

heterogeneity than prior work and did not, might instead provide support for considerable homogeneity in the FFA. Çukur *et al.*'s three clusters, one of which appears highly similar in response and location to the body-selective area situated between FFA1 and FFA2 [6] and which is typically not considered FFA, are consistent with a model in which all FFA voxels contain one homogeneous population of neurons: neurons that become tuned to features of objects we learn to individuate, with more neurons developing selectivity as the degree of experience increases. The size of face-selective areas in any one subject would be determined by how many of these neurons in the lateral fusiform gyrus have developed selectivity for faces. Subsets of this population (clusters) would emerge, because face-selective neurons also develop selectivity for other categories the subjects may individuate but for which experience levels rarely match that for faces. In other words, clusters may result from differences in expertise between categories, but functionally all neurons in this area may be *a priori* capable of responding to many categories. Such multiplexing is observed in earlier visual areas [9]. Neurons that can participate in the representation of faces and other objects of expertise, as part of neural ensembles, which may not be able optimally to represent objects from distinct categories simultaneously, is one way to account for competition observed between faces and cars in car experts [10].

Acknowledgments

This work was supported by the NSF (Grant SBE-0542013), VVRC (Grant P30-EY008126), and NEI (Grant R01 EY013441-06A2).

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Norms and expectations in social decision-making

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Recent research has shown that stimulating right lateral prefrontal cortex (rLPFC) via transcranial direct current stimulation (tDCS) changes social norm compliance in economic decisions, with different types of compliance affected in different ways. More broadly considering the norms involved in decision-making, and in particular expectations held by players, can help clarify the mechanisms underlying these results.

The rapidly growing field of decision neuroscience has made great strides in utilizing converging theories and methods from multiple disciplines (most prominently neuroscience, psychology, and economics) to specify more accurate models

of human decision-making. An important focus of this work is to understand the brain processes underlying social preferences, which can ultimately explain often puzzling behavior in social scenarios. For example, why do experimental participants often reject unequal splits of a monetary amount, when the alternative is receiving nothing at all, as in the well-studied ultimatum game (UG) [1]? In addition, why do participants often choose to make fair offers to others when under no obligation to do so? In recent years, neuroscientific approaches have been brought to bear on these types of question, and the current paper by Ruff *et al.* [2] is a prime example of how a convergence of innovative methods can greatly assist in better identifying the specific neural processes implicated in these types of complex decision.

Here, the experimenters tested decision-making in two treatment conditions, one in which making an unequal offer to a participant had no consequence (baseline condition), and one in which the partner could punish the participant if they deemed the offer unfair (punishment condition). Three groups of participant made these offer decisions while un-

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1364-6613/\$ – see front matter

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dergoing different types of tDCS to the rLPFC, an area previously implicated in social norm compliance [3]. Results showed that anodal tDCS (which enhances neural excitability) increased the difference in contribution between the punishment and baseline conditions, suggesting that this stimulation increased sensitivity to the sanction threat, whereas cathodal tDCS (suppressing neural excitability) reduced this difference, both relative to a sham stimulation condition. Demonstrating shifts in decision-making in these interactive scenarios via a technique that allows for more causal inferences, such as tDCS, is an important advance for the study of how social norms are implemented, and this study is an excellent example of how such causal manipulations can extend theory beyond the largely correlational findings emerging from neuroimaging. Here, the rLPFC appears to be causally involved in applying a pre-existing social norm to decision-making. However, enhancing LPFC response increased offers in the sanction-threat condition, but decreased offers (compared with sham) in the no-punishment baseline condition, and it remains an open question as to why different types of LPFC stimulation produce differential effects on decision behavior. One possible way to reconcile these interesting findings is to consider social norms more broadly.

The authors suggest that participants are using a fairness norm of ‘equity’, whereby the optimal decision would be to split the pot of money equally between both players. Fairness norms have been particularly well studied, and considerable work has supported the notion that most people care about ensuring that others receive similar payoffs [4]. However, other beliefs may also matter in social decision-making, a variety of which have been described by psychologists, and formalized by economists as probability distributions. For

example, people may have second-order beliefs, reflecting what people think their partner expects them to do [5]. In addition, people generally have beliefs about descriptive social norms, that is, the typical behavior of others, and often behave in accordance with this knowledge [6]. For example, UG recipients are more likely to accept unfair offers if they believe that low offers are the norm [7]. In addition, players can learn the distributions of offers they encounter, and reject offers that violate their expectations, suggesting that descriptive social norms are malleable [8].

One hypothesis that could help explain the current results is that people have different beliefs about the descriptive norm across the two game conditions, expecting most people to offer less money in the baseline condition. Stimulation may be changing participants’ motivations to comply with these different respective beliefs. More specifically, if the goal is to adhere to a social norm and the rLPFC is involved in the motivation to comply with this norm, then enhancing activity in this region, such as via anodal stimulation, should change the amount of money one gives a partner. Similarly, alternative stimulation that decreases degree of compliance (i.e., cathodal) should show the opposite effects, as is evident (Figure 1).

