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Autistic Traits Modulate Mimicry of Social but not Nonsocial Rewards

Anthony Haffey, Clare Press, Garret O'Connell and Bhismadev Chakrabarti

Autism Spectrum Conditions (ASC) are associated with diminished responsiveness to social stimuli, and especially to social rewards such as smiles. Atypical responsiveness to social rewards, which reinforce socially appropriate behavior in children, can potentially lead to a cascade of deficits in social behavior. Individuals with ASC often show diminished spontaneous mimicry of social stimuli in a natural setting. In the general population, mimicry is modulated both by the reward value and the sociality of the stimulus (i.e., whether the stimulus is perceived to belong to a conspecific or an inanimate object). Since empathy and autistic traits are distributed continuously in the general population, this study aimed to test if and how these traits modulated automatic mimicry of rewarded social and nonsocial stimuli. High and low rewards were associated with human and robot hands using a conditioned learning paradigm. Thirty-six participants from the general population then completed a mimicry task involving performing a prespecified hand movement which was either compatible or incompatible with a hand movement presented to the participant. High autistic traits (measured using the Autism Spectrum Quotient, AQ) predicted lesser mimicry of high-reward than low-reward conditioned human hands, whereas trait empathy showed an opposite pattern of correlations. No such relations were observed for high-reward vs. low-reward conditioned robot hands. These results demonstrate how autistic traits and empathy modulate the effects of reward on mimicry of social compared to nonsocial stimuli. This evidence suggests a potential role for the reward system in underlying the atypical social behavior in individuals with ASC, who constitute the extreme end of the spectrum of autistic traits. *Autism Res* 2013, ••: ••–••. © 2013 International Society for Autism Research, Wiley Periodicals, Inc.

Keywords: reward; imitation; social; nonsocial; autism; empathy; mimicry

Introduction

Autism Spectrum Conditions (ASC) are a set of neurodevelopmental conditions marked by atypical social behavior and repetitive behavior/restricted range of interests. Autistic traits are distributed continuously in the general population, and individuals with ASC represent the high end of this distribution [Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001; Robinson et al., 2011]. Individuals with ASC show reduced interest toward social stimuli, which is thought to reflect reduced social motivation [Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012; Dawson et al., 2002]. At a neural level, individuals with autism show reduced activity in reward processing regions of the brain such as the ventral striatum when processing social rewards (e.g., happy faces) relative to controls from the general population [Scott-Van Zeeland, Dapretto, Ghahremani, Poldrack, & Bookheimer, 2010]. This diminished interest in socially rewarding stimuli could potentially cause a cascade of other developmental deficits as the social rewards (e.g., smiles) do not act as effective reinforcers for

shaping socially appropriate behavior. A series of behavioral, electrophysiological, and neuroimaging studies provide further support for atypical reward system functioning in ASC [Dawson et al., 2005; Kohls et al., 2011; Schmitz et al., 2008; Scott-Van Zeeland et al., 2010].

Mimicry is a crucial part of our social behavioral repertoire. We use the term “mimicry” in this paper to refer to motor acts in which an individual copies a motor act of another individual, regardless of the extent of cognitive/neural processing involved. “Automatic mimicry” refers to mimicry that operates without any intention to have produced such behavior [Heyes, 2011]. In some paradigms investigating this behavior, the tendency to mimic operates with or counter to an explicitly instructed movement [Bird, Leighton, Press, & Heyes, 2007; Press, Richardson, & Bird, 2010]. In such paradigms, participants are typically asked to execute a hand movement congruent or incongruent with an observed movement, and it is found that they are faster on congruent trials. The automaticity of mimicry is consistent both with theories that supporting mechanisms are innate [Ferrari & Gallese, 2007; Ferrari et al., 2006] and that they

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develop through domain-general processes of learning [Heyes, 2001]. If mimicry occurs in the absence of any specific task instruction to produce behavior of *any* type, it is referred to as “spontaneous mimicry.” Spontaneous mimicry is commonly studied in experiments where the participants are required to merely observe movements (commonly facial expressions) [Beall, Moody, McIntosh, Hepburn, & Reed, 2008; Sims, Van Reekum, Johnstone, & Chakrabarti, 2012].

