Neural Circuitry of Social Valuation

by

David Victor Smith

Department of Psychology & Neuroscience
Duke University

Date:_______________________

Approved:

___________________________
Scott A. Huettel, Supervisor

___________________________
Roberto Cabeza

___________________________
Timothy J. Strauman

___________________________
Michael L. Platt

Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology & Neuroscience in the Graduate School of Duke University

2012
ABSTRACT

Neural Circuitry Social Valuation

by

David Victor Smith

Department of Psychology & Neuroscience
Duke University

Date:_______________________

Approved:

___________________________
Scott A. Huettel, Supervisor

___________________________
Roberto Cabeza

___________________________
Timothy J. Strauman

___________________________
Michael L. Platt

An abstract of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology & Neuroscience in the Graduate School of Duke University

2012
Abstract

Few aspects of human cognition are more personal than the choices we make. Our decisions—from the mundane to the impossibly complex—continually shape the courses of our lives. In recent years, researchers have applied the tools of neuroscience to understand the mechanisms that underlie decision making, as part of the new discipline of decision neuroscience. A primary goal of this emerging field has been to identify the processes that underlie specific decision variables, including the value of rewards, the uncertainty associated with particular outcomes, and the consequences of social interactions. Here, across three independent studies, I focus on the neural circuitry supporting social valuation—which shapes our social interactions and interpersonal choices. In the first study (Chapter 2), I demonstrate that social valuation relies on the posterior ventromedial prefrontal cortex (pVMPFC). Extending these findings, I next show that idiosyncratic responses within pVMPFC predict individual differences in complex social decision scenarios (Chapter 3). In addition, I also demonstrate that decisions involving other people (e.g., donations to a charitable organization) produce increased activation in brain regions associated with social cognition, particularly the temporal-parietal junction (TPJ). Finally, in my last study (Chapter 4), I employ functional connectivity analyses and show that regions supporting social cognition—including the TPJ—exhibit increased connectivity with pVMPFC during social valuation,
an effect that depends upon individual differences in preferences for social stimuli. Collectively, these results demonstrate that the computation of social value relies on distributed neural circuitry, including regions implicated in processing value and regions implicated in social cognition. Future research on social valuation and interpersonal choice must build upon this emerging theme by linking neural circuits and behavior.
Dedication

To those who do what they love.
Contents

Abstract.................................................................................................................................iv

List of Tables ......................................................................................................................... xi

List of Figures ....................................................................................................................... xiv

Acknowledgments ............................................................................................................... xix

1. Decision Neuroscience: Neuroeconomics ........................................................................ 1

   1.1 Decision Variables ....................................................................................................... 1

   1.1.1 Value: Dopamine and Reward Prediction ................................................................. 2

   1.1.2 Value: Alternative Explanations .............................................................................. 5

   1.1.3 Uncertainty .............................................................................................................. 9

   1.1.4 Social Interactions ................................................................................................. 14

   1.2 Value Comparison ...................................................................................................... 19

   1.3 Open Questions ......................................................................................................... 21

2. Distinct Value Signals Within Anterior and Posterior Ventromedial Prefrontal Cortex
................................................................................................................................................24

   2.1 Introduction ................................................................................................................... 24

   2.2 Materials and Methods ................................................................................................. 27

   2.2.1 Participants ............................................................................................................. 27

   2.2.2 Stimuli and Tasks .................................................................................................... 27

   2.2.3 Estimating Decision Value ..................................................................................... 31

   2.2.4 Image Acquisition ................................................................................................. 31

   2.2.5 FMRI Data Analysis ............................................................................................... 32
2.3 Results .............................................................................................................................. 35
  2.3.1 Behavioral Data........................................................................................................... 35
  2.3.2 Activation in Anterior VMPFC Reflects Experienced Value ................................. 35
  2.3.3 Activation in Posterior VMPFC Reflects Decision Value ..................................... 42
  2.4 Discussion......................................................................................................................... 45

