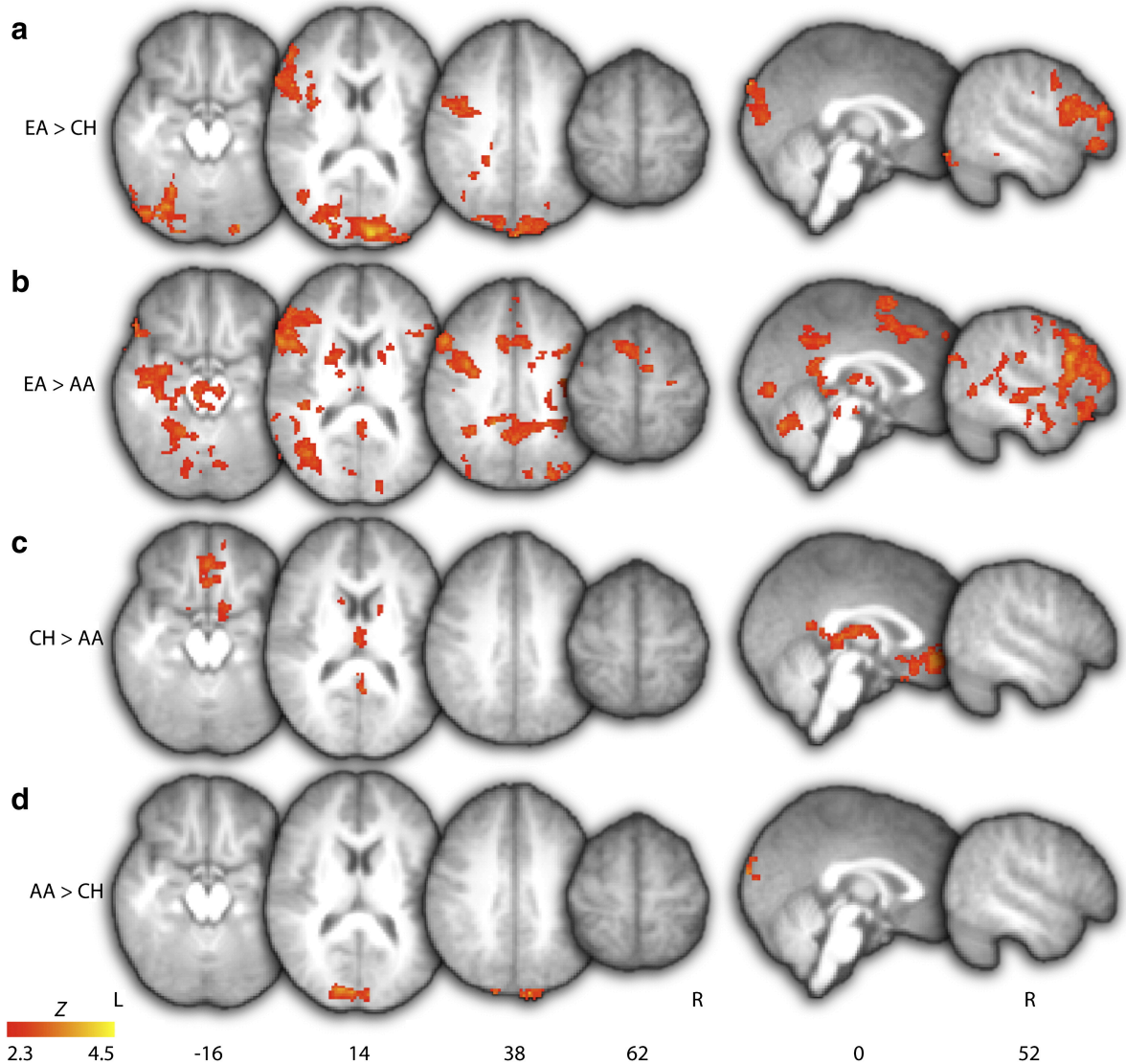
Figure 4.4. Neural regions differentiating between viewing the portraits of individuals from three different racial groups, European American (EA; own-race) and two racial outgroups: Chinese American (CH) and African American (AA). (a–d) Whole-brain racial comparisons yielding significant differences from all possible pairwise racial comparisons. Greater fusiform gyrus activity was observed during own-race portrait viewing as compared to the two racial outgroups.

(a–b). Functional activity is thresholded at Z > 2.3 with whole-brain correction for multiple

comparisons 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.
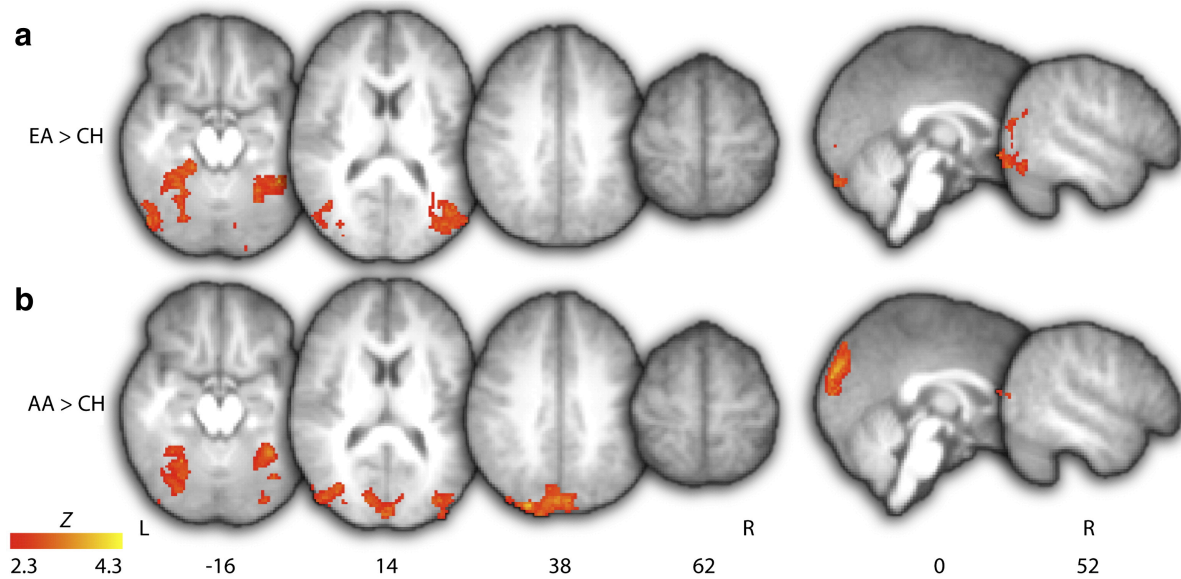
Figure 4.5. Neural regions differentiating between observation of the gestures of individuals from three different racial groups, European American (EA; own-race) and two racial outgroups: Chinese (CH) and African American (AA). (a–b) Whole-brain racial comparisons yielding significant differences from all possible pairwise racial comparisons. These contrasts (EA > CH, AA > CH) are the same as those exhibiting racial differences during imitation, but racial differences during gesture observation are confined to visual regions. The remaining racial contrast exhibiting differences during imitation, (AA > EA) also resulted in significant differences in visual regions during gesture observation at a lower statistical threshold ($Z > 1.7$, corrected, data not shown). 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.

Table 4.3. Anatomical regions differentiating between races during portrait viewing

Anatomical Regions	x	y	z	Z
View Portrait EA > CH				
R Frontal pole	50	38	16	3.50
R Precentral gyrus	62	10	22	3.00
R Middle temporal gyrus, temporoccipital part	60	-42	-12	2.84
R Occipital fusiform gyrus	34	-74	-12	4.57
L Occipital fusiform gyrus	-26	-82	-20	3.63
L Occipital pole	-8	-92	14	4.11
R Lateral occipital cortex	24	-82	28	3.69
L Superior lateral occipital cortex	-20	-76	44	3.13
View Portrait EA > AA				
R Inferior frontal gyrus, pars opercularis	52	14	26	3.75
R Frontal pole	54	38	8	3.64
L Frontal orbital cortex	-28	26	-6	3.63
R Precentral gyrus	46	0	56	3.62
R Paracingulate gyrus	8	14	44	3.46
L Superior frontal gyrus	-14	4	72	3.43
L Middle frontal gyrus	-36	10	36	3.34

L Posterior cingulate gyrus	-10	-50	28	3.65
R Parietal operculum cortex	58	-28	24	3.35
R Temporal occipital fusiform cortex	36	-42	-24	3.68
R Temporal pole	52	20	-16	3.48
L Occipital pole	-10	-94	4	4.52
R Cuneal cortex	10	-80	-32	3.96
L Superior lateral occipital cortex	-12	-82	40	3.71
R Inferior lateral occipital cortex	62	-62	0	3.28
R Superior lateral occipital cortex	38	-84	32	3.04
R Thalamus	10	-10	2	3.27
L Putamen	-28	-20	2	2.96
L Cerebellum	-20	-62	-46	3.09

View Portrait CH > AA

Paracingulate gyrus	0	40	-8	3.47
L Precuneus	-2	-54	14	3.12
R Caudate	8	6	0	3.77
L Caudate	-14	0	20	2.51

View Portrait AA > CH

R Occipital pole	24	-96	24	4.45

L Occipital pole	-12	-98	26	4.15

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.

Table 4.4. Anatomical regions differentiating between races during gesture observation

Anatomical Regions	x	y	z	Z
Observe Gesture EA > CH				
Temporal occipital fusiform cortex	32	-44	-12	3.60
Occipital fusiform gyrus	24	-76	-6	4.22
Occipital pole	-20	-98	-4	3.49
Superior lateral occipital cortex	42	-64	20	3.36
Cerebellum	-10	-90	-32	3.25
Observe Gesture AA >CH				
Occipital fusiform gyrus	28	-74	-12	4.32
Occiptial pole	26	-88	34	4.09
Occipital fusiform gyrus	-28	-72	-6	3.98
Cuneal cortex	-4	-84	42	3.49
Lingual gyrus	22	-44	-10	3.24
Occipital pole	2	-94	14	3.19
Inferior lateral occipital cortex	52	-74	12	2.80

Note: See Table S1 for notes concerning table organization and assignment of anatomical labels.