Mimicry is associated with empathy, such that positive correlations have been found between spontaneous mimicry and levels of empathy [Hess, Philippot, & Blairy, 1999; Maringer, Krumhuber, Fischer, & Niedenthal, 2011; Sonnby-Borgström, 2002]. Furthermore, individuals with ASC have been found to exhibit lower trait empathy as well as reduced spontaneous mimicry of social stimuli [Chakrabarti & Baron-Cohen, 2006; Hermans, Putman, & Van Honk, 2006]. Interestingly, while individuals with ASC generally display comparable levels of automatic mimicry of face and body parts [e.g., hands; Bird et al., 2007; eyes/mouth; Press et al., 2010] they often show reduced spontaneous mimicry of social stimuli in more natural settings [Beall et al., 2008; Rogers, Hepburn, Stackhouse, & Wehner, 2003; Stel, van den Heuvel, & Smeets, 2008]. This raises the possibility that while the underlying machinery for mimicry maybe intact in autism, it is not brought online spontaneously in social situations. This may be because of the low reward value ascribed to social stimuli.

To test this possibility, we investigated the hypothesis that the response to rewarding social stimuli (i.e., stimuli that can reasonably be recognized as belonging to a conspecific) and their spontaneous mimicry are directly related. According to this hypothesis, valence (positive/negative) of social stimuli will not modulate mimicry in individuals with ASC in the way that it would influence neurotypical individuals [Likowski, Muehlberger, Seibt, Pauli, & Weyers, 2008; Sims et al., 2012; Stel et al., 2010].

This study investigated *individual differences* in how reward modulates mimicry of *social vs. nonsocial stimuli*, in the general population. *Individual differences* were measured using measures of autistic traits [Autism Quotient; Baron-Cohen et al., 2001], and empathy [Empathy Quotient; Baron-Cohen & Wheelwright, 2004]. Behavioral genetic studies suggest a similar etiology of autistic traits both in the general population as well as in its extreme end [Robinson et al., 2011]. This suggests that observed associations with the AQ in the general population are potentially generalizable to groups characterized by high AQ scores (such as individuals with ASC). For determining the impact of reward on *social vs. nonsocial* stimuli, human and robot hands were conditioned with high and low rewards, and then participants were tested on an automatic mimicry reaction time task as described in Bird et al. [2007]. This task has been associated with greater

automatic mimicry of human than robot hands in neurotypical individuals [Press, Bird, Flach, & Heyes, 2005] and comparable levels of automatic mimicry of human and robot hands in ASC compared to controls [Bird et al., 2007].

We predicted that trait empathy will be positively associated with the extent of automatic mimicry for rewarding human hands compared to non-rewarding human hands. In parallel, we predicted that autistic traits will be negatively correlated with the extent of automatic mimicry for rewarding human hands compared to non-rewarding human hands. No such association was expected for automatic mimicry of rewarding vs. non-rewarding robot hands. The robot hands were included as a control condition since there is no evidence to suggest a direct relationship between empathy/autistic traits and reward value for nonsocial objects.

Participants

Forty-seven participants aged between 18 and 40 were recruited, 11 of whom were excluded from the data leaving 36 participants (18 males, 18 females; mean age = years months, s.d. = years and months). Participants were excluded if they did not complete the experiment (two participants), or there were technical issues with the equipment (two participants), or if they had less than 75 valid trials in the motion task (see section on EMG Measurement for criteria; seven participants). All participants had normal or corrected to normal vision and were right handed. Participants completed the Autism Quotient (AQ) and Empathy Quotient (EQ) online (see Table 1). The study was approved by the University of Reading Research Ethics Committee.

Table 1. Distribution of the Scores of the $n = 36$ Participants (18 = males, 18 = females) in the Questionnaires

Trait	Mean	SD	Range
AQ	16.69	5.69	7–31
EQ	41.22	11.83	18–64

Stimuli

The human and robotic hands used in the conditioning and testing phase were silhouettes derived from previous research [Press et al., 2005]. All silhouettes were matched for image dimensions and luminescence. The human and robotic hands were each presented in two colors on a black background (one associated with high reward, and the other with low reward). During the conditioning phase, the hands were presented in the neutral position (see Fig. 1). In the test phase, motion was simulated by presenting the hand in the neutral position followed by