3. Neural Predictors of Self and Charity Framing Effects ................................................. 50
  3.1 Introduction...................................................................................................................... 50
  3.2 Materials and Methods .................................................................................................. 52
     3.2.1 Participants............................................................................................................... 53
     3.2.2 Stimuli and Task...................................................................................................... 53
     3.2.3 Image Acquisition ................................................................................................. 55
     3.2.4 Preprocessing ......................................................................................................... 56
     3.2.5 FMRI Analysis ........................................................................................................ 58
  3.3 Results ............................................................................................................................ 59
     3.3.1 Behavioral Data........................................................................................................ 59
     3.3.2 Loss Frame Evokes Activation in DMPFC ............................................................... 62
     3.3.3 Decisions Involving Charity Recruit Social Cognition Regions ........................... 63
     3.3.4 Posterior VMPFC Predicts Relative Framing Biases ............................................ 64
  3.4 Discussion......................................................................................................................... 66

4. Social Cognition Regions Modulate Value Regions in a Preference-Specific Manner . 71
  4.1 Introduction...................................................................................................................... 71
  4.2 Materials and Methods .................................................................................................. 74
4.2.1 Participants.................................................................................................................................. 74
4.2.2 Stimuli and Tasks ....................................................................................................................... 74
4.2.3 Image Acquisition ...................................................................................................................... 78
4.2.4 Preprocessing ............................................................................................................................ 78
4.2.5 FMRI Analyses .......................................................................................................................... 79
4.2.6 Trial-to-Trial Analysis ................................................................................................................. 81
4.3 Results ........................................................................................................................................... 82
   4.3.1 Ratings and Choice Behavior .................................................................................................. 82
   4.3.2 Parametric Effects of Attractiveness ....................................................................................... 83
   4.3.3 Increased Functional Connectivity with Posterior VMPFC Predicts Social Valuation............... 87
4.4 Discussion ....................................................................................................................................... 93
5. Moving Beyond Value Systems: Linking Circuits and Behavior ...................................................... 97
   5.1 Value Computations Rely on Interacting Brain Systems ............................................................ 97
   5.2 Exploiting the Strengths of FMRI ............................................................................................... 99
      5.2.1 Multivariate Pattern Analyses Extract Information Within Brain Regions ......................... 100
      5.2.2 Multivariate Network Analyses Extract Information Across Brain Regions ......................... 104
   5.3 Future Studies ............................................................................................................................ 109
      5.3.1 Manipulating Valuation Processes ......................................................................................... 109
      5.3.2 Exploiting Dynamic Social Interactions ................................................................................ 110
      5.3.3 Characterizing Individual Differences .................................................................................. 111
   5.4 Summary and Conclusions ......................................................................................................... 111
List of Tables

Table 1: The attractiveness categories used in the present experiment. All are drawn from the distribution of normalized attractiveness ratings, with ratings here expressed as z-scores........................................................................................................................................29

Table 2: Regions exhibiting increased activation to photographs of their faces, regardless of their attractiveness, compared to monetary rewards. Coordinates of cluster maxima are in MNI space. Cluster size is provided in terms of the number of 2 mm³ voxels. Abbreviations: BA (Brodmann Area).......................................................................................................................................36

Table 3: Regions exhibiting increased activation to monetary rewards, regardless of their value, compared to photographs of faces. Coordinates of cluster maxima are in MNI space. Cluster size is provided in terms of the number of 2 mm³ voxels. Abbreviations: BA (Brodmann Area).......................................................................................................................................36

Table 4: Regions exhibiting sensitivity to monetary value, defined as increased activation to large gains (+$5 & +$2) compared to large losses (-$5 & -$2). Coordinates of local maxima within clusters of activation are in MNI space. Cluster size is provided in terms of the number of 2 mm³ voxels. Distinct clusters are separate by blank rows. Abbreviations: BA (Brodmann Area).......................................................................................................................................36

Table 5: Regions whose activation increases with increasing monetary reward size. Coordinates of local maxima within clusters of activation are in MNI space Coordinates of local maxima within clusters of activation are in MNI space. Cluster size is provided in terms of the number of 2 mm³ voxels. Abbreviations: BA (Brodmann Area).......................................................................................................................................36

