Commentary: Decoding the Charitable Brain: Empathy, Perspective Taking, and Attention Shifts Differentially Predict Altruistic Giving

Vanessa Era [1,2†], Martina Fusaro [1,2*†] and Selene Gallo [3†]

[1] Social Cognitive Neuroscience Laboratory, Department of Psychology, Sapienza University of Rome, Rome, Italy, [2] Social Cognitive Neuroscience Laboratory, Fondazione Santa Lucia, IRCCS, Rome, Italy, [3] Social Brain Lab, The Netherlands Institute for Neuroscience, Royal Netherlands Academy of Arts and Sciences (KNAW), Amsterdam, Netherlands

A commentary on

Decoding the Charitable Brain: Empathy, Perspective Taking, and Attention Shifts Differentially Predict Altruistic Giving
by Tusche, A., Böckler, A., Kanske, P., Trautwein, F. M., and Singer, T. (2016). J. Neurosci. 36, 4719–4732. doi: 10.1523/JNEUROSCI.3392-15.2016

Altruism is acting to promote someone else's welfare, even at a risk or cost to ourselves. In altruistic decision making the emotional sharing of the other person's affective state needs to be integrated with cognitive evaluations of the social context in which the decision takes place. More specifically, in the case of charitable donation the donor needs to evaluate the mission of the charity in order to make an informed decision. In a recent paper by Tusche et al. (2016), the authors explored the specific contribution of empathy and perspective taking (PT) in altruistic behavior. Empathy is the capacity to understand the affective experience of another person (Decety and Jackson, 2004) while PT is the cognitive process of inferring others' thoughts and intentions (Frith and Frith, 2006). The paper focused on disentangling the specific role of empathy and PT and of their neural correlates, anterior insula (AI), and the temporo-parietal junction (TPJ), respectively, in altruistic behavior.

In this commentary, we discuss Tusches' and colleagues interesting results, paying special attention to the role of prefrontal areas in higher-level cognitive processes involved in the charitable decision-making process. In their study, the authors asked participants to donate money to different charities during fMRI. Participants were later asked to rate how processes previously associated with altruistic behavior, including empathic responses and PT, characterized each charity. An additional task was performed to independently measure participants' empathy and PT neural correlates (EmpaToM, Kanske et al., 2015). Activity in different areas, including those traditionally associated with affective sharing (AI), PT (TPJ), and decision making (ventromedial and dorsolateral prefrontal cortices), distinguished between selfish and generous donation.

The authors focused on the finding of a segregated role of TPJ and AI in supporting donations promoted by PT and empathy, respectively. Interestingly, medial prefrontal cortex (mPFC) activity was found across tasks. Firstly, the activity of this region distinguished between generous and selfish donation. Secondly, its activity coded for degrees of empathy (but not PT) toward the charities when the authors disentangled the contribution of empathy and PT to donation trial-by-trial. Finally, mPFC activity predicted donation generosity supported by PT (but not by empathy)

when looking at its activity during EmpaToM. Not being the focus of their study, the authors did not clarify these ambiguous results about the involvement of the prefrontal cortices in altruistic giving. Charitabile donations are shaped by moral motivations, evaluations of risks and costs, guilt, personal values, prospective evaluations, and the ability to understand another person (Batson, 1989). This latter ability might be supported by affectively resonating with the other (empathy) or by cognitively evaluating other's state (PT). Both of these processes might be modulated by the beneficiary of the donation (social context). Thus, investigating the role of the prefrontal cortices in charitable donations can also clarify the relationship between empathy and PT in this process.

Tusche et al. showed that the activation of mPFC supported both empathy's and PT's contribution to donation. However, this activation was not consistent across different tasks. The technique used in the study might have underestimated the shared modulation of empathy and PT by mPFC in supporting donations. More specifically, the technique employed used a linear decision boundary applied to a small local cluster of voxels. Multi Voxel Pattern Analysis (MVPA) is in general more sensitive to high frequency spatial difference between conditions than a univariate general linear model (GLM) approach. This feature was fundamental in finding distinct neural underpinnings for empathy and PT in different regions of the brain supporting donations, a task in which the GLM failed. It is important to note that classification algorithms tend to focus on discriminative features and ignore features that are shared across the categories. Tusche et al. tested whether local clusters in specific regions represented empathy and/or PT. They found that areas having information regarding one of the two processes did not contain information about the other in supporting altruism. This does not exclude that the relationship between covariance of those areas, or between those areas and control ones, carries the information about the degree in which empathy and PT influence charitable donation.

Social contexts might, in fact, influence the recruitment of empathy and PT, contributing to the flexibility of the altruistic behavior. This context-based top-down modulation of social behaviors (Lakin et al., 2003) has been proposed to rely on a specific brain network in which mPFC is an important node (Wang et al., 2011). Wang and Hamilton (2012) proposed a model regarding the control of imitative behavior: the social top-down response modulation (STORM). The STORM model assumes that mimicry plays an important role in communication and affiliation and makes individuals more prone to be engaged in positive social interactions (Lakin and Chartrand, 2003; Lakin et al., 2003). Spontaneous mimicry is modulated by social signals requiring the engagement of empathy and perspective taking

processes (Chartrand et al., 2005). The same processes also seem to be involved in prosocial behavior, such as charitable donations (Mathur et al., 2010; Telzer et al., 2011; Morelli et al., 2014). For this reason we suggest that the STORM model could also explain the modulation of charitable donation based on social context. Imitation is guided by social cues (Lakin and Chartrand, 2003), and the same cues could also guide prosocial behavior (i.e., group diversity, Andreoni et al., 2016). More specifically, the STORM model assumes that imitative behavior is modulated by social context. Responses evoked in the mirror neuron system are subjected to top-down control. This control mechanism is supported by the activity of mPFC. The modulation is based on an evaluation of both the current context and the social situation. We suggest that a similar top-down mechanism, in which empathy and PT are not two independent processes but are controlled together by mPFC, might be generalized to the modulation of altruistic donation, where the social context is represented by the beneficiary of the prosocial behavior.