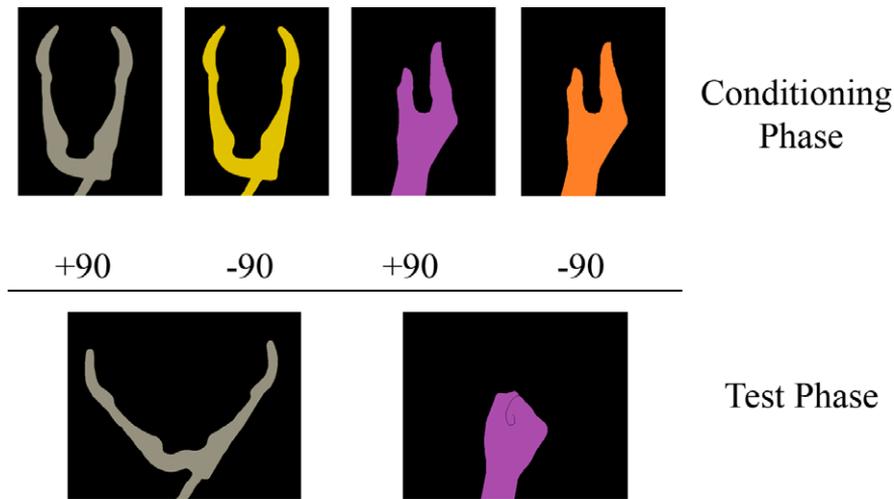


Figure 1. Images of the four different colored hands (neutral positions) that were implicitly conditioned with different reward values in the conditioning phase (90% win and 90% loss). This was followed by the test phase where participants observed opening and closing hand movements made by the four hands. Only the open robot hand and the closed human hands have been shown in this figure.

an image of the hand either open or closed (see Fig. 1). The original photos of the human and robot hands were used as the stimuli for the practice trials.

Eight emotionally neutral objects were taken from the International Affective Pictures System [IAPS; Lang, Bradley, & Cuthbert, 1999] to present during both parts of the tasks (see below) to serve as stimuli for a memory task that participants were ostensibly performing, and to ensure that participants were paying attention to the stimuli on the screen. These *distractor images* were rated as producing little arousal and consisted of unrelated objects. All stimuli were displayed using E-Prime 2.0 (Psychology Software Tools, PA, USA).

Procedure

After giving informed consent participants were briefed about completing the conditioning task and sat 50 cm away from a Viewsonic VE510s monitor (ViewSonic Corporation, California, USA). After completing the conditioning task, the electrodes were attached to the participants (see EMG Measurement for more detail). Participants were then briefed about how to complete the motion task. After completing the motion task, the electrodes were removed and the participants were debriefed.

Phase 1: Conditioning: During each trial a hand (in a neutral position, see Fig. 1) was presented on the right hand side of the screen while participants completed a card guessing game on the left hand side. A card between a 2 and 7 was presented on the screen face up, next to a face down card. Participants were required to guess whether the face-down card was higher or lower than the face-up card [Sims et al., 2012]. Each hand was presented 30 times. There were four *distractor images* also included

which participants were instructed to remember for a later task. Each distractor image was presented twice, contributing to a total of 128 trials. Participants won 90% of the trials against one human and one robot hand (“positive” hands), and lost 90% of the trials against the other human and robot hand (“negative” hands). The color of winning and losing hands was counterbalanced across participants. To make participants attend to the hands, they were instructed to look at the images at the side as part of a subsequent memory task.

Phase 2: Motion task: Participants were instructed to either open or close their right hand when presented with simulated motion of one of the robot or human hands opening or closing (see Fig. 1). This instruction “open” or “close” was presented for 1,000 ms before presenting the hand stimuli. The hand would then be presented in a neutral posture for 1,000 ms, followed by an opened or closed posture for 1,000 ms. Upon the presentation of this posture, the participant was required to complete the instructed motion. The instructed motion would either match that of the presented motion (“compatible” trials), or would conflict (“incompatible” trials). The response time (RT) from the onset of the image of the closed or open hand was recorded. Contrasts between compatible and incompatible motion RTs were used to calculate the extent of mimicry (see *Data Analysis* for more detail). There were 16 compatible and 16 incompatible trials for each of the four hand types. This resulted in 32 trials per hand and 128 trials in total. The order of trials was random for every participant. After the electrodes were attached, participants were instructed to rest their right arm on the table at an angle of 45 degrees away from them and the screen. This posture prevented the participants’ hand position matching that of the hand on the