Table 6: Regions exhibiting sensitivity to social value, defined as increased activation to attractive faces (those from the 4-star category) compared to unattractive faces (those from the 1-star category). Coordinates of local maxima within clusters of activation are in MNI space. Cluster size is provided in terms of the number of 2 mm³ voxels. Distinct clusters are separate by blank rows. Abbreviations: BA (Brodmann Area).......................................................................................................................................36

Table 7: Regions whose activation increases with increasing social reward size. Coordinates of local maxima within clusters of activation are in MNI space. Cluster size is provided in terms of the number of 2 mm³ voxels. Distinct clusters are separate by blank rows. Abbreviations: BA (Brodmann Area).......................................................................................................................................36

Table 8: Regions whose activation increases with increasing social reward (see Figure 16). Coordinates of local maxima within the five clusters of activation are in MNI space. ..................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................................
Probabilistic labels reflect the probability (or likelihood) that a coordinate belongs to a given region. For clarity, we only show labels whose likelihood exceeds 5%.

Abbreviations: WM (white matter); sLOC (lateral occipital cortex, superior division); iLOC (lateral occipital cortex, inferior division); ACC (anterior cingulate cortex); OFG (occipital fusiform gyrus); SFG (superior frontal gyrus); TOFC (temporal occipital fusiform cortex).

Table 9: Regions whose activation follows a nonlinear, U-shaped pattern in response to social reward. Coordinates of local maxima within the two clusters of activation are in MNI space. Probabilistic labels reflect the probability (or likelihood) that a coordinate belongs to a given region. For clarity, we only show labels whose likelihood exceeds 5%.

Abbreviations: WM (white matter); OFC (Frontal Orbital Cortex); IFG (Inferior Frontal Gyrus, pars triangularis); MPFC (Frontal Medial Cortex); ParaCG (Paracingulate Gyrus); F Operculum (Frontal Operculum Cortex), ACC (anterior cingulate cortex).

Table 10: Regions whose functional connectivity with pVMPFC increases as a function of increasing attractiveness ratings and increasing economic exchanges (see Fig. 17). Coordinates of local maxima within the four clusters of activation are in MNI space. Probabilistic labels reflect the probability (or likelihood) that a coordinate belongs to a given region. For clarity, we only show labels whose likelihood exceeds 5%.

Abbreviations: pMTG (middle temporal gyrus, posterior division); pSTG (superior temporal gyrus, posterior division); WM (white matter); aMTG (middle temporal gyrus, anterior division); sLOC (lateral occipital cortex, superior division); iLOC (lateral occipital cortex, inferior division); ACC (anterior cingulate cortex); PCC (posterior cingulate cortex).

Table 11: Hierarchical regression results. To examine the incremental contribution of additional regions of interest, we performed a hierarchical regression analysis with four sequential levels: confound terms (Block 1); value terms (Block 2); functional connectivity terms (Block 3); regional interaction terms (Block 4). We found that a model incorporating the functional connectivity regions was significantly better at predicting trial-to-trial social valuations compared to value-region-only model.

Table 12: Complete regression statistics. For completeness, here we show the complete regression model with all four blocks and all terms.

Table 13: Cognitive processes can be misrepresented by focusing on average levels of activation within a given brain regions (e.g., dorsolateral prefrontal cortex). Across 27 spatial locations (i.e., a cubical region of interest), hypothetical activation levels are shown across three cognitive processes. Importantly, although the average activation
and variance of activation is mathematically equivalent across all three cognitive processes, each process evokes a distinct pattern of activation.
List of Figures

Figure 1: Brain regions supporting reward processing and value computation. Reward experience and evaluation evokes activation in several interconnected brain regions within the brain’s dopaminergic system. Key regions include the ventral tegmental area (VTA), the ventral striatum (vSTR), and the ventromedial prefrontal cortex (VMPFC).... 5

Figure 2: Brain regions supporting decision uncertainty. Several brain regions respond to uncertainty, or situations lacking desired information about the timing, content, value, or certainty of rewards. These include the insular cortex (Ins), anterior cingulate cortex (ACC), lateral prefrontal cortex (LPFC), and posterior parietal cortex (PPC)....... 12

Figure 3: Brain regions supporting social cognition. Assessing the intentions of others reliably evokes activation in the temporal parietal junction (TPJ)... 18