Ruff *et al.* did indeed measure some beliefs that the participants held, including those regarding the perceived fairness of the offer, the punishment expected, and the anger they believed their partner would feel. The authors found no difference as a function of tDCS, suggesting that stimulation is not changing the belief itself, but rather the willingness to comply with the norm. Unfortunately, the experimenters did not measure beliefs separately for each treatment condition, or directly assess the participants’ beliefs about descriptive norms. For example, it could have

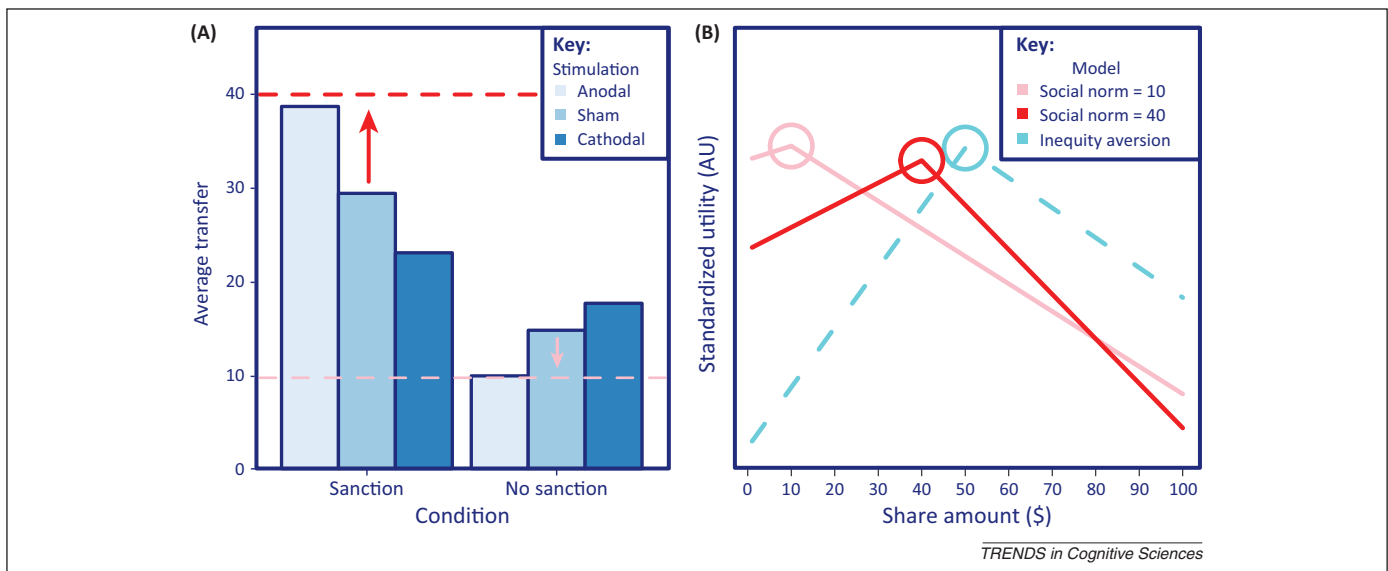


Figure 1. Behavioral results and model predictions. **(A)** The behavioral results from [2] with the average transfer amounts as a function of context (sanction, no sanction) and transcranial direct current stimulation (tDCS) level (anodal, sham, or cathodal). There is a significant context by stimulation interaction, such that transfers are highest in the sanction condition with anodal stimulation and lowest when receiving anodal stimulation in the no sanction context. In addition, people in general transfer less money when there is no possibility of sanction, which is suggestive of a lower descriptive social norm. **(B)** The standardized utility functions for inequity aversion [4] and expectation [7] models. The expected utility $U_c(x)$ associated with a context c for the set of offers $x \in [0,100]$ is $U_c(x) = \pi_x - \alpha \cdot \max(E[\varphi_c] - x, 0) - \beta \cdot \min(x - E[\varphi_c], 0)$, where α and $\beta > 0$, π_x refers to the player’s payoff, and $E[\varphi_c]$ describes the mean of the probability distribution of the type of transfers the player believes most other players would make in a given context [e.g., \$40 (red), \$10 (pink)]. The maxima of these utility functions indicate the theoretically optimal behavior, which is effectively matching the social norm. Inequity aversion makes identical predictions in both contexts (i.e., a transfer of \$50), likely reflecting the fairness ratings reported by [2]. The expectation model makes differential predictions based on context-specific norms (e.g., a norm of \$40 or \$10) and tDCS to right lateral prefrontal cortex (rLPFC) is likely increasing compliance to these different respective norms [see (A), red = \$40 and pink = \$10].

been informative to ask participants what they thought 'typical' behavior would be in each of the situations.

Support for the hypothesis that tCDS to LPFC modulates compliance comes from previous work showing that this brain region has an important role in the processing of expectations. For example, there appears to be a system involved in monitoring deviations from a social norm that includes the anterior cingulate cortex and insula [7,9] and the LPFC may interact with this system by maintaining goal information in working memory and also exerting cognitive control to comply with the goal [10].

Ruff *et al.* conclude their article with a plea to extend the experimental work on norm-based decision-making towards populations in which norm compliance is often a problem. We certainly agree with this suggestion, and would also encourage future studies to explore the psychological and neural mechanisms underlying social norm compliance in more realistic settings.

Actual social norms that guide decision-making in everyday settings can be difficult to elicit in a laboratory setting, and most studies examine the response to incentives administered by other experimental participants. However, in reality, incentives are usually overseen by a formal authority, and not by those with whom one directly interacts. Furthermore, these incentives are typically temporally removed from the decision itself. Additionally, although some everyday behaviors are influenced by monetary incentives, such as parking tickets, or subsidies for installing solar panels, much of our behavior is enforced by social incentives. For example, sanctions such as social disapproval or public

embarrassment, as well as the corresponding social rewards, are being increasingly applied to produce behavioral change effectively [6]. Future work should explore how social and monetary incentives may differentially influence social norm compliance. Deeper psychological and neural insights into these mechanisms can help in designing more effective public policy by specifically targeting the relevant underlying processes, providing a much-needed bridge between the theory and practice of social decision-making.

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