screen; eliminating spatial compatibility between the participant's hand and the human or robot hand. They were instructed how to open and close their hands, and 10 practice trials were conducted to ensure the participants' open and close movements produced a clear electromyography (EMG) signal. At the end of the task participants were shown all eight *distractor images*, and asked to identify which images had already been presented in the conditioning task. All participants were 75% or more accurate in identifying the presence of novel distractor stimuli, suggesting they attended to the stimuli during the conditioning phase.

EMG Measurement

EMG activity was measured during the test phase using sensors placed over the first dorsal interosseous muscle. A ground electrode was placed on the central forehead. The raw signal was recorded by an ML-870 Power Lab (AD Instruments, Australia), and passed through a ML-138 Octal Bio amplifier (AD Instruments, Australia) with a gain of 10,000. The raw signal was sampled at 1 kHz, which was then digitally filtered with a band-pass filter of 20-500Hz. Baselines were calculated by recording standard deviation (SD) of the EMG activity for 100 ms before the onset of each motion image. A median baseline was calculated for every 32 consecutive trials. Response onset was defined as when the SD of the signal was a) at least 1.2 times the SD of a sliding 30s window, individually selected to most accurately detect response periods by eye, and b) when the SD of a 20-ms epoch was greater than 2.75 times the median baseline as calculated above [Press et al., 2005]. Trials were rejected if participants failed to produce activity greater than 2.75 times the standard deviation of the baseline. Trials in which the participant responded before 100ms or after 1000ms after the presented motion image were manually removed.

Data Analysis

Three sets of dependent variables were generated for testing correlations with the personality trait measures. First, to calculate the participants' tendency to mimic each hand, the average response time for the compatible hands was subtracted from the average response time of the incompatible hands, producing a measure of *hand mimicry*. This was done separately for human and robot hands. To test the impact of reward conditioning on this measure, *hand mimicry* of the negatively conditioned stimulus (e.g., the negative human hand mimicry) was subtracted from the *hand mimicry* of the positively conditioned stimulus (e.g., the positive human hand mimicry) to produce *conditioned mimicry*. This too was done separately for human and robot hands. Higher *conditioned mimicry* indicates a greater mimicry of positively than negatively conditioned hands.

All test statistics presented in the following section include two-tailed *P*-values.

Results

To measure whether an interaction between sociality and conditioning existed independently of the predicted effects of autistic traits and empathy, a 2 x 2 x 2 analysis of variance (ANOVA; Sociality x Conditioning x Compatibility) was run. This showed that there was no Sociality x Reward x Compatibility interaction ($F(1,35) = 0.215$, $P = 0.646$; see Table 2). However, when AQ was covaried out a significant Sociality x Reward x Compatibility interaction was observed ($F(1,34) = 5.201$, $P = 0.029$). Similarly, when EQ was covaried out of the ANOVA, a significant three-way interaction (Sociality x Reward x Compatibility) was observed ($F(1,34) = 4.544$, $P = 0.04$).

To explore the relationship of the trait measures with the interaction reported above, AQ and EQ were examined for their correlations with human and robot *conditioned mimicry*. AQ showed a significant negative correlation with human *conditioned mimicry* ($r(34) = -0.367$, $P = 0.028$; see Fig. 2) but not with robot *conditioned mimicry* ($r(34) = 0.266$, $P = 0.118$). To directly test the difference between these two dependent correlations, Steiger's *Z* was calculated [Steiger, 1980]. This showed a significant difference between the correlations (Steiger's $Z = 2.398$, $P = 0.017$; See Fig. 3).

The EQ showed a significant positive correlation with human *conditioned mimicry* ($r(34) = 0.477$, $P = 0.003$), but not with robot *conditioned mimicry* ($r(34) = -.072$, $P = 0.675$). Steiger's *Z* test showed that these two correlations were significantly different ($Z = 2.151$, $P = 0.032$; See Fig. 3).