Figure 4: Overview of studies. We conducted three fMRI studies to examine the neural circuitry of social valuation.......................................................... 23

Figure 5: Experimental tasks. (A) Trial structure for the multimodal reward task. Male, heterosexual young adults passively viewed a randomized sequence of images of female faces and monetary rewards (2 s event duration; 2 s fixation interval). The face images varied in valence from very attractive to very unattractive, based on ratings from an independent group of participants. The monetary rewards, whose value ranged from $5 to -$5, influenced the participant’s overall payout from the experiment. To ensure task engagement, participants responded to infrequent visual targets that appeared as small yellow borders around the image. (B) Trial structure for the economic exchange task. Trials began with a decision phase (lasting 4 s) in which the participant was forced to spend a small amount of money to view a face. Participants could choose to spend more money to view a more attractive face or less money to view a less attractive face. Following the decision phase, there was an anticipation phase that lasted either 2 s or 4 s. Then a single face, randomly selected from the chosen attractiveness category, was displayed for 2 s. Trials were separated by a variable interval whose duration ranged from 2 s to 6 s. .... 28

Figure 6: Neurometric measures of monetary and social experienced value. (A) To identify brain regions whose activation tracked monetary value, we contrasted large monetary gains (+$5 and +$2) minus large monetary losses (-$5 and -$2). Within anterior medial prefrontal cortex [x12, y58, z2] and adjacent frontopolar cortex [x-2, y68, z-2] there was a clear effect of the valence of monetary rewards (shown in green). We additionally identified brain regions whose activation tracked social value by
contrasting the response to faces drawn from our most-attractive category (4-star) and that to faces drawn from our least-attractive category (1-star). Activation was modulated by the valence of social rewards in the ventral striatum [vSTR; x-8, y18, z-6] and ventromedial prefrontal cortex [VMPFC; x0, y48, z-8] (shown in red). Using a conjunction analysis, we identified a small region of anterior VMPFC [aVMPFC; x0, y46, z-8] whose activation increased to increasing value for both forms of rewards (shown in yellow), and survived an additional cluster correction of 15 contiguous voxels. All areas of activation passed a cluster significance threshold of z > 2.3, with whole-brain cluster-correction at p < 0.05. (B) Interrogation of the aVMPFC region that responded to both rewards revealed that activation within this area increased with increasing monetary reward. Error bars indicate standard error of the mean (SEM). (For display purposes, error bars were calculated without correcting for normalized values.) (C) Within the aVMPFC region, activation increased with increasing attractiveness, with least response to the most unattractive faces and greatest response to the most attractive faces. Error bars indicate SEM. (For display purposes, error bars were calculated without correcting for normalized values.)

Figure 7: Individual differences in exchange rate. In our economic exchange task, participants had the opportunity to exchange small amounts of money for the opportunity to view a more attractive face. This task afforded an opportunity to examine each participant’s relative economic valuation of social and monetary rewards. We observed substantial inter-individual differences in participants’ willingness to make these exchanges; shown in the plot is a ranking of participants (N = 23) by the proportion of time they sacrificed a larger amount of money to purchase a more attractive face.

Figure 8: Posterior VMPFC encodes information about decision value. (A) We investigated whether neurometric representations of value (in the multimodal reward task) could predict whether a given individual was likely to subsequently trade money to view faces (in the economic exchange task). To do this, we introduced exchange rate (as a proportion of total opportunities) as a factor in an across-participants analyses. We found one region within the posterior VMPFC (pVMPFC; x6, y26, z-14) in which differential neurometric representations of value, defined as Social Value (4-star minus 1-star) minus Monetary Value (large gains minus large losses), predicted exchanges. Shown are voxels passing a significance threshold of p < 0.001 (uncorrected); the pVMPFC peak of activation was highly significant [z = 3.24]. (B) Within pVMPFC, increasing neurometric value for social compared to monetary rewards predicted increasing likelihood of economic exchanges (r = 0.72). That is, those individuals who had the greatest neurometric value for social compared to monetary rewards, as defined by a double subtraction of Social Value (4-star minus 1-star) minus Monetary Value
(large monetary gains minus large monetary losses), readily exchanged money to view more-attractive faces. In contrast, those individuals with the least neurometric value for social compared to monetary rewards were unlikely to sacrifice that money for a better social reward. The line represents the least-squares fit to the data points; each point reflects the average response within pVMPFC for each participant.