CHAPTER 5

Imitation alters the neural encoding of race: self-similarity versus social status

ABSTRACT

People preferentially imitate others who are similar to them or have high social status. Such imitative biases are thought to have evolved because they increase the efficiency of cultural acquisition. Here we investigated whether self-similarity or social status drives neural responses to a person's race during imitation. We used fMRI to measure neural responses when 20 African American (AA) and 20 European American (EA) young adults imitated AA, EA and Chinese American (CA) models and also passively observed their gestures and faces. We found that both AA and EA participants exhibited more activity in lateral fronto-parietal and visual regions when imitating AAs compared to EAs or CAs. These results demonstrate that racial self-similarity does not modulate neural responses to race during imitation, in contrast with findings from previous neuroimaging studies of face perception and action observation. Furthermore, AA and EA participants associated AAs with lower social status than EAs or CAs, suggesting that race-associated status modulates neural activity during imitation. Finally, the fusiform gyrus was differentially modulated by race during imitation (consistent with social status) as compared to face and action observation (consistent with self-similarity), indicating that neural responses to race in the fusiform gyrus are task-dependent. Taken together, these findings suggest that neural responses to race during imitation are driven by socially-learned associations rather than self-similarity. This may reflect the adaptive role of imitation in social learning, where learning from higher-status models may be more beneficial. This study provides neural evidence in support of evolutionary theories of cultural acquisition.

INTRODUCTION

People preferentially imitate others whom they perceive to be similar to themselves or high in status. These imitative biases are thought to increase the efficiency of cultural learning (Boyd and Richerson, 1987). A person's race can indicate his or her self-similarity and social status (Van den Berghe, 1987) and is known to influence whom people imitate. Preferences for own-race models (Feinman, 1980; Karunanayake and Nauta, 2004; Kelly et al., 2005; King and Multon, 1996; Zirkel, 2002) and higher-status-race models (Clark and Clark, 1947; Liebert et al., 1972; Neely et al., 1973; Thelen, 1971) are well documented. Surprisingly, however, the vast majority of studies on the neural mechanisms of imitation have not considered the race of the person being imitated (the model) (Caspers et al., 2010). Most prior studies on neural responses to race during face perception and action observation have drawn distinctions between ingroup and outgroup to frame the interpretation of their findings (for reviews see Eberhardt (2005) and Ito and Bartholow (2009)), suggesting that the neural encoding of another person's race may be based primarily on shared racial group membership. Here we investigated whether neural responses to the model's race during imitation are also modulated by shared racial group membership (similarity hypothesis), or are instead modulated by the social status associated with different racial groups (status hypothesis), as suggested by status biases in imitative learning.

Previously (Losin et al., 2012), we used fMRI to measure neural activity while European American (EA) participants imitated EA, African American (AA) and Chinese American (CA) models. Participants exhibited more activity in lateral fronto-parietal and visual regions when imitating AA compared to EA models. Activity did not follow the same pattern, however, when participants imitated members of the other racial outgroup (CA) compared to their ingroup (EA). Therefore, it was unclear whether more activity during imitation of AAs was due to their

membership in a racial outgroup, consistent with the similarity hypothesis, or the fact that AAs are typically perceived to be lower in social status than EAs or CAs (Fiske et al., 1999; Fiske et al., 2002), consistent with the status hypothesis.

To disentangle these two possibilities, here we collected data in a sample of AA participants performing the same tasks and directly compared the results to those previously observed in our sample of EA participants. This comparison allowed us to clearly distinguish between the similarity and status hypotheses. This is because although AAs are the racial group in our stimuli typically perceived to be the lowest in status by both EAs and AAs, the AA models were a racial ingroup to one group of participants (AAs) and a racial outgroup to the other (EAs). Furthermore, we compared race effects during imitation to those during face perception and action observation. This comparison allowed us to determine whether the *same* neural regions previously found to exhibit racial similarity effects when people passively view the faces and actions of others are instead modulated by race-associated status during imitation, or alternatively whether racial similarity and race-associated status are simply encoded by *different* neural regions.

METHODS

Participants

Participants were 20 (10 male) right-handed, 18-30 year old African Americans (AAs). We compare these participants to a prior sample of 20 (10 male) right-handed, 18-26 year old European American (EA) participants whose data were previously reported in (Losin et al., 2012). The two racial groups were matched in age, handedness (Edinburgh Handedness Inventory, (Oldfield, 1971)) and socioeconomic status (participant's self-reported jobs were

converted to a numerical score using the nine job categories in the Barratt Simplified Measure

of Social Status (Barratt, 2005) and added to their years of education). See Table 5.1 for group

demographic means and between-group comparisons. Participants were recruited through free

online bulletins (e.g., Craigslist), university (UCLA) e-mail lists, and local newspapers.

Participants 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. Participants were compensated for their participation

and written informed consent was obtained from all participants.

Hand Sign Imitation Paradigm

The same fMRI task used with EA participants in (Losin et al., 2012) was also used with

the AA participants in the present study. Stimuli in this task were waist-up color videos of 12

models (6 male), of 3 different ethnicities (EA, AA, and Chinese American (CA)). Group

differences will be discussed in terms of 'race' because this is the construct most likely

perceived by participants based on visual information alone. Models performed 16 bimanual,

symmetrical hand signs derived from New Zealand Sign Language that were described as

meaningless to both models and participants. Stimuli were presented in the following four

conditions: 1) *imitate gesture*, in which participants imitated the models performing the hand

signs during the video presentation; 2) *observe gesture*, in which participants passively

observed the models performing hand signs; 3) *view portrait*, in which participants passively

viewed still portraits of each model; and 4) *baseline*, in which participants fixated on a black

cross in the center of a white screen (Figure 5.1a). Participants were cued to either imitate or

passively observe the stimuli by a colored border (green for imitation, red for passive observation).

Four stimuli of the same condition and portraying the same model were presented in a block (Figure 5.1b). An instruction screen that was either green with the word "imitate" or red with the word "observe" preceded all blocks. Stimulus blocks were organized into four balanced runs, such that each model, each hand sign, and each condition were seen an equal number of times in each run. Five 22.5-second baseline blocks were evenly spaced throughout each run. Over the course of the experiment, each participant saw 64 stimuli (16 blocks) portraying models from each of the three racial groups in each of the three conditions. The presentation order of these blocks was pseudorandomized within a run, ensuring fewer than two models of the same gender in a row, no two models of the same race in a row, and no two of the same hand sign in a row. A unique pseudorandomized stimulus order was created for each participant. Total task time was 55 minutes (13:45 / run). 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.

Self-report and Behavioral Measures

In order to assess whether participants from both racial groups perceived the stimuli and performed the imitation task in a similar way, we collected participants' ratings of the attractiveness of the models and also assessed the accuracy of their imitation while in the scanner. Measures of model attractiveness were collected immediately following the scanning session. Participants viewed the still portraits of each stimuli model on a laptop in the order they first appeared in the scanner. They were asked to "rate how attractive each person is". Ratings

were made on a visual analogue scale depicted under each portrait that ranged from 1 "very unattractive" to 9 "very attractive", with "average" as the scale mid-point. An average of the attractiveness ratings for the 4 models from each racial group for each participant was entered into a linear mixed effects model (lme) in R (R Development Core Team, 2010) in which participant race and model race were fixed factors and participant was a random factor.

Task compliance and hand sign imitation accuracy was assessed during fMRI data acquisition by watching the participants' hands through the control room window. During the gesture imitation blocks, hand sign imitation accuracy was assessed for 16/20 EA participants and 20/20 AA participants (for the remaining four EA participants the performance of imitation was still verified, just not rated). Each sign was assigned a rating of 2 if the sign was imitated correctly, a rating of 1 if the sign was imitated but with errors, and a rating of 0 if the sign was not imitated. Imitation accuracy was compared between groups for the percentage of hand signs receiving each accuracy rating in each participant (averaged across four runs) using two-tailed independent-samples T-tests.

We also collected self-report measures on the two behavioral factors of interest: participant's feelings of similarity to the models from each racial group and the social status they associated with each racial group represented in the stimuli. We collected these measures in order to verify whether both groups of participants felt more similar to own-race models (Bandura, 1977; Tarr and Gauthier, 2000; Karunanayake and Nauta, 2004) but rated AAs as lower status than EAs and CAs regardless of their own race (Dunham et al., 2006; Wong et al., 1998), as predicted based on the literature. Participants' feeling of similarity to the stimuli models were assessed using the same procedure used to assess their perception of model attractiveness. While viewing portraits of each model, each participant was asked to "rate how similar you feel each person is to you" on a scale from 1 "very dissimilar to me" to 9 "very similar to me". The similarity scores for the 4 models from each racial group were then averaged to

create a similarity score for each racial group of models, which was used in subsequent analyses.

Social status is a multi-dimensional construct including both subjective and objective components (Adler et al., 2000; Henrich and Gil-White, 2001). We did not have an *a priori* hypothesis as to whether objective or subjective social status would most closely relate to racial modulation of neural activity during imitation. Therefore, we measured both the objective and subjective social status that participants associated with the different racial groups in the fMRI task. We used the Barratt Simplified Measure of Social Status (BSMSS) (Barratt, 2005) and the MacArthur Scale of Subjective Social Status (MSSSS) (Adler et al., 2000), both of which we modified to apply to the different racial groups represented in the stimuli (rather than to the self). For both measures we used the terms White, Black and Asian rather than European American, African American and Chinese American, as these broad racial categories were those most likely perceived by participants during the fMRI task based on visual information alone.

The BSMSS (Barratt, 2005) is a version of the widely-used Hollingshead Four Factor Index of Social Status (Hollingshead, 1975) with updated job categories. For this measure, participants were asked to choose which level of education and which type of job they most closely associated with the different United States racial groups represented in the stimuli. Participants were given seven choices for education ranging from 1 "less than 7th grade" to 7 "graduate degree" and nine groups of occupations ranging from 1, a group that included day laborers and house cleaners, to 9, a group that included physicians and attorneys. Participants' choices on these two measures were multiplied by the factor weight of 3 for occupation and 5 for education and then summed to get a composite objective SES score that ranged from 8 to 66. The Hollingshead Four Factor Index of Social Status has been found to have substantial inter-rater reliability with a Cohen's kappa value of 0.68.

In the MSSSS (Adler et al., 2000), participants were shown a picture of a ladder with ten rungs and instructed to "think of the ladder as representing where different groups stand in the United States." They were told that "at the top of the ladder are the groups that are the best off - those who have the most money, the most education and the most respected jobs" and that "at the bottom are the groups that are the worst off - who have the least money, least education, and the least respected jobs or no jobs." They were asked to select the ladder with the red arrow pointing to the rung where they thought each racial group represented in the study (AA, EA and CA) stands relative to other racial groups in the United States. The MSSSS has been found to predict outcomes such as psychosocial and health measures above and beyond objective measures of SES (Cundiff et al., 2011). Thus, the MSSSS likely captures important aspects of social status not accounted for by the BSMSS. The MSSSS has also been found to have adequate test-retest reliability (Spearman's rank correlation) $\rho = 0.62$ ($p < 0.01$) (Operario et al., 2004).