No correlations were predicted or found between individual traits and *hand mimicry* for human (AQ: $r(34) = 0.158$, $P = 0.358$; EQ: $r(34) = 0.002$, $P = 0.992$) or robot hands (AQ: $r(34) = 0.273$, $P = 0.107$; EQ: $r(34) = -0.146$, $P = 0.394$) once collapsed across reward conditions.

Table 2. Mean Response Times to Each of the Conditions of the Study

Sociality	Mean RTs (ms)			
	Human		Robot	
Conditioning	Positive	Negative	Positive	Negative
Compatible	328.459	322.102	324.337	322.169
Incompatible	357.606	348.514	355.546	342.965
Incompatible-Compatible	29.147	26.412	31.209	20.796

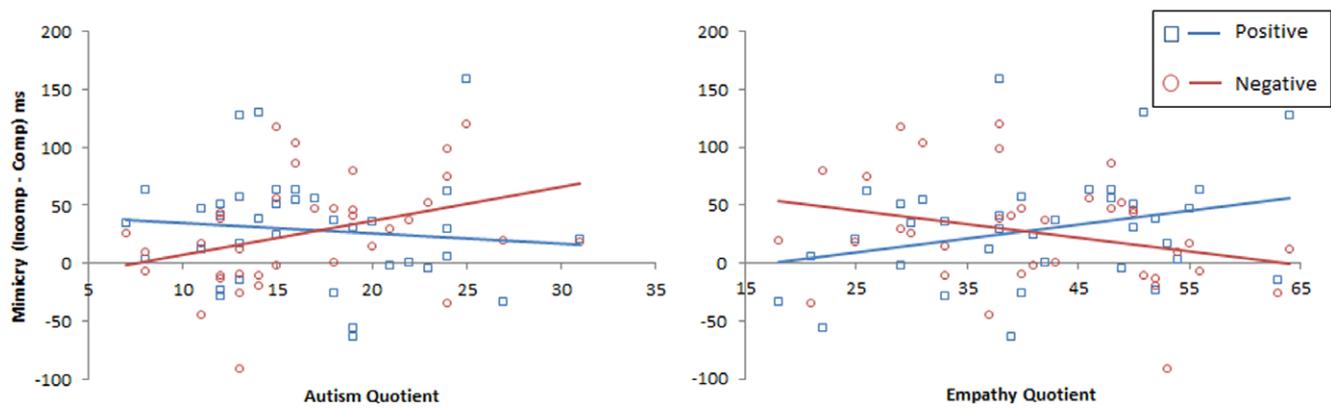


Figure 2. Scatter plots of mimicry of positively (blue lines) and negatively (red lines) conditioned human hands across participants' Autism Quotient and Empathy Quotient scores.

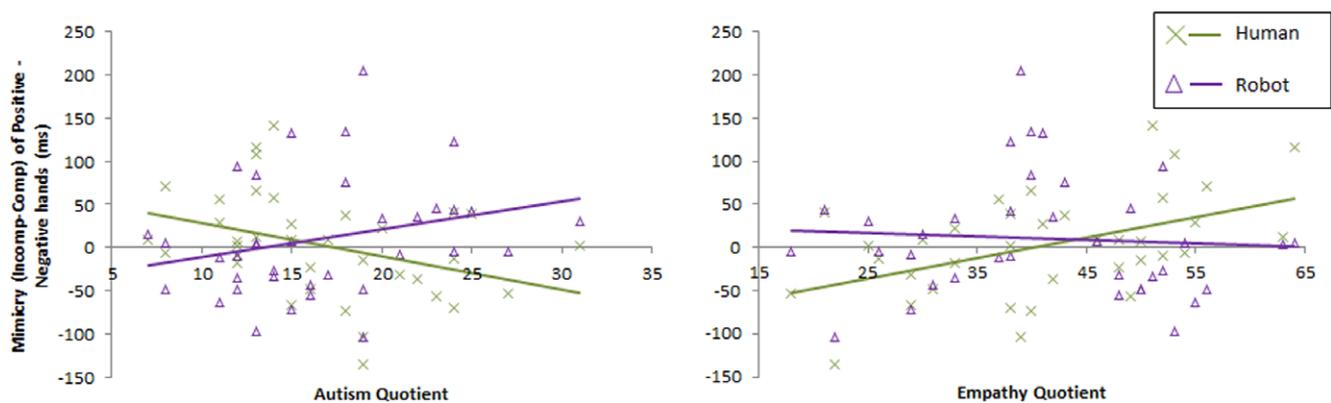


Figure 3. Scatter plots of mimicry of human *conditioned* (green lines) and robot *conditioned* (purple lines) hands across participants' Autism and Empathy Quotient scores.