Figure 9: Regions identified as pVMPFC and aVMPFC. We identified two distinct subregions of VMPFC that responded to different forms of value. Shown in red is anterior VMPFC (aVMPFC; x0, y46, z-8). This region was the sole point of overlap for monetary and social value, indicating a role for processing experienced rewards. Shown in blue is posterior VMPFC (pVMPFC; x6, y26, z-14). This region was identified in a whole-brain analysis in which we regressed relative neural value (Social > Money reward responses) against relative economic value (Social > Money; proportion of exchanges for faces).

Figure 10: Experimental task. Participants engaged in a financial decision-making task. At the beginning of each trial, an initial endowment was presented that indicated the target of the decision (self or charity; equally split). Following this cue, participants had the opportunity to choose between a gamble where they could keep or lose all of the initial endowment or a safe option where they would receive a guaranteed proportion of the initial endowment. The safe option was presented in two conditions: (A) a keep frame; and (B) a lose frame. Crucially, these two frames were mathematically identically and only differed in the presentation of the option ("keep" or "lose"). After the participants made their choice, a fixation was presented for 2.5 to 6.5 second. At the end of the experiment, we chose one trial at random to be resolved for payment purposes.

Figure 11: Behavioral data. (A and B) For both self (red) and charity (blue) decision targets, we observed a robust effect of frame where participants increased their willingness to gamble when the safe option was presented as a potential loss. (C and D) Relative to the keep frame, participants were substantially slower to respond during in the loss frame, but this effect was not modulated by decision target. (E and F) The magnitude of the framing effect (i.e., proportion of gamble trials chosen in loss frame minus keep frame) was highly variable across participants, with framing susceptibility in one condition predicting the other condition.

Figure 12: Neural framing effects irrespective of choice. (A) To examine the neural basis of framing effects, we contrasted loss frame trials against gain frame trials. This contrast revealed activation within DMPFC. All areas of activation passed a permutation-based whole-brain corrected threshold of p < 0.05. (B) Within DMPFC, we found that loss
frame trials evoked greater activation than keep frame trials. (C) In an independent sample, we observed a partial replication where charity trials framed as losses evoked greater DMPFC activation than charity trials framed as gains.

Figure 13: Brain activation associated with playing for charity compared to self. (A) To examine how different decision targets are processed, we contrasted charity trials against self trials. This contrast revealed activation within middle temporal gyrus (mTG) and temporal-parietal junction (TPJ). All areas of activation passed a permutation-based whole-brain corrected threshold of p < 0.05. (B) Within TPJ, we found that charity trials evoked greater activation than self trials. (C) In an independent sample, we replicated our TPJ effect, observing increased activation for charity trials relative to self trials.

Figure 14: Posterior VMPFC predicts individual differences in relative framing biases. (A) From prior work examining decision value (Smith et al., 2010), we defined an anatomical region of interest within posterior ventromedial prefrontal cortex (pVMPFC). (B) Using this pVMPFC region, we extracted the average neural effect size, for each subject (white dots), for Self Framing effects minus Charity Framing effect [(Self Loss – Self Gain) – (Charity Loss – Charity Gain)]. We then regressed these neural Self-Charity Framing effects onto the behavior Self-Charity Framing effects and found a positive relationship trending toward significance.

Figure 15: Experimental tasks. (A) Trial structure for the ratings task. Male, heterosexual young adults viewed a randomized sequence of images of female faces and provided, for each image, an attractiveness rating using an 8-point scale. To control for motor anticipation, the ordering of the 8-point scale was randomly flipped across trials; on some trials, the highest rating was the left-most option, and on other trials, the highest rating was the right-most option (as shown in the example). (B) Trial structure for the economic exchange task. Each trial began with a choice phase (lasting 4 s) in which the participant was forced to spend a small amount of money to view a face. Participants could choose to spend more money to view a more attractive face (denoted with increasing stars) or less money to view a less attractive face. After a variable delay period, a single face, randomly selected from the chosen attractiveness category, was displayed for 2 s.