Social status measures were collected from 15 EA and 14 AA participants through an online survey subsequent to the fMRI data collection. In order to test for the predicted patterns of racial self-similarity and status, we entered individual participant scores on these measures as the dependant variables in separate linear mixed effects models (lme) in R (R Development Core Team, 2010). For these analyses, subject race and model race were fixed factors and participant was a random factor. We performed post-hoc pair-wise comparisons to assess any interactions using Tukey's Honestly Significant Difference (HSD) test.

MRI Data Acquisition

Data were collected using a 3 Tesla 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 (3x3x4 mm voxels, TR: 2250 ms, TE: 28 ms, slices: 34, flip angle: 90 degrees, FoV read: 192 mm, echo spacing: 47 ms, bandwidth: 2442 Hz/Px, time: 13:45); 2) one co-planar high resolution T2-weighted structural scan (1.5x1.5x4mm voxels, TR: 5000ms, TE: 34ms, slices: 34, flip angle: 90 degrees, FOV Read: 192 mm, echo spacing: .89 ms, bandwidth: 1302 Hz/Px, time: 1:30); and 3) one high resolution T1-weighted magnetization-prepared rapid gradient echo (MPRAGE) structural scan (1x1x1 mm voxels, TR: 1900 ms, TE: 2.26 ms, Flip angle: 90 degrees, TI: 900 ms, FoV Read: 250 mm, echo spacing 6.9 ms, bandwidth: 200 hz/px, time: 6:50).

MRI Data Analysis

Data analyses were performed using FSL version 4.1.6 (Centre for Functional Magnetic Resonance Imaging of the Brain software library, www.fMRIb.ox.ac.uk/fsl) (Smith et al., 2004), AFNI (Cox, 1996) and the Automatic Registration Toolbox (ART, (Ardekani et al., 1995)). Functional data were preprocessed by skull-stripping (AFNI), realignment to the mean functional image (FSL's MCFLIRT), temporal filtering with a high-pass filter cutoff of 100s (FSL), and spatial smoothing with a 6mm full width half maximum Gaussian kernel in three dimensions (FSL).

Although head motion was low (~ 0.7 mm mean maximum relative displacement) and did not differ between groups (See Table 5.2 for group means and between-group comparison), several data quality control measures were implemented prior to statistical 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 that 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 and 6 out of 80 runs for EA and AA participants, respectively). From the EA group, we also previously removed one male participant (all 4 runs) 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 70 runs from 19 EA participants (10 female) and 74 runs from 20 AA participants being utilized in the present statistical analyses. Within these runs, less than 1.5 percent of 362 volumes per run were removed due to motion artifacts in each group and the groups did not differ in the number of volumes removed (See Table 5.2 for group means and between-group comparisons).

Statistical analyses were performed at the single subject level using a general linear model (GLM) with FSL's fMRI Expert Analysis Tool (FEAT). We examined neural activity related to the race of the model in the AA participants using the same statistical model previously applied to the EA participants (Losin et al., 2012). The time courses of blocks containing each racial group of models (EA, AA, CA), in each condition (imitate gesture, observe gesture, view portrait), were convolved with a canonical double-gamma hemodynamic response function and included as regressors in the GLM. The five 22.5-second rest blocks were used as the implicit baseline.

In order to investigate race effects in each condition, all possible pairwise contrasts of model racial groups were estimated for each condition (e.g., imitate gesture EA > imitate gesture AA) and each racial group of models was also compared to the fixation baseline for each condition (e.g. imitate gesture EA > baseline). Additionally, in order to determine whether race effects during gesture imitation differed from those during the non-imitative conditions, interaction contrasts were 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 $_{AA > EA}$).

First level contrast estimates were computed for each run and contrast estimates for each subject were computed by averaging over the four runs, treating each run as a fixed effect. For group analysis, contrast estimates were registered to standard space (Montreal Neurological Institute, MNI) in three stages. The mean volume of each run of individual EPI data was registered to the in-plane high-resolution T2-weighted image (3-parameter affine) and, in turn, to the T1-weighted MPRAGE (7-parameter affine) using FSL's FLIRT. Finally, registration of the MPRAGE to MNI space (FSL's MNI Avg152, T1 2x2x2mm) was carried out with FLIRT (12-parameter affine) and refined using ART (non-linear transformation). Group level analyses were then performed to calculate a group mean for each contrast for each racial group of subjects and between-racial-group differences using using FSL's FLAME stages 1 and 2. All analyses were performed across the whole-brain. Group images 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. Peak activation coordinates were determined using an automated search for relative maxima with a minimum separation of 15 mm. Coordinates with the highest Z value within an individual anatomical region (determined using the FSL Harvard-Oxford probabilistic atlases) are reported in tables.

RESULTS

Behavioral and Self-Report Measures

We first assessed whether any between-group differences existed in participants'

perceptions of actor attractiveness or imitation accuracy in order to rule out these possible

confounds to interpretation of the race effects of interest. Our analysis revealed that participants'

assessments of actor attractiveness did not vary based on the race of the model or their own

race, nor was there a significant interaction between these factors (all p > 0.05; Table 2). These

data suggest that both EA and AA participants perceived the attractiveness of models from the

three different racial groups as slightly above average (ratings ranging from 5-6 / 9). These data

additionally suggest that both EA and AA participants viewed the models they observed and

imitated in a similar way despite the participants' own different racial group membership. Thus, it

is highly unlikely that differences in perceived model attractiveness account for any observed

race effects. We also found that imitation accuracy was high in both groups (> 94% of signs

receiving the highest accuracy rating), and did not differ between groups (See Table 5.2 for

group means and between-group comparisons). Equivalent imitative performance indicates that

participants in both groups were able to perform the hand sign imitation task accurately and that

task performance is unlikely to confound the interpretation of any observed between-group

differences.

We next investigated participants' feelings of similarity to the different models and their

assessment of the social status typically associated with the different racial groups represented

in the stimuli. We did so in order to verify that participants' self reports on these measures

matched those previously reported in the literature on which our neural predictions for the

similarity and status hypotheses were based. Specifically, based on prior literature (Bandura,

1977; Tarr and Gauthier, 2000; Karunanayake and Nauta, 2004) we predicted that participants

would report feeling more similar to the models from their own racial group. Consistent with this

prediction, we found that participants' feelings of similarity to the models did vary based on

model race, $F(2, 74) = 12.53$, $p < 0.0001$, and that the effects of model race varied based on the

participant's own race (subject race x model race interaction) $F(2, 74) = 39.77$, $p < 0.0001$.

Pairwise comparisons (Tukey's HSD) revealed that, as predicted, this interaction resulted from participants feeling more similar to models from their own racial group than models from each of their two respective racial outgroups (EA and CA models for AA participants, and AA and CA models for EA participants) (Figure 5.2a).

We also made predictions about participants' assessment of the social status associated with the different racial groups of the models represented in the stimuli (White, Black and Asian) based on prior studies (Dunham et al., 2006; Fiske et al., 1999; Fiske et al., 2002; Freeman et al., 2011; Penner and Saperstein, 2008; Wong et al., 1998). We predicted that 1) participants would rate the status associated with each of these racial groups similarly, regardless of their own race (Dunham et al., 2006; Wong et al., 1998), and 2) participants would rate Blacks as being associated with lower status than either Whites (Freeman et al., 2011; Penner and Saperstein, 2008) or Asians (Fiske et al., 1999; Fiske et al., 2002) while the latter two groups would be rated as being similar in status (Wong et al., 1998). Consistent with our first prediction, we found no main effect of participants' race on their assessment of the subjective social status (SSS) or socioeconomic status (SES) associated with the different racial groups represented in the stimuli (all $p > 0.8$). Consistent with our second prediction, we found a significant effect of model race on perceived SSS $F(2, 54) = 80.84$, $p < 0.0001$, and SES $F(2, 54) = 94.01$, $p < 0.0001$ such that both groups of participants rated Blacks as being associated with lower SSS and SES than either Whites or Asians (Figure 5.2b-c).

Although status ratings for Whites and Asians were closer to one another than to those for Blacks, some significant differences between White and Asian status ratings were found. For the SSS measure, AA participants rated Whites as being associated with higher social status than Asians while EA participants' ratings of the status of Whites and Asians were not significantly different. This difference resulted in participant race x racial group interaction that

approached significance $F(2, 54) = 2.89$, $p = 0.06$. For the SES measure, AA participants rated the SES of Whites and Asians as equivalent while EA participants rated Asian SES as higher than White SES. This difference resulted in a participant race x racial group interaction for SES $F(2, 54) = 4.6$, $p = 0.02$. Despite these interactions due to inconsistencies in the assessment of the relative status of Whites compared to Asians, data from both status measures largely fit the predicted pattern of similar ratings of race-associated status regardless of the participant's race and higher status ratings for Whites and Asians than for Blacks. Taken together, these data suggest that our participants self reports of racial similarity and race-associated status were consistent with those reported in the literature supporting our neural predictions based on racial self-similarity and status.

Effects of Model Race During Imitation in AA Participants

We first examined which neural systems were modulated by the model's race during imitation in our AA participants. To do so we compared imitation of actors from the three different racial groups. Out of all possible pair-wise racial comparisons, significant differences were found during imitation of AA > EA, AA > CA and EA > CA models, the same three racial comparisons where differences were previously observed in our EA sample (Losin et al., 2012). Also similar to what we previously found for the EA participants, we found increased activity during imitation of AA models compared to either EA or CA models in an extended bilateral network of regions previously shown to be important for imitation by a recent, large meta-analysis (Caspers et al., 2010), including the inferior frontal gyrus and neighboring premotor cortex, the inferior and superior parietal lobules and visual regions including the fusiform gyrus and inferior and superior lateral occipital cortex (Figure 5.2a-b, blue and green activity). In contrast, there was an absence of neural differences between imitation of EA and CA models in lateral fronto-parietal regions. Instead, differences were observed mainly in primary and

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secondary visual regions (V1-V3) and the fusiform gyrus, with more activity present during

imitation of EA compared to CA models (Figure 5.2c, blue and green activity).

Effects of Model Race During Imitation in AA vs. EA Participants

In order to discriminate between the similarity and status hypotheses, we next

investigated whether the effects of the model's race on neural activity during imitation varied

based on the race of the imitator. We did so by directly comparing model race effects during

imitation between the AA participants to those previously observed in the EA participants. The

status hypothesis predicts that the effect of the model's race will be similar regardless of the

participants' own race as assessments of race-associated status are typically invariant of the

race of the assessor (Dunham et al., 2006; Wong et al., 1998), largely consistent with the status

ratings of our own participants. In contrast, the similarity hypothesis predicts a model race x

subject race interaction such that AA participants would exhibit more activity in response to

imitating one or both of their racial outgroups (EA or CA), just as had been the case for the EA

participants (Losin et al., 2012).

In support of the status hypothesis, we found that the effect of the model's race did not

differ between AA and EA participants for two out of the three racial comparisons exhibiting

these effects in each group (imitating AA vs CA models and imitating EA vs CA models).