Discussion

This study tested whether autistic traits and empathy were associated with mimicry of rewarding social stimuli (human hands). As a control condition, we measured the mimicry of rewarding nonsocial stimuli (robot hands). In support of our hypotheses, we found that low autistic traits and high empathy were associated with greater mimicry of social stimuli (human hands) associated with rewards. No such relationship was found between these trait measures and the mimicry of nonsocial stimuli (robot hands). This suggests that the extent of automatic mimicry of social stimuli associated with rewards is modulated by autistic traits. Using a very similar study design, Sims et al. [2012] have recently shown that individuals with high autistic traits (AQ) demonstrate lower spontaneous mimicry of more rewarding faces. Together, these results support and extend previous reports that show that autism and autistic traits are associated with the reduced spontaneous mimicry of social stimuli in unconstrained observation paradigms [Hermans et al.,

2006; Minio-Paluello, Baron-Cohen, Avenanti, Walsh, & Aglioti, 2009] by suggesting that it is due to the low reward value ascribed to social stimuli. In addition, AQ has been found to negatively predict performance in a mentalization task specifically for socially rewarding ("likeable") targets [Marsh et al., 2010].

Trait empathy predicted greater mimicry of human hands associated with high rewards compared to those associated with low rewards. As with the AQ, no significant association was observed between the EQ and the mimicry of conditioned robot hands. Questionnaire measures of empathy have previously been associated with spontaneous mimicry in multiple paradigms [Harrison, Morgan, & Critchley, 2010; Sonnby-Borgström, 2002; Stel et al., 2008]. Our results are consistent with these reports, and extend these further by suggesting that empathy modulates the impact of reward value on the spontaneous mimicry of social stimuli.

However, it is important to note that there was no significant relationship between autistic traits and mimicry of stimuli (when conditions are collapsed across

reward values); confirming that autistic traits are not associated with a fundamental deficit in the neural machinery for mimicry. This is consistent with recent behavioral and neuroimaging results which find no differences in automatic mimicry and operation of mirror mechanisms between individuals with ASC and typically developing controls [Bird et al., 2007; Dinstein et al., 2008; Press et al., 2010].

Together, these results further the view that social motivation plays a central role in automatic mimicry. Individuals with high empathy (and low autistic traits) may find the human hands more salient, and thus be more susceptible to reward value manipulations associated with those stimuli. This, in turn, could explain a greater automatic mimicry for rewarding human hands, alongside an absence of similar effects of robot hands. Conversely, those with lower empathy (and high autistic traits) may lack this interest in the human hands, and hence demonstrate a lack of the reward conditioning effect on mimicry. The lack of any correlations between empathy measures and mimicry of robot hands (positive and negative) further supports the idea that the social/nonsocial nature of the target object is paramount to investigate the determinants of automatic mimicry. Our results are compatible with the mirror system-based explanation of automatic imitation [Catmur, Walsh, & Heyes, 2009; Iacoboni, 2009]. There is evidence that mirror systems located in the ventral pre-motor cortex underlie automatic mimicry [Catmur et al., 2009], which would imply atypical modulation of the mirror system activity in response to rewarding social stimuli in individuals with high autistic traits (and low trait empathy). Based on these results as well as from Sims et al. [2012], we speculate that the mirror systems per se might be spared in autism, but that they may be atypically modulated by reward signals in response to social stimuli.