Figure 16: Brain regions tracking increasing attractiveness judgments. (A) To identify brain regions whose activation tracked attractiveness judgments, we constructed parametric model based on each participant’s ratings and examined regions exhibiting a linear relationship with ratings. Brain regions tracking attractiveness ratings included the ACC (x,y,z = 6,18,34), right caudate (x,y,z = 8,12,8), and parts of visual cortex (x,y,z =
-4,-100,4; x,y,z = -28,-82,2). All areas of activation passed an initial cluster-forming threshold of z=2.3, with whole-brain cluster correction at p=0.05. (B) Interrogation of the ACC region revealed a quasi-linear trend of activation, with higher activation predicting higher ratings and lower activation predicting lower activation. Error bars reflect SEM.

Figure 17: Functional connectivity between pVMPFC and regions involved in social cognition predicts social valuations. We employed a PPI analysis to identify regions whose functional connectivity with posterior VMPFC increases as a function of both increasing attractiveness ratings and increasing willingness to exchange money for faces. Shown on the left is a depiction of our seed region, posterior VMPFC, which represents a canonical valuation region. The middle panel shows a schematic of the trial-to-trial modulator (subjective attractiveness) and the participant covariate (proportion of exchanges). Shown on the right are areas whose connectivity with posterior VMPFC increases with increasing attractiveness ratings and increasing willingness to trade money for faces. These regions included the frontal pole (x,y,z = 4,70,-4), TPJ (x,y,z = -40,-60,32), middle temporal gyrus (x,y,z = -66,-32,-6), and posterior cingulate (x,y,z = -2,-46,20). All areas of activation passed an initial cluster-forming threshold of z=2.3, with whole-brain cluster correction at p=0.05.
Acknowledgments

My professional and personal development are inextricably linked to my experiences in graduate school at Duke. These experiences were shaped by my advisors, colleagues, and friends—and without them, this dissertation would not be possible. I have many people to thank, and I regret that this list will inevitably be woefully incomplete.

I first want to acknowledge that the studies presented in this dissertation represent collaborative efforts, and I thank my collaborators for their insights and contributions to each of the projects presented in this dissertation (as well as the projects that are not represented in this dissertation). I specifically want to thank John Clithero, McKell Carter, Chris Coutlee, and Vinod Venkatraman, for helping shape my understanding of neuroimaging and its application to decision neuroscience. I am also thankful that I have had the opportunity to pursue both neuroimaging and electrophysiological experiments with Michael Platt and Ben Hayden. Their healthy skepticism of neuroimaging research has always encouraged me to try and go beyond typical neuroimaging work by grasping the methodological details and limitations of this technique. Finally, I also want to thank my former mentor, Chris Rorden, for his continued support throughout graduate school, including the opportunity to work on several cutting-edge methodological problems in neuroimaging. His guidance and
expertise have been instrumental in helping me become an independent neuroimaging researcher.

My academic home, the Huettel Lab, has been extremely supportive—both intellectually and personally. Its members, both past and present, have always been there for me, through the most challenging times and the most rewarding times. I especially want to thank John Clithero, Chris Coutlee, Adrienne Taren, Amy Winecoff, McKell Carter, and Vinod Venkatraman, for their unwavering and continued support. Without them, the challenging times would have been insurmountable and the rewarding times would have been far less rewarding.

In addition, I want to thank my dissertation committee—Roberto Cabeza, Tim Strauman, and Michael Platt—for their input and guidance over the years. Their diverse perspectives have forced me to think about my work in broader terms, and I look forward to integrating their viewpoints into my future work.

I also thank my family, for their support and their perspectives on my work. Though indirectly, they have encouraged me to think about the practical implications and interpretations of my research—i.e., why science is important.