Furthermore, we found only a single cluster exhibiting differential responses between AA and

EA participants for the third racial comparison, imitating AA vs EA models. This cluster was

located in the pre-supplementary motor area (pre-SMA) and extended into the anterior cingulate

cortex (ACC) (Figure 5.3d, Table 5.4). Plotting average parameter estimates extracted from this

cluster (for imitation of AA and EA models compared to baseline) revealed greater activity

during imitation of EA models for AA participants, and AA models for EA participants. In order to

gain further insight into neural responses to race within this region, we also extracted parameter estimates for imitation of CA models and compared them to those for the other two racial groups using 2-tailed paired T-tests (Figure 5.3d). Both groups of participants exhibited no difference between imitation of CA models and models form their own racial group and both groups also exhibited less activity during imitation of CA models and their other racial outgroup (EA models for AA participants and AA models for EA participants), suggesting effects of model race within the pre-SMA and ACC were not simply related to shared group membership.

We observed a substantial degree of overlap between the neural regions modulated by the race of the model during imitation in the AA and EA participants (green areas in Figure 5.3a-c), further strengthening support for the status hypothesis. For the imitate AA > EA and imitate AA > CA contrasts these regions included the fusiform gyrus and inferior and superior lateral occipital cortices, the inferior frontal gyrus and neighboring premotor cortex, and inferior and superior parietal lobules. For the imitate EA > CA contrast, these regions included visual regions V1-V2 and the fusiform gyrus. Taken together, these results revealed only a single between-group difference in model race effects during imitation and a high degree of overlap between AA and EA participants. Thus, the race of the model modulates neural activity during imitation largely independently of the imitator's own race arguing against the similarity hypothesis in favor of the status hypothesis.

Effects of Model Race During Imitation vs. the Non-imitative Conditions

We next sought to determine whether the *same* neural regions exhibiting effects consistent with the status hypothesis during imitation were exhibiting previously reported racial similarity effects when people passively view the faces and actions of others. Alternatively, it was possible that race-associated status simply modulated activity within *different* neural

regions during imitation than racial similarity did during passive face and action viewing. To address this question, we directly compared race effects across both groups during gesture imitation to those in the observe gesture and view portrait conditions (3-way participant race x model race x condition interactions). We confined our investigation to neural regions exhibiting effects consistent with the status hypothesis (i.e. those exhibiting overlapping race effects in the EA and AA participants during imitation) using a post-threshold mask (green regions in Figure 5.3a-c).

If the *same* neural regions exhibiting effects consistent with the status hypothesis during imitation were instead modulated by racial similarity during the non-imitative conditions, we predicted 3-way interactions in those regions. Specifically, we predicted that these 3-way interactions would result from the same region exhibiting more activity when 1) imitating AA compared to either EA or CA models and 2) when passively viewing the faces or actions of own-race compared to other-race models, as previously found. If race-associated status and racial similarity simply modulated neural activity in *different* neural regions during imitation and the non-imitative conditions, we also predicted 3-way interactions. In this case, however, we predicted interactions would result from those regions exhibiting status effects during imitation instead not being modulated by the race of the model during passive action and face viewing and vice versa.

In line with the first prediction, we found clusters of activity in the fusiform gyrus that exhibited significantly different responses to the race of the model during gesture imitation than during either gesture observation or portrait viewing for the AA vs EA contrast (Figure 5.3a-b). Parameter estimates revealed that both AA and EA participants exhibited more activity within the fusiform gyrus and lateral occipital cortex during imitation of AA vs EA models, consistent with the status hypothesis. However, during gesture observation and portrait viewing, the same region exhibited more activity in response to own-race compared to other-race models (Figure

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5.3a-b, red and blue bars, Table 5.4), consistent with prior studies on neural responses to race during these tasks (Eberhardt, 2005; Ito and Bartholow, 2009).

To further test the status hypothesis during imitation and the similarity hypothesis during the non-imitative conditions, we extracted parameters from the fusiform clusters exhibiting task-related differences to AA vs EA models for the third group of models, CAs. CA individuals are racial outgroup for both groups of participants and also a group considered to be higher in perceived status than AAs. Therefore, if racial similarity were driving the effects of model race on neural activity in the fusiform gyrus during passive action and face viewing, we expected to see less activity associated with CA individuals than participants' own racial group within these conditions. If the race of the model were influencing fusiform activity during imitation instead based on race-associated status we expected to see less activity associated with imitation of CA than AA models for both groups of participants, as CAs are considered to be higher in perceived status than AAs (Fiske et al., 1999; Fiske et al., 2002). Consistent with the status hypothesis during imitation, we found less activity during imitation of CA models relative to AA models in both groups of participants (Figure 4a-b green bars). Additionally, consistent with the similarity hypothesis during the non-imitative conditions, we found less activity during either observing the gestures or viewing the portraits of CA models than own-race models for both groups of participants, though this difference was only a nonsignificant trend for EA vs CA models in EA participants during portrait viewing. We also found a similar level of activity in response to the CA models as the other racial outgroup for each group of participants (EA models for AA participants and AA models for EA participants), in further support of the similarity hypotheses during passive face and action viewing (Figure 3a-b green bars).

Taken together, results from the 3-way interactions demonstrate that one of the neural regions exhibiting status effects during imitation, namely the fusiform gyrus, exhibits activity consistent with the similarity hypothesis instead during the non-imitative conditions across both

EA and AA participants and models from *three* racial groups. Thus, these data suggest that the fusiform gyrus is differentially modulated by the race of the model depending on the task.

DISCUSSION

Our results suggest that social status, rather than racial similarity, drives racial modulation of neural activity during imitation. In Losin (2011), we found that European American (EA) participants exhibited more activity in lateral fronto-parietal and visual regions when imitating African American (AA) compared to Chinese American (CA) or EA models. Because people preferentially imitate those from groups perceived to be high in status (Boyd and Richerson, 1987), and AAs are typically perceived to have lower social status than either EAs or CAs (Fiske et al., 1999; Fiske et al., 2002), we hypothesized that imitation of models from racial groups perceived to be lower in social status may require greater recruitment of imitation-related neural regions as a result of less familiarity with imitating these individuals in daily life (the status hypothesis) (Losin et al., 2012). This hypothesis was further supported by studies demonstrating that imitating unfamiliar actions is associated with greater neural activity in some of the same sensory-motor regions as were more active during imitation of AA models (Buccino et al., 2004; Vogt et al., 2007). Importantly, because AAs were also a racial outgroup for the EA participants, the alternative explanation of this effect relating to racial group membership (the similarity hypothesis) could not be ruled out.

In the present study, we found that the race of the person being imitated influenced neural activity in AAs in largely the same manner as it had in EAs. Both EAs and AAs exhibited more activity when imitating AA compared to EA or CA models in visual and lateral fronto-parietal regions. There was also a high degree of overlapping activity between AAs and EAs and only a single region exhibiting different responses between AAs and EAs when compared

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directly. Importantly, as predicted, both AA and EA participants also rated AAs as being associated with lower subjective social status and socioeconomic status than either EAs or CAs, regardless of their own race. Thus, our data are consistent with the hypothesis that imitation-related neural regions (Caspers et al., 2010) are recruited to a greater degree when people imitate individuals from groups they perceive to be lower in social status.

That the perceived social status of the model influences neural activity during imitation supports cultural learning theories from evolutionary psychology, which posit that people preferentially imitate high status individuals, both in terms of prestige (similar to subjective social status) and success (similar to objective social status) (Boyd and Richerson, 1987; Boyd and Richerson, 1985; Henrich and Gil-White, 2001; Henrich and McElreath, 2003; Laland, 2004). Such imitative biases are thought to have evolved because they automatically direct attention to the individuals most likely to exhibit high quality behaviors, thus increasing the efficiency with which these behaviors are learned and ultimately increasing the fitness of the imitator. Thus, our study provides neural data to support predictions made by theories regarding the evolution of human cultural capacities. Our findings are also consistent with 1) studies demonstrating that individuals from lower status racial groups (mostly AAs) may preferentially imitate models from higher status racial groups (usually EAs), rather than their own (Clark and Clark, 1947; Liebert et al., 1972; Neely et al., 1973; Thelen, 1971), 2) evidence of a tight link between the perceptions of race and perceptions of social status (Macrae and Bodenhausen, 2001; Tajfel, 1982; Penner and Saperstein, 2008; Freeman et al., 2011), and 3) studies demonstrating that another person's social status (not related to race) modulates neural activity in the lateral frontal and parietal cortices and the fusiform gyrus (Zink et al., 2008; Ly et al., 2011; Chiao et al., 2009).

Surprisingly, however, this is the first finding related to social status in either the literature on neural mechanisms of action imitation/observation, or the literature on racial (face)

perception. Although a few studies have investigated the effects of the race or ethnicity of the model during action observation, all of these studies have suggested that such effects were modulated by shared group membership (Désy and Théoret, 2007; Liew et al., 2010; Molnar-Szakacs et al., 2007). Similarly, among studies investigating the neural responses to faces of people from different racial groups, most studies drew distinctions between ingroup and outgroup to frame the interpretation of their findings (Eberhardt, 2005; Ito and Bartholow, 2009). One possible reason for the dearth of status-related findings in these literatures is the infrequency with which such studies include participants from more than one racial group, or models from more than two racial groups, both of which can help disambiguate group membership effects from others (Losin et al., 2010). An exception is a study by Lieberman and colleagues (2005), who found increased activity in the amygdala of both EA and AA participants in response to AA compared to EA faces, which they interpret as relating to negative associations with AAs. Though this interpretation has been debated (Phelps and LeDoux, 2005), we propose that inclusion of two racial groups of participants in studies on race-related neural mechanisms will reveal more race effects related to status, as in the present study, as well as other factors beside racial similarity.

The only neural region in our study that did not exhibit activity consistent with the status hypothesis during imitation was the pre-supplementary motor area (pre-SMA). Here EA participants showed heightened activity when imitating AA models whereas AA participants showed increased activity when imitating EA models, suggesting that activity in this region may be modulated by group membership (i.e., both EA and AA participants displaying higher responses to outgroup members). However, data from the additional outgroup used in the present study (CA) revealed that this interpretation is not accurate as both EA and AA participants' responses to CA models were similar to those observed for their respective ingroup. These findings generally caution against interpreting race effects in terms of ingroup

vs. outgroup biases in the absence of appropriate control conditions (i.e., more than one outgroup) and suggest that neural responses to race within the pre-SMA are likely affected by the interaction of several factors (e.g., self-similarity, social status, and majority/minority status).