In summary, we have shown how autistic traits and empathy are associated with the extent of automatic mimicry of rewarding social stimuli. This relationship is specific to social stimuli, and did not hold true for non-social control stimuli used in our study. This finding fits well with the idea that atypical mimicry of social stimuli often seen in individuals with ASC may be related to a lack of social motivation. The inferences that we draw from these results are limited by the fact that none of the participants with high AQ had a clinical diagnosis. Future studies should test this paradigm in individuals with ASC. One potential avenue for future research is to test how these results based on automatic mimicry generalize to spontaneous mimicry, seen in real-life social interactions. Ongoing studies in our lab are testing the impact of these manipulations at a neural level, by measuring the activity of the brain involved in reward processing [e.g., ventral striatum, orbitofrontal cortex; Haber & Knutson, 2009] and mimicry [e.g., inferior parietal lobule, inferior frontal

gyrus; Keysers, Kaas, & Gazzola, 2010]. This study thus provides a bridge for two distinct sets of observation about atypical reward processing [Kohls et al., 2011; Scott-Van Zeeland et al., 2010] and socially inappropriate mimicry in ASC [Hobson & Hobson, 2008; McIntosh, Reichmann Decker, Winkielman, & Wilbarger, 2006].

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References

- Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: An investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *Journal of Autism and Developmental Disorders*, 34, 163–175.
- Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, 31, 5–17.
- Beall, P.M., Moody, E.J., McIntosh, D.N., Hepburn, S.L., & Reed, C.L. (2008). Rapid facial reactions to emotional facial expressions in typically developing children and children with autism spectrum disorder. *Journal of Experimental Child Psychology*, 101, 206–223.
- Bird, G., Leighton, J., Press, C., & Heyes, C. (2007). Intact automatic imitation of human and robot actions in autism spectrum disorders. *Proceedings of the Royal Society B: Biological Sciences*, 274, 3027–3031.
- Catmur, C., Walsh, V., & Heyes, C. (2009). Associative sequence learning: The role of experience in the development of imitation and the mirror system. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 2369–2380.
- Chakrabarti, B., & Baron-Cohen, S. (2006). Empathizing: Neurocognitive developmental mechanisms and individual differences. *Progress in Brain Research*, 156, 403–417.
- Chevallier, C., Kohls, G., Troiani, V., Brodtkin, E.S., & Schultz, R.T. (2012). The social motivation theory of autism. *Trends in Cognitive Sciences*, 16, 231–239.
- Dawson, G., Carver, L., Meltzoff, A.N., Panagiotides, H., McPartland, J., & Webb, S.J. (2002). Neural correlates of face and object recognition in young children with autism spectrum disorder, developmental delay, and typical development. *Child Development*, 73, 700–717.
- Dawson, G., Webb, S.J., Wijsman, E., Schellenberg, G., Estes, A., et al. (2005). Neurocognitive and electrophysiological evidence of altered face processing in parents of children with autism: Implications for a model of abnormal development of social brain circuitry in autism. *Development and Psychopathology*, 17, 679–697.