The involvement of prefrontal regions in altruistic behavior has been highlighted in many studies (Hare et al., 2010; Waytz et al., 2012). Tusche et al. found that the recruitment of empathy and PT predicting altruistic behavior is flexible and dependent on the different charitable organizations (social context) to which participants were asked to donate. This contextual influence can be interpreted in light of the STORM model. Prefrontal cortices might evaluate different charities (social context) and modulate the amount of empathy or PT recruited, resulting in different levels of generosity. We highlighted the role of prefrontal areas in higher-level cognitive processes involved in the charitable decision-making process. Although empathy and PT support charitable donation separately as showed by Tusche et al., it is also important to consider that both of them are modulated by the same high-level regions. We suggest that those regions preferentially support PT or empathy depending on the social context, and also modulate the degree to which PT and empathy are engaged to promote altruistic choices that represent a social reward.

AUTHOR CONTRIBUTIONS

VE, MF, and SG have made substantial, direct, and intellectual contribution to the work and approved it for publication.

ACKNOWLEDGMENTS

REFERENCES

Andreoni, J., Payne, A. A., Smith, J., and Karp, D. (2016). Diversity and donations: the effect of religious and ethnic diversity on charitable giving. *J. Econ. Behav. Organ.* 128, 47–58. doi: 10.1016/j.jebo.2016.05.010

Batson, C. D. (1989). "Personal values, moral principles, and a three-path model of prosocial motivation," in *Social and Moral Values: Individual and Societal Perspectives*, eds N. Eisenberg, J. Reykowski and E. Staub (Mahwah, NJ: L. Erlbaum Associates), 213–228.

Chartrand, T. L., Maddux, W. W., and Lakin, J. L. (2005). "Beyond the perception-behavior link: The ubiquitous utility and motivational moderators of nonconscious mimicry," in *The New Unconscious*, eds R. R. Hassin, J. S. Uleman, and J. A. Bargh (New York, NY: Oxford University Press), 334–361.

Decety, J., and Jackson, P. L. (2004). The functional architecture of human empathy. *Behav. Cogn. Neurosci. Rev.* 3, 71–100. doi: 10.1177/1534582304267187

Frith, C. D., and Frith, U. (2006). The neural basis of mentalizing. *Neuron* 50, 531–534. doi: 10.1016/j.neuron.2006.05.001

Hare, T. A., Camerer, C. F., Knoepfle, D. T., O'Doherty, J. P., and Rangel, A. (2010). Value computations in ventral medial prefrontal cortex during charitable decision making incorporate input from regions involved in social cognition. *J. Neurosci.* 30, 583–590. doi: 10.1523/JNEUROSCI.4089-09.2010

Kanske, P., Böckler, A., and Singer, T. (2015). "Models, mechanisms and moderators dissociating empathy and Theory of Mind," in *Social Behavior from Rodents to Humans: Neural Foundations and Clinical Implications*, Current Topics in Behavioral Neurosciences, eds M. Wöhr and S. Krach (Luxemburg: Springer), 1–14. doi: 10.1007/7854_2015_412

Lakin, J. L., and Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychol. Sci.* 14, 334–339. doi: 10.1111/1467-9280.14481

Lakin, J. L., Jefferis, V. E., Cheng, C. M., and Chartrand, T. L. (2003). The chameleon effect as social glue: evidence for the evolutionary significance of nonconscious mimicry. *J. Nonverbal Behav.* 27, 145–162. doi: 10.1023/A:1025389814290

Mathur, V. A., Harada, T., Lipke, T., and Chiao, J. Y. (2010). Neural basis of extraordinary empathy and altruistic motivation. *Neuroimage* 51, 1468–1475. doi: 10.1016/j.neuroimage.2010.03.025

Morelli, S. A., Rameson, L. T., and Lieberman, M. D. (2014). The neural components of empathy: predicting daily prosocial behavior. *Soc. Cogn. Affect. Neurosci.* 9, 39–47. doi: 10.1093/scan/nss088

Telzer, E. H., Masten, C. L., Berkman, E. T., Lieberman, M. D., and Fuligni, A. J. (2011). Neural regions associated with self control and mentalizing are recruited during prosocial behaviors towards the family. *Neuroimage* 58, 242–249. doi: 10.1016/j.neuroimage.2011.06.013

Tusche, A., Böckler, A., Kanske, P., Trautwein, F. M., and Singer, T. (2016). Decoding the charitable brain: empathy, perspective taking, and attention shifts differentially predict altruistic giving. *J. Neurosci.* 36, 4719–4732. doi: 10.1523/JNEUROSCI.3392-15.2016

Wang, Y., and Hamilton, A. F. (2012). Social top-down response modulation (STORM): a model of the control of mimicry in social interaction. *Front. Hum. Neurosci.* 6:153. doi: 10.3389/fnhum.2012.00153

Wang, Y., Ramsey, R., and Hamilton, A. F. (2011). The control of mimicry by eye contact is mediated by medial prefrontal cortex. *J. Neurosci.* 31, 12001–12010. doi: 10.1523/JNEUROSCI.0845-11.2011

Waytz, A., Zaki, J., and Mitchell, J. P. (2012). Response of dorsomedial prefrontal cortex predicts altruistic behavior. *J. Neurosci.* 32, 7646–7650. doi: 10.1523/JNEUROSCI.6193-11.2012