We also found that the fusiform gyrus and neighboring lateral occipital cortex are differentially modulated by another person's race during imitation compared to passive viewing of the actions or faces of others. While these regions exhibited a pattern consistent with the status hypothesis during imitation, during passive viewing of faces and actions, the same regions were more responsive to racial ingroup than outgroup members, as previous studies reported (Eberhardt, 2005; Ito and Bartholow, 2009). Importantly, increased activity in response to ingroup relative to outgroup members was found across two racial outgroups of models in two racial groups of participants, providing more support than previous studies for increased activity in the fusiform gyrus in response to ingroup members when people passively observe other's faces and actions. More broadly, this finding demonstrates that neural regions encoding a person's race encode different racial associations based on the task performed, rather than exclusively encoding racial similarity, as suggested by previous studies on neural mechanisms of racial perception (Eberhardt, 2005; Ito and Bartholow, 2009). The exhibition of this contextual modulation by the fusiform gyrus suggests fusiform gyrus activity related to race is not exclusively related to this region's sensitivity to familiarity and expertise (Tarr and Gauthier, 2000). Effects of socially learned associations have previously been demonstrated within the fusiform gyrus (Singer et al., 2004), even in relation to social status (Chiao et al., 2009; Zink et al., 2008), albeit less frequently. Prior to the present study, however, such socially learned associations had not been demonstrated in the fusiform gyrus in relation to race.

An alternative explanation for the present findings during imitation is that different factors are driving increased activity in response to AAs in AA and EA individuals. A similar explanation was proposed by (Phelps and LeDoux, 2005), who suggested that the heightened amygdala

responses to AAs observed in Lieberman (2005) were driven by the motivational salience of AAs for the AA participants and negative associations with AAs for the EA participants. We think this type of explanation of our findings is unlikely for two reasons: 1) effects were seen in sensory-motor and association regions rather than exclusively in regions tied to motivational salience (e.g., the amygdala and ventral striatum), and 2) *both* groups exhibited ingroup effects during action observation and portrait viewing, making a two-factor account for the similar activity observed during imitation less likely.

In conclusion, our findings demonstrate that the race of the person being imitated modulates neural activity during imitation, independent of the imitator's own race. Furthermore, they suggest that social status, rather than racial similarity, is responsible for this racial modulation during imitation. In terms of the neural mechanisms underlying imitation, these findings suggest that complex socially-learned associations beyond mere similarity can be represented in lower- and higher-order sensory-motor systems. In terms of the neural responses to race, these findings suggest that the neural encoding of another person's race is flexibly modulated by specific task demands, rather than being based primarily on shared racial group membership. Finally, in terms of cultural learning, our findings provide the first neural evidence supporting evolutionary theories of imitation biases as adaptive mechanisms of cultural acquisition.

Figure 5.1. 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.
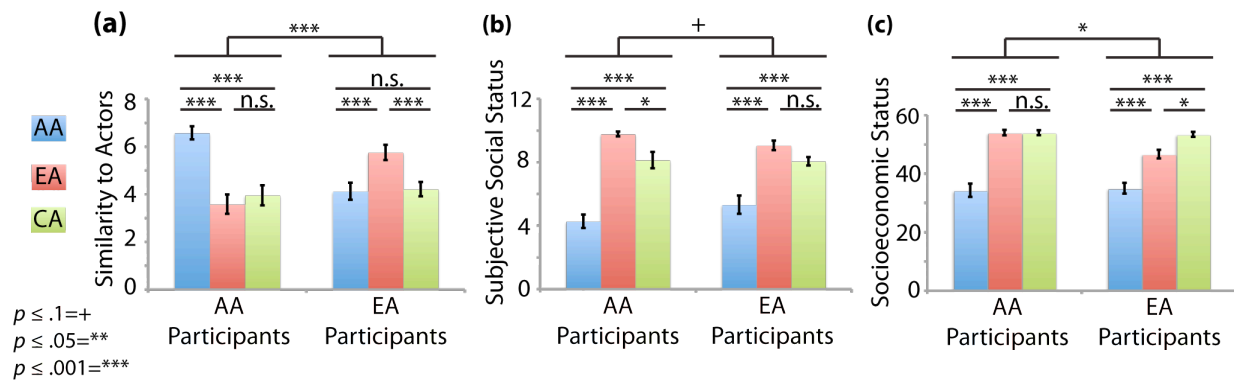
Figure 5.2. Results from self-report measures of racial self-similarity and race-associated social status in both AA and EA participants. (a) Participants' ratings of their feelings of similarity to stimuli models from the different racial groups (made while looking at model portraits) on a scale from 1 (very dissimilar to me) to 9 (very similar to me). (b) Participants' ratings of the socioeconomic status associated with each of the racial groups represented in the stimuli using the MacArthur Scale of Subjective Social Status (MSSSS) (Adler et al., 2000). (c) Participants' ratings of the socioeconomic status associated with each of the racial groups represented in the stimuli obtained using a modified version of the Barratt Simplified Measure of Social Status (BSMSS) (Barratt, 2005). Individual participant values for each measure were entered into a linear mixed effects model (lme) in R (Development Core Team, 2010) in which subject race and model race or racial group were fixed factors and participant was a random factor. Upper significance bar indicates a participant-race x model race or racial group interaction. Lower significance markers are the result of *post hoc* pairwise comparisons made using Tukey's Honestly Significant Difference (HSD) test. Error bars are standard error of the mean.
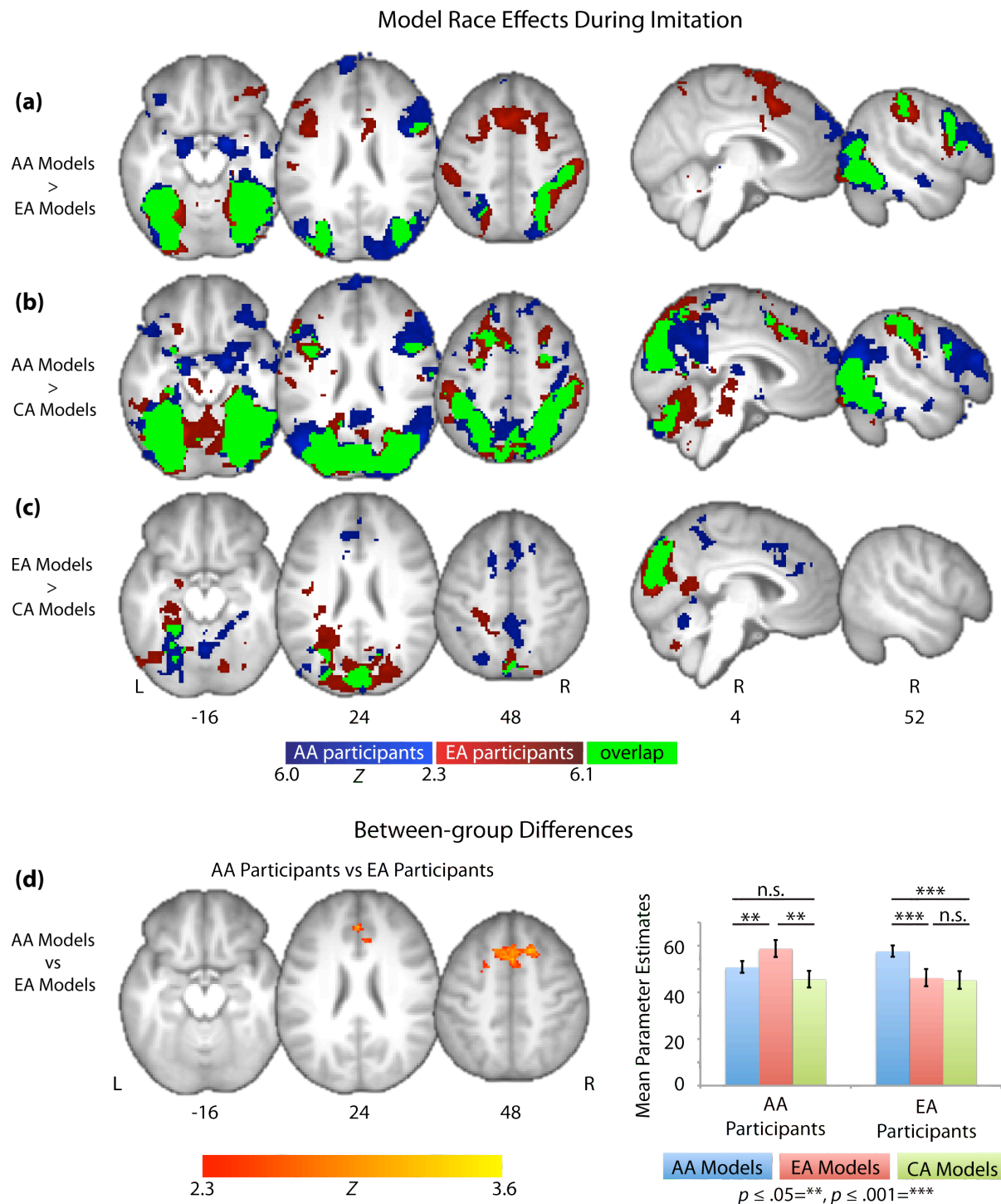
Figure 5.3. Comparison between neural regions differentiating between imitation of models from

three different racial groups: European American (EA), Chinese American (CA), and African

American (AA), in AA and EA participants. 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 an average T1 weighted structural scan across both groups of participants (n = 39).

Values under brains represent the MNI coordinate of the axial (z) or sagittal slice (x). L=left and

R=right side of the brain. (a-c) Whole-brain racial comparisons yielding significant differences

from all possible pairwise racial comparisons in AA participants (dark blue activity), EA

participants (dark red activity) and their overlap (green activity). (d) Results from the only

between-group comparison (i.e. participant race x model race interaction) that yielded a

significant difference during imitation. Parameter estimates are averaged across the entire

significant cluster from the four conditions contributing to the interaction compared to baseline

(red bars= EA models and blue bars = AA models). For comparison, parameters are also

extracted from the same region for imitation of the CA group compared to baseline (green bars).

Error bars represent within subject standard error of the mean, calculated with Cousineau's

adaptation of Loftus & Masson's method with Morey's correction (Cousineau, 2005; Loftus and

Masson, 1994; Morey, 2008).