- Dinstein, I., Thomas, C., Humphreys, K., Minshew, N.J., Behrmann, M., & Heeger, D.J. (2008). Dysfunctional mirror neurons and Autism—A doubtful connection. London, UK: International Meeting for Autism Research.
- Ferrari, P.F., & Gallese, V. (2007). Mirror neurons and intersubjectivity. *Advances in Consciousness Research*, 68, 73–88.
- Ferrari, P.F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., & Suomi, S. (2006). Neonatal imitation in rhesus macaques. *PLoS Biology*, 4, e302.
- Haber, S.N., & Knutson, B. (2009). The reward circuit: Linking primate anatomy and human imaging. *Neuropsychopharmacology*, 35, 4–26.
- Harrison, N.A., Morgan, R., & Critchley, H.D. (2010). From facial mimicry to emotional empathy: A role for norepinephrine? *Social Neuroscience*, 5, 393–400.
- Hermans, E.J., Putman, P., & Van Honk, J. (2006). Testosterone administration reduces empathetic behavior: A facial mimicry study. *Psychoneuroendocrinology*, 31, 859–866.
- Hess, U., Philippot, P., & Blairy, S. (1999). Mimicry: Facts and fiction.
- Heyes, C. (2001). Causes and consequences of imitation. *Trends in Cognitive Sciences*, 5, 253–261.
- Heyes, C. (2011). Automatic imitation. *Psychological Bulletin*, 137, 463–483.
- Hobson, R.P., & Hobson, J.A. (2008). Dissociable aspects of imitation: A study in autism. *Journal of Experimental Child Psychology*, 101, 170–185.
- Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology*, 60, 653–670.
- Keysers, C., Kaas, J.H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, 11, 417–428.
- Kohls, G., Peltzer, J., Schulte-Rüther, M., Kamp-Becker, I., Remschmidt, H., et al. (2011). Atypical brain responses to reward cues in autism as revealed by Event-related potentials. *Journal of Autism and Developmental Disorders*, 41, 1523–1533.
- Lang, P.J., Bradley, M.M., & Cuthbert, B.N. (1999). International affective picture system (IAPS): Instruction manual and affective ratings. Gainesville, Florida, USA: The Center for Research in Psychophysiology, University of Florida.
- Likowski, K.U., Muehlberger, A., Seibt, B., Pauli, P., & Weyers, P. (2008). Modulation of facial mimicry by attitudes. *Journal of Experimental Social Psychology*, 44, 1065–1072. doi:10.1016/j.jesp.2007.10.007.
- Maringer, M., Krumhuber, E.G., Fischer, A.H., & Niedenthal, P.M. (2011). Beyond smile dynamics: Mimicry and beliefs in judgments of smiles. *Emotion*, 11, 181–187.
- Marsh, A.A., Kozak, M.N., Wegner, D.M., Reid, M.E., Henry, H.Y., & Blair, R.J.R. (2010). The neural substrates of action identification. *Social Cognitive and Affective Neuroscience*, 5, 392–403.
- McIntosh, D.N., Reichmann Decker, A., Winkielman, P., & Wilbarger, J.L. (2006). When the social mirror breaks: Deficits in automatic, but not voluntary, mimicry of emotional facial expressions in autism. *Developmental Science*, 9, 295–302.
- Minio-Paluello, I., Baron-Cohen, S., Avenanti, A., Walsh, V., & Aglioti, S.M. (2009). Absence of embodied empathy during pain observation in Asperger syndrome. *Biological Psychiatry*, 65, 55–62.
- Press, C., Bird, G., Flach, R., & Heyes, C. (2005). Robotic movement elicits automatic imitation. *Brain Research. Cognitive Brain Research*, 25, 632–640.
- Press, C., Richardson, D., & Bird, G. (2010). Intact imitation of emotional facial actions in autism spectrum conditions. *Neuropsychologia*, 48, 3291–3297.
- Robinson, E.B., Koenen, K.C., McCormick, M.C., Munir, K., Hallett, V., et al. (2011). Evidence that autistic traits show the same etiology in the general population and at the quantitative extremes (5%, 2.5%, and 1%). *Archives of General Psychiatry*, 68, 1113–1121.
- Rogers, S.J., Hepburn, S.L., Stackhouse, T., & Wehner, E. (2003). Imitation performance in toddlers with autism and those with other developmental disorders. *Journal of Child Psychology and Psychiatry*, 44, 763–781.
- Schmitz, N., Rubia, K., Van Amelsvoort, T., Daly, E., Smith, A., & Murphy, D.G.M. (2008). Neural correlates of reward in autism. *British Journal of Psychiatry*, 192, 19–24.
- Scott-Van Zeeland, A.A., Dapretto, M., Ghahremani, D.G., Poldrack, R.A., & Bookheimer, S.Y. (2010). Reward processing in autism. *Autism Research*, 3, 53–67.
- Sims, T.B., Van Reekum, C.M., Johnstone, T., & Chakrabarti, B. (2012). How reward modulates mimicry: EMG evidence of greater facial mimicry of more rewarding happy faces. *Psychophysiology*, 49, 998–1004.
- Sonnby-Borgström, M. (2002). Automatic mimicry reactions as related to differences in emotional empathy. *Scandinavian Journal of Psychology*, 43, 433–443.
- Steiger, J.H. (1980). Tests for comparing elements of a correlation matrix. *Psychological Bulletin*, 87, 245–251.
- Stel, M., van Baaren, R.B., Blascovich, J., van Dijk, E., McCall, C., et al. (2010). Effects of a priori liking on the elicitation of mimicry. *Experimental Psychology*, 57, 412–418.
- Stel, M., van den Heuvel, C., & Smeets, R.C. (2008). Facial feedback mechanisms in autistic spectrum disorders. *Journal of Autism and Developmental Disorders*, 38, 1250–1258.