(a) Model Race Effects During Gesture Imitation vs Gesture Observation

AA Participants vs EA Participants
AA Models vs EA Models

L -16   -2 R

2.3   *Z*   3.7

AA Models   EA Models   CA Models

$p \le .05 = *$, $p \le .01 = **$, $p \le .001 = ***$

(b) Model Race Effects During Gesture Imitation vs Portrait Viewing

AA Participants vs EA Participants
AA Models vs EA Models

L -16   -2 R
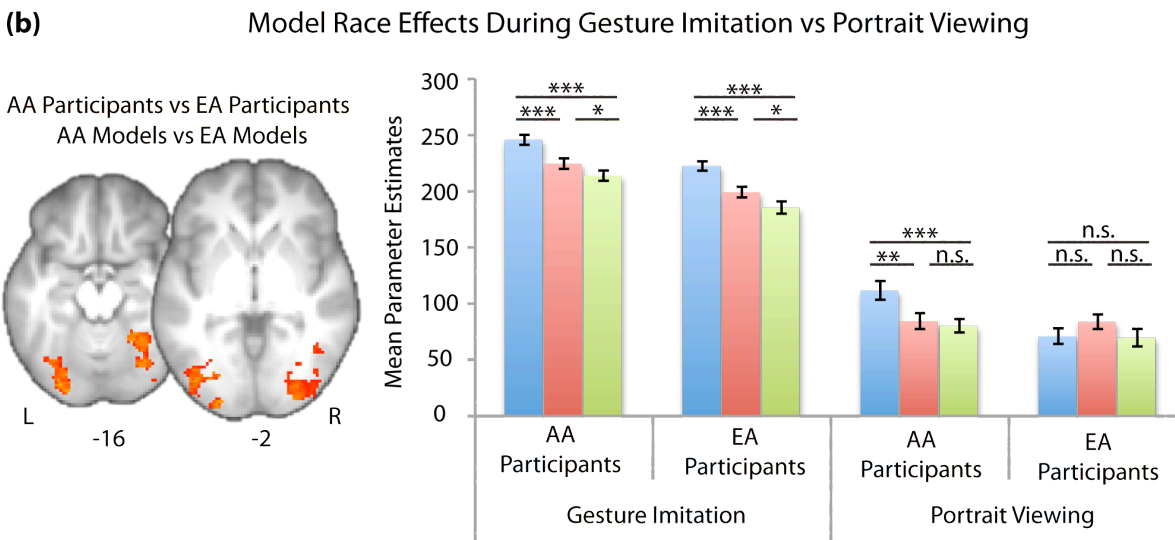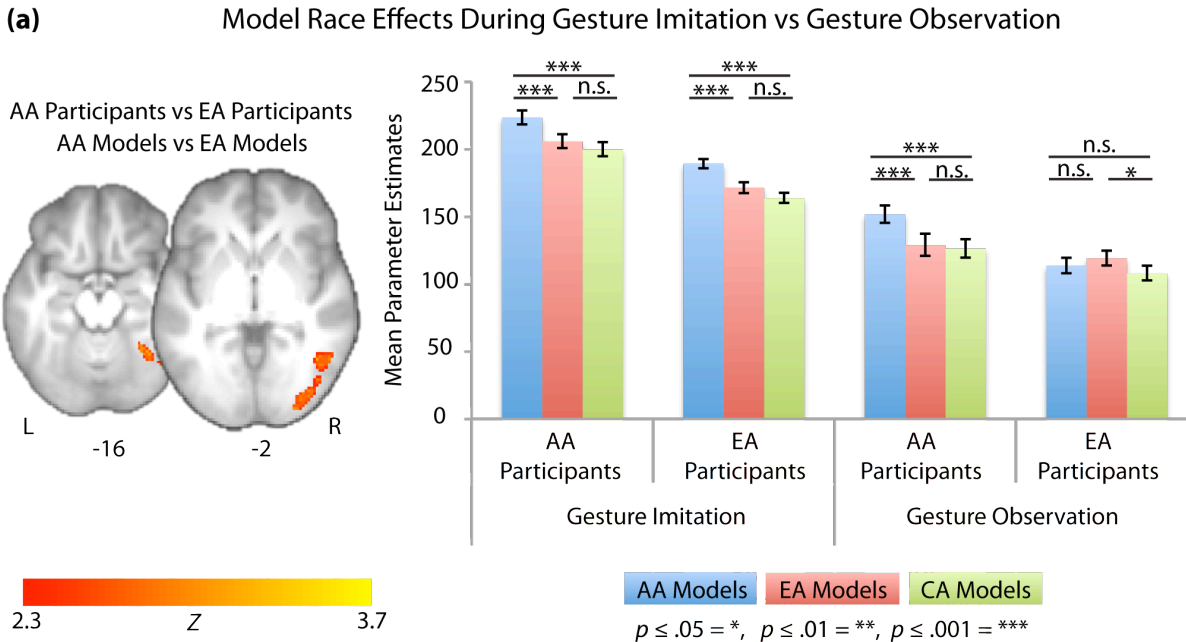
Figure 5.4. Regions exhibiting differential race effects (model race x participant race interactions) in the imitation condition compared to the non-imitative conditions (3-way interactions). Results are confined to those regions exhibiting effects consistent with the status hypothesis during imitation using a post-threshold mask of overlapping activity between EA and AA participants during imitation (green regions in Figure 5.3a). Bar graphs are of average parameter estimates from each condition contributing to the interaction compared to baseline

(red bars= EA models and blue bars = AA models). For comparison, parameters for the CA models (green bars) are also extracted from the same regions. Error bars represent within subject standard error of the mean, calculated with Cousineau's adaptation of Loftus & Masson's method with Morey's correction (Cousineau, 2005; Loftus and Masson, 1994; Morey, 2008). (a) Regions exhibiting differential race effects between gesture imitation and gesture observation. (b) Regions exhibiting differential race effects between gesture imitation and portrait viewing.

Table 5.1: Participant demographics by race

Measure	EA Mean	SD	AA Mean	SD	p
Age (years)	23.06	2.14	23.10	2.98	0.96
Handedness (1 = right, -1 = left)	0.69	0.18	0.69	0.26	0.98
Socioeconomic status	22.11	2.85	20.53	2.93	0.10

Note: Handedness scores are from the (Edinburgh Handedness Inventory, (Oldfield, 1971)). Socioeconomic status scores were calculated by converting participant's self-reported jobs to a numerical score using the nine job categories in the Barratt Simplified Measure of Social Status (Barratt, 2005) and adding them to their self-reported years of education. *P* values are the result of 2-tailed independent sample t-tests between the AA and EA participants.

Table 5.2: Participant task-related self-report and behavioral measures

Measure	EA Mean	SD	AA Mean	SD	p
Attractiveness EA models	5.58	1.01	5.21	1.09	0.93
Attractiveness AA models	5.5	0.92	6.06	1.42	0.67
Attractiveness CA models	5.59	1.01	5.58	1.56	1
Signs imitated correctly (%)	94.08	5.07	95.61	4.22	0.33
Signs imitated with errors (%)	5.81	5.13	4.14	4.19	0.29
Signs not imitated (%)	0.11	0.21	0.25	0.68	0.41
Mean relative displacement (mm)	0.08	0.04	0.07	0.04	0.59
Max. relative displacement (mm)	0.65	0.62	0.70	0.71	0.64
Motion excluded volumes	5.26	6.39	4.45	5.42	0.41

Note: Model attractiveness scores are participants' self-reported ratings of the attractiveness of each model (made while looking at a portrait of that model) averaged across the 4 models from each racial group. Attractiveness ratings were made on a scale from 1 (very unattractive to 9 (very attractive). Imitation accuracy scores are the percentage of hand signs receiving each accuracy rating (sign imitated correctly = 2, sign imitated with error = 1, and sign not imitated = 0). *P* values for attractiveness ratings reflect between-group comparisons performed using Tukey's Honestly Significant Difference (HSD) test after all attractiveness scores were entered into a linear mixed effects model (lme) in R (R Development Core Team, 2010) in which subject race and model race or racial group were fixed factors and participant was a random factor. All other *p* values come from 2-tailed independent sample t-tests between the AA and EA participants.

Table 5.3. Anatomical regions differentiating between model races during imitation for AA participants

Anatomical Region	side	x	y	z	Z
Imitate AA Models > Imitate EA Models					
Superior frontal gyrus	**L**	**-2**	**54**	**40**	**4.03**
Inferior Frontal Gyrus, po	**R**	**58**	**16**	**30**	**3.74**
Frontal Pole	**R**	**54**	**44**	**8**	**3.18**
Postcentral Gyrus	**R**	**48**	**-24**	**42**	**3.37**
Supramarginal Gyrus, ad	**L**	**-44**	**-38**	**42**	**3.35**
Temporal Occipital Fusiform	**R**	**36**	**-42**	**-20**	**4.60**
Temporal Pole	L	-42	24	-28	3.45
Middle Temporal Gyrus, pd	**R**	**68**	**-8**	**-16**	**3.43**
Middle Temporal Gyrus,to	R	64	-50	-8	3.06
Lateral Occipital Cortex, sd	**L**	**44**	**-80**	**18**	**4.69**
	R	**28**	**-60**	**42**	**4.00**
Lateral Occipital Cortex, id	L	-36	-66	-14	5.40
	R	38	-74	-12	5.74
Occipital Pole	L	-34	-94	0	4.53
	R	14	-88	34	3.46
Intracalcarine Cortex	R	14	-76	6	3.20
Amygdala	L	-20	-4	-20	3.80
	R	20	-6	-14	4.69
Parahippocampal Gyrus, pd	L	-16	-34	-4	3.17
Thalamus	R	16	-28	10	2.89
Imitate AA Models > Imitate CA Models					
Inferior Frontal Gyrus, po	**R**	**38**	**10**	**26**	**4.35**
Frontal Pole	**L**	**-2**	**64**	**24**	**3.76**
Precentral Gyrus	**L**	**-40**	**2**	**30**	**3.61**

	R	38	-2	54	3.50
Frontal Orbital Cortex	L	-28	36	2	2.90
	R	32	32	-18	3.55
Paracingulate Gyrus	L	-4	12	50	3.34
Middle Frontal Gyrus	L	-32	-4	62	3.16
Superior Frontal Gyrus	L	-18	38	44	3.12
Superior Parietal Lobule	L	-34	-54	56	4.34
Supramarginal Gyrus, pd	R	44	-36	50	4.08
Postcentral Gyrus	L	-40	-28	42	3.65
	R	62	-16	28	3.36
Angular Gyrus	R	56	-50	24	3.28
Amygdala	L	-16	-8	-14	4.30
	R	18	-6	-14	4.60
Inferior Temporal Gyrus, to	R	58	-54	-18	3.67
Middle Temporal Gyrus, ad	R	64	-6	-18	3.62
Temporal Pole	L	-38	20	-24	3.34
Occipital Fusiform Gyrus	R	36	-74	-10	6.06
Temporal Occipital Fusiform	L	-34	-62	-16	5.83
Lateral Occipital Cortex, sd	L	-28	-74	24	5.23
	R	32	-78	20	5.17
Occipital Pole	L	-32	-94	-4	4.38
Supracalcarine Cortex	L	-4	-86	10	3.72
Lingual Gyrus	R	18	-40	-4	3.43
Cerebellum	L	-6	-84	-42	3.61
	R	34	-74	-54	3.63
Cingulate Gyrus, pd	L	-4	-48	32	4.00
Precuneus Cortex	L	-2	-80	40	3.74

Imitate EA Models > CA Models

Superior Frontal Gyrus	L	-24	6	58	3.03
	R	12	16	70	3.37
Paracingulate Gyrus		0	46	26	3.25
Postcentral Gyrus	L	-6	-48	68	3.44
Cingulate Gyrus, pd	R	10	-38	42	3.19
Precuneus	**R**	**18**	**-68**	**42**	**2.51**
Cuneal Cortex	**R**	**8**	**-84**	**18**	**3.94**
Occipital Fusiform Gyrus	L	-28	-78	16	3.55
Lateral Occipital Cortex, sd	**L**	**-22**	**-70**	**52**	**3.52**
Temporal Occipital Fusiform	**L**	**-32**	**-54**	**-16**	**3.24**
Occipital Fusiform Gyrus	L	-18	-88	-14	3.09
Caudate	R	10	6	10	3.30
Cerebellum		**0**	**-62**	**-16**	**3.77**

Note: Bolded regions are those where a corresponding local maximum in the EA group fell in the same anatomical region. 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. po = pars opercularis, ad = anterior division, sd = superior division, id = inferior division, to = temporooccipital part.

Table 5.4. Between-group differences in anatomical regions differentiating between model races during imitation (2-way interactions) and their differences with the non-imitative conditions (3-way interactions)

Anatomical Region	side	x	y	z	Z
AA Participants vs EA Participants					
2-way Interaction					
Imitate AA Actors vs Imitate EA Actors					
Superior Frontal Gyrus	R	16	-8	60	3.62
Superior Frontal Gyrus	L	-24	6	62	3.22
Cingulate Gyrus, ad	L	-2	6	40	3.32
3-way Interactions					
Imitate AA Actors vs Imitate EA Actors					
Gesture Imitation > Gesture Observation					
Temporal Occipital Fusiform	R	34	-50	-10	3.54
Lateral Occipital Cortex, id	R	52	-62	14	3.14
Occipital Pole	R	30	-92	-4	3.11
Imitate AA Actors vs Imitate EA Actors					
Gesture Imitation > Portrait Viewing					
Occipital Fusiform Gyrus	L	-28	-74	-10	3.75
	R	28	-70	-4	3.25
Occipital Pole	L	-28	-96	14	2.94

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. id = inferior division.

REFERENCES

Adler NE, Epel ES, Castellazzo G, Ickovics JR (2000) Relationship of subjective and objective

    social status with psychological and physiological functioning: Preliminary data in

    healthy, White women. Health Psychology 19:586-592.

Ardekani BA, Braun M, Hutton BF, Kanno I, Iida H (1995) A fully automatic multimodality image

    registration algorithm. Journal of Computer Assisted Tomography 19:615-623.

Bandura A (1977) Social learning theory. New Jersey: Prentice-Hall.

Barratt W (2005) The Barratt simplified measure of social status (BSMSS): Measuring SES.

    Unpublished manuscript. Indiana State University, available at

    http://wbarratt.indstate.edu/socialclass/Barratt_Simplifed_Measure_of_Social_Status.pdf

Boyd R, Richerson PJ (1985) Culture and the evolutionary process. University of Chicago

    Press.

Boyd R, Richerson PJ (1987) The evolution of ethnic markers. Cultural Anthropology 2, 65-79.

Buccino G, Vogt S, Ritzl A, Fink GR, Zilles K, Freund HJ, Rizzolatti G (2004) Neural circuits

    underlying imitation learning of hand actions: an event-related fMRI study. Neuron

    42:323-334.

Caspers S, Zilles K, Laird AR, Eickhoff SB (2010) ALE meta-analysis of action observation and

    imitation in the human brain. Neuroimage 50:1148-1167.

Chiao JY, Harada T, Oby ER, Li Z, Parrish T, Bridge DJ (2009) Neural representations of social

    status hierarchy in human inferior parietal cortex. Neuropsychologia 47:354-363.

Clark KB, Clark MP (1947) Racial identification and preference in Negro children. Readings in
social psychology 169-178.

Cousineau D (2005) Confidence intervals in within-subject designs: A simpler solution to Loftus
and Masson's method. Tutorial in Quantitative Methods for Psychology 1:42-45.

Cox RW (1996) AFNI: software for analysis and visualization of functional magnetic resonance
neuroimages. Computers and Biomedical Research 29:162-173.

Cundiff JM, Smith TW, Uchino BN, Berg CA (2011) Subjective social status: Construct validity
and associations with psychosocial vulnerability and self-rated health. International
Journal of Behavioral Medicine 1-11.

R Development Core Team (2010) R: A language and environment for statistical computing. R
Foundation for Statistical Computing Vienna Austria.

Désy MC, Théoret H (2007) Modulation of motor cortex excitability by physical similarity with an
observed hand action. PLoS ONE 2:e971.

Dunham Y, Baron AS, Banaji MR (2006) From American city to Japanese village: a cross-
cultural investigation of implicit race attitudes. Child Development 77:1268-1281.

Eberhardt JL (2005) Imaging race. The American Psychologist 60:181-190.

Feinman S (1980) Infant response to race, size, proximity, and movement of strangers. Infant
Behavior and Development 3:187-204.

Fiske ST, Cuddy AJC, Glick P, Xu J (2002) A model of (often mixed) stereotype content:
Competence and warmth respectively follow from perceived status and competition.
Journal of Personality and Social Psychology 82:878-902.

Fiske ST, Xu J, Cuddy AC, Glick P (1999) (Dis) respecting versus (dis) liking: Status and
        interdependence predict ambivalent stereotypes of competence and warmth. Journal of
        Social Issues 55:473-489.

Freeman JB, Penner AM, Saperstein A, Scheutz M, Ambady N (2011) Looking the part: social
        status cues shape race perception. PLoS ONE 6:e25107.

Henrich J, Gil-White FJ (2001) The evolution of prestige - Freely conferred deference as a
        mechanism for enhancing the benefits of cultural transmission. Evolution and Human
        Behavior 22:165-196.

Henrich J, McElreath R (2003) The evolution of cultural evolution. Evolutionary Anthropology
        12:123-135.

Hollingshead AA (1975) Four factor index of social status. Unpublished Manuscript.

Ito TA, Bartholow BD (2009) The neural correlates of race. Trends in the Cognitive Sciences
        13:524-531.

Karunanayake D, Nauta MM (2004) The relationship between race and students' identified
        career role models and perceived role model Influence. Career Development Quarterly
        52: 225-234.

Kelly DJ, Quinn PC, Slater AM, Lee K, Gibson A, Smith M, Ge L, Pascalis O (2005) Three-
        month-olds, but not newborns, prefer own-race faces. Developmental Science 8:F31-
        F36.

King MM, Multon KD (1996) The effects of television role models on the career aspirations of
        African American junior high school students. Journal of Career Development 23:111-
        125.

Laland KN (2004) Social learning strategies. Learning & behavior 32:4-14.

Lieberman MD, Hariri A, Jarcho JM, Eisenberger NI, Bookheimer SY (2005) An fMRI
investigation of race-related amygdala activity in African-American and Caucasian-
American individuals. Nature Neuroscience 8:720-722.

Liebert RM, Sobol MP, Copemann CD (1972) Effects of vicarious consequences and race of
model upon imitative performance by black children. Developmental Psychology 6:453-
456.

Liew SL, Han S, Aziz-Zadeh L (2010) Familiarity modulates mirror neuron and mentalizing
regions during intention understanding. Human Brain Mapping 11:1986-1987.

Loftus GR, Masson MEJ (1994) Using confidence intervals in within-subject designs.
Psychonomic Bulletin & Review 1:476-490.

Losin EAR, Iacoboni M, Martin A, Cross KA, Dapretto M (2012) Race modulates neural activity
during imitation. Neuroimage 59:3594-3603

Losin EAR, Dapretto M, Iacoboni M (2010) Culture and neuroscience: additive or synergistic?
Social Cognitive and Affective Neurosceince 5:148-158.

Ly M, Haynes MR, Barter JW, Weinberger DR, Zink CF (2011) Subjective socioeconomic status
predicts human ventral striatal responses to social status information. Current Biology
21:794-797.

Macrae CN, Bodenhausen GV (2001) Social cognition: Categorical person perception. British
Journal of Psychology 92:239-255.

Molnar-Szakacs I, Wu AD, Robles FJ, Iacoboni M (2007) Do you see what I mean? Corticospinal excitability during observation of culture-specific gestures. PLoS ONE 2:e626.

Morey RD (2008) Confidence intervals from normalized data: A correction to Cousineau (2005). Tutorial in Quantitative Methods for Psychology 4:61-64.

Neely JJ, Hechel RV, Leichtman HM (1973) The effect of race of model and response consequences to the model on imitation in children. Journal of Social Psychology 89:225-231.

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97-113.

Operario D, Adler NE, Williams DR (2004) Subjective social status: reliability and predictive utility for global health. Psychology & Health 19:237-246.

Penner AM, Saperstein A (2008) How social status shapes race. Proceedings of the National Academy of Sciences 105:19628-19630.

Phelps EA, LeDoux JE (2005) Contributions of the amygdala to emotion processing: from animal models to human behavior. Neuron 48:175-187.

Singer T, Kiebel SJ, Winston JS, Dolan RJ, Frith CD (2004) Brain responses to the acquired moral status of faces. Neuron 41:653-662.

Smith SM, Jenkinson M, Woolrich MW, Beckmann CF, Behrens TE, Johansen-Berg H, Bannister PR, De Luca M, Drobnjak I, Flitney DE, Niazy RK, Saunders J, Vickers J, Zhang Y, De Stefano N, Brady JM, Matthews PM (2004) Advances in functional and

structural MR image analysis and implementation as FSL. Neuroimage 23 Suppl 1:S208-S219.

Tajfel H (1982) Social psychology of intergroup relations. Annual Review of Psychology 33:1-39.

Tarr MJ, Gauthier I (2000) FFA: a flexible fusiform area for subordinate-level visual processing automatized by expertise. Nature Neuroscience 3:764-770.

Thelen MH (1971) The effect of subject race, model race, and vicarious praise on vicarious learning. Child Development 42:972-977.

Van den Berghe PLB (1987) Ethnicity and Other Bases of Sociality. In: The Ethnic Phenomenon. Elsevere.

Vogt S, Buccino G, Wohlschläger AM, Canessa N, Shah NJ, Zilles K, Eickhoff SB, Freund HJ, Rizzolatti G, Fink GR (2007) Prefrontal involvement in imitation learning of hand actions: effects of practice and expertise. Neuroimage 37:1371-1383.

Wong P, Lai CF, Nagasawa R, Lin T (1998) Asian Americans as a model minority: Self-perceptions and perceptions by other racial groups. Sociological Perspectives 41:95-118.

Zink CF, Tong Y, Chen Q, Bassett DS, Stein JL, Meyer-Lindenberg A (2008) Know your place: neural processing of social hierarchy in humans. Neuron 58:273-283.

Zirkel S (2002) Is there a place for me? Role models and academic identity among White students and students of color. The Teachers College Record 104:357-376.

CHAPTER 6

Conclusions of the dissertation

Preferential imitation of certain individuals over others, i.e., imitative bias, is a critical component of cultural learning (Boyd & Richerson, 1985; Henrich & McElreath, 2003). Prior to the present studies, however, how these imitative biases were instantiated in the brain was unknown. In a first step towards answering this question, I used fMRI to measure neural responses to the race and gender of the person being imitated (the model). I found that the gender of the model was represented primarily in the reward system during imitation, with greater activity during imitation of own-gender compared to other-gender models. In contrast, I found that the race of the model modulated activity in a large bilateral network of neural regions previously found to be important for imitation including the putative human mirror neuron system, related sensorymotor regions, and primary and secondary visual cortices including the fusiform gyrus. All of these regions were more active when people imitated African American models compared to either European American or Chinese American models regardless of whether the participant's own race was African American or European American. Finally, I found that both the gender and race of the model were represented differently in the brain during imitation than when people passively observed others' actions or faces. These data provide the first insight into the neural mechanisms that underlie processes of cultural acquisition.

At the most basic level, these data demonstrate that *who* is being imitated rather than just what *actions* they are performing is being encoded by neural systems underlying imitation. Prior to the present studies, the vast majority of neuroimaging studies on imitation used stimuli in which only an isolated effector (e.g. a hand or a foot) was shown. Therefore, it was unclear whether the neural systems identified as playing a role in imitation (Caspers, Zilles, Laird, & Eickhoff, 2010) were only those involved in the basic sensorymotor aspects of imitation or also instantiated the more socially complex aspects of imitation, such as model-based imitative biases. Data from this dissertation suggest the latter. Furthermore, the effects of model gender and especially model race were large (of a high magnitude), and, in the case of model race,

affected virtually every node of the imitation network (Caspers et al., 2010). Thus, these findings suggest that imitative biases may be an integral part of imitative behavior at the neural level rather than a separate process governed by a separate neural system primarily implicated in social processing such as the default mode network (Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008). Furthermore, these findings highlight the importance of employing more ecologically valid stimuli in studies of imitation and either including or controlling for characteristics of the model including gender and race.

A second important finding across all three empirical studies was that gender and race modulate neural activity in a unique way during imitation, as compared to passive viewing of others' faces and actions. Imitation was the only condition in which the model's gender differentially influenced neural activity. Furthermore, the model's race was associated with different patterns of neural activity during imitation as compared to when people passively viewed the same models' actions or faces. These differing patterns of neural activity along with participants' self-report measures suggested that self-similarity was driving neural responses to race when people passively viewed faces and actions while social status was driving neural responses to race during imitation. Taken together, these findings demonstrate that there is no single mechanism through which the brain encodes another person's gender or race; rather, there is a range of neural systems that can respond flexibly to gender and race based on task demands.

A third conclusion that can be drawn from this suite of studies is that the brain responds differently to a model's gender compared to a model's race during imitation. This difference was manifested both in terms of the neural regions that encode gender versus race and the manner in which they do so. These findings refute the hypothesis that gender and race are two equivalent primary social dimensions by which people automatically and inflexibly categorize others as suggested by prior work (Brewer, 1988; Hamilton, Stroessner, & Driscoll, 1994;

Messick & Mackie, 1989). Instead, these findings are consistent with a more evolutionarily motivated theory put forth by Kurzban and colleagues (Kurzban, Tooby, & Cosmides, 2001). This theory suggests that gender and race are two fundamentally different types of social categories likely processed by different cognitive mechanisms. Although humans have been divided by gender throughout their evolutionary history, it is unlikely that ancestral hunter-gatherers encountered populations genetically distant enough from themselves to be viewed as different races (Kurzban et al., 2001). Therefore, Kurzban et al. (2001) suggest that it is reasonable to expect gender encoding may be associated with an evolved cognitive mechanism, and that because the reproductive implications of gender are constant, this mechanism may be relatively inflexible. In contrast, they suggest that race encoding may be subserved by cognitive mechanisms that evolved for another purpose – to flexibly associate physical appearance with different types of social relationships (coalitions). In line with this hypothesis, the reward circuitry that we found to encode gender during imitation is a relatively evolutionarily ancient system, whereas the cortical regions associated with imitation that we found to encode race are evolutionarily more recent. Furthermore, the neural encoding of gender appeared to relate to a single association, self-similarity, whereas racial encoding appeared to be flexibly modulated by different racial associations (self-similarity and social status), based on task demands.

A final conclusion suggested by these data is that a person's own gender and race influence how his or her brain processes others' gender and race during imitation. This notion is best supported by the differences in race processing between African American and European American participants during imitation. Both European American and African American participants exhibited more activity in lateral fronto-parietal and visual regions during imitation of African American models compared to either European American or Chinese American models. We have proposed that this difference arises from social status associations with race that are

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held by both African American and European American participants. The fact remains, however, that European Americans exhibited more activity in response to imitating models from a racial out-group versus in-group whereas African American participants exhibited more activity in response to imitating members of a racial in-group versus out-group. Thus, it is possible that the observed difference arises in part due to the participants' own cultural experience as members of a racial majority or minority group. This hypothesis could be tested by comparing the present results to those from individuals living in regions with a different demographic makeup (e.g., regions in which African Americans comprise the majority).

The present studies represent the first steps into a vast new domain of neuroscientific inquiry – the study of the neural mechanisms of cultural acquisition. Following are some of the questions left unanswered by the present studies and some future directions for research to address these questions.

First, although many behavioral measures thought to underlie differences in neural responses to gender and race were collected, none were found to relate directly to the neuroimaging findings. This lack of a relationship between behavioral and neuroimaging measures could be explained by a number of factors. It is possible that the observed neural differences are in fact *not* related to the behavioral constructs we linked them to (i.e., self-similarity for gender and social status for race). It is more likely, however, that the lack of significant relationships between neuroimaging and self-report measures may reflect the fact that perceptions of self-similarity and social status associated with gender and race function on a relatively implicit level, one that is not easily accessible through self-report. The potential for inaccurate self-reports is also increased by the sensitive nature of stating one's views about gender and race and the related self-presentational biases. For example, several studies on the neural correlates of racial processing have found brain-behavior correlations only with implicit race-related measures (e.g., the Implicit Association Test) rather than with explicit measures

such as self-reported racial preferences (e.g., Cunningham et al., 2004). Thus, we hypothesize that our fMRI results may to some degree reflect implicit gender and racial associations. This hypothesis could be tested in future studies by including more implicit measures related to self-similarity and social status.

A second limitation of the present studies is that it is unclear whether the differential encoding of gender and race we observed during imitation truly reflects the imitative preferences that are suggested by cultural learning theories and demonstrated in behavioral studies. This is because in our study design, participants were asked to explicitly imitate models, whereas much real world imitation and imitation learning occurs implicitly. Secondly, participants were required to imitate all models an equal number of times. To address the relationship between imitative biases and neural activity during imitation directly, future research could utilize a design in which participants are required to choose between different models or are presented with two models simultaneously with eyetracking being used to assess attentional biases. These measures of imitative preference could then be related directly to neural activity during imitation. Finding a relationship between the differential encoding of race and gender during imitation and imitative preferences related to race and gender would allow us to more directly link patterns of neural activity found in the present studies to the imitative biases important for cultural learning.

A third question left unanswered by the present studies is how the race and gender of the model impacts the learning and memory of imitated actions. Because in the current studies all models performed the same set of actions, distinguishing between the learning of different actions based on model gender and race was not possible. A difference in the *degree of learning* from different models is not predicted by cultural learning theories (only a difference in *model preference*). Whether model race and gender affects learning is, however, an obvious and interesting question and one that may link the present findings to potential clinical

applications. This question could be addressed by assigning a subset of modeled actions to male and female models of different races and comparing the quality of imitation and memory for actions performed by these models. Relating individual differences in learning or memory to neural differences related to race and gender during imitation would provide a direct link between the present findings and imitative learning. If such differences were found, they could inform behavioral modeling strategies (e.g., using own-gender models) in clinical fields such as stroke rehabilitation (Small, Buccino, & Solodkin, 2012).

In conclusion, the present studies have demonstrated that both the gender and the race of the person being imitated modulate neural activity during imitation, providing a first step in exploring the neural systems underlying imitative learning and, ultimately, cultural acquisition. Although the field of cultural neuroscience is growing rapidly, the focus has been almost entirely on how differential cultural experience shapes the brain. Understanding the mechanisms by which cultural information is initially acquired is arguably an even more fundamental question to be addressed. Thus, future studies of the kind contained in this dissertation will be necessary to fully understand the complex and bidirectional interactions between culture and the brain.

REFERENCES

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. University of Chicago Press.

Brewer, M. B. (1988). *A dual process model of impression formation*. Lawrence Erlbaum Associates, Inc.

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, *50*(3), 1148-67. doi:10.1016/j.neuroimage.2009.12.112

Cunningham, W. A., Johnson, M. K., Raye, C. L., Chris Gatenby, J., Gore, J. C., & Banaji, M. R. (2004). Separable neural components in the processing of Black and White faces. *Psychological Science: A Journal of the American Psychological Society*, *15*(12), 806-13. doi:10.1111/j.0956-7976.2004.00760.x

Hamilton, D. L., Stroessner, S. J., & Driscoll, D. M. (1994). Social cognition and the study of stereotyping. In *Social cognition: Impact on social psychology* (pp. 291-321). Academic Press.

Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology*, *12*(3), 123-135. doi:10.1002/evan.10110

Kurzban, R., Tooby, J., & Cosmides, L. (2001). Can race be erased? Coalitional computation and social categorization. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(26), 15387-92. doi:10.1073/pnas.251541498

Messick, D. M., & Mackie, D. M. (1989). Intergroup relations. *Annual Review of Psychology*, *40*(1), 45-81.

Schilbach, L., Eickhoff, S. B., Rotarska-Jagiela, A., Fink, G. R., & Vogeley, K. (2008). Minds at rest? Social cognition as the default mode of cognizing and its putative relationship to the "default system" of the brain. *Consciousness and Cognition, 17*(2), 457-467.

Small, S. L., Buccino, G., & Solodkin, A. (2012). The mirror neuron system and treatment of stroke. *Developmental Psychobiology*, *54*(3), 293-310. doi:10.1002/dev.20504