Last, but certainly not least, I would like to thank Scott Huettel, who has been an amazing mentor and academic advisor. I cannot say enough kind words about him and his influence on me as a scientist and as a person. I can only hope to eventually pay it forward and model my own lab after his wonderful example.
1. Decision Neuroscience: Neuroeconomics

Humans and other animals continually make decisions: Should I give up a sure immediate reward for a larger, but risky reward in the future? Should I take an aggressive or passive stance toward my competitor? Is this a fair trade? Poor decision making is a hallmark of many cognitive disorders, from addiction to schizophrenia. Over the past decade, there has been dramatic growth in the use of neuroscience methods to study the mechanisms of decision making. Here, I summarize some key insights and describe ongoing challenges from this new interdisciplinary of “decision neuroscience” or “neuroeconomics”. Although these two terms have been used synonymously throughout the literature, I use the former term hereafter for clarity and breadth.

1.1 Decision Variables

The cardinal goal of decision neuroscience research has been to identify the neural mechanisms that shape individual choice behavior (Doya, 2008; Glimcher & Rustichini, 2004; Platt & Huettel, 2008; Rangel, Camerer, & Montague, 2008; Sanfey, 2007; Sanfey, Loewenstein, McClure, & Cohen, 2006). Most studies have adopted a “decision variable” approach: first identify an economic phenomenon of interest, then abstract that phenomenon into a format amenable to neuroscience research, next choose

---

1 This chapter uses material from a coauthored review paper published in Wiley Interdisciplinary Reviews: Cognitive Science (Smith & Huettel, 2010).
one or more variables that modulate decision, and finally identify aspects of brain function that track changes in those decision variables. In this section, we focus on the three most common classes of decision variables: value, uncertainty, and social interactions.

1.1.1 Value: Dopamine and Reward Prediction

The fundamental elements of any decision are its potential outcomes, and specifically their values. An extensive literature implicates the neurotransmitter dopamine in assigning value based on environmental stimuli (Schultz, 2000, 2006, 2007; Wise & Rompre, 1989). Dopaminergic neurons in the brainstem’s ventral tegmental area (VTA) project to several subcortical and cortical targets, most notably to the nucleus accumbens in the ventral striatum (vSTR). It was originally believed that dopamine coded for the hedonic impact of rewards (Bishop, Elder, & Heath, 1963; Olds & Milner, 1954; Olds & Fobes, 1981; Wise, 1982; Wise, Spindler, deWit, & Gerberg, 1978), and this viewpoint remains common within popular accounts of dopamine as the “pleasure chemical”. More recent work, however, emphasizes dopamine’s role in motivated behavior, including altering the salience of incentives (Berridge, 1996; Berridge, 2007; Berridge & Robinson, 1998) and updating models of future rewards (Schultz, Dayan, & Montague, 1997). It should be also noted that some authors have questioned whether dopamine specifically contributes to reward processing, in itself (e.g., Cannon & Bseikri, 2004).
Reward prediction errors (RPE) arise when a stimulus provides information that changes expectations of the timing, amount, or content of future rewards. Early studies by Schultz and colleagues (Schultz, 1998a, 1998b; Schultz et al., 1997; Schultz, Tremblay, & Hollerman, 1998) used electrophysiological methods to track changes in neuron firing rate to cues that predicted a reward (e.g., fruit juice) that was delivered a few seconds later. At the beginning of the experiment, before the monkey learned that a given cue predicted any subsequent reward, the neuronal activity in VTA only increased to the delivery of the rewarding fruit juice. As the monkeys learned that the cue predicted future rewards, the cue evoked increasing VTA activity but activity to the reward itself diminished. Once the cue-reward contingency was established, the researchers omitted some expected rewards and found that VTA activity decreased below baseline firing rates. Based on these results, Schultz and colleagues interpreted the firing rate of dopaminergic neurons to carry RPE signals (Schultz et al., 1997), which provides a computationally tractable method for tracking changes in value.

Signals consistent with reward prediction errors have since been identified in neurons in the ventral striatum (vSTR) (Schultz et al., 1998) and ventromedial prefrontal cortex (Schultz et al., 1998; Tremblay & Schultz, 2000). Similar prediction errors have recently been reported in human dopaminergic neurons in the substantia nigra (Zaghloul, Blanco, Weidemann, McGill, Jaggi, Baltuch, & Kahana, 2009). Studies using functional magnetic resonance imaging (fMRI) also have shown that reward
predictability modulates the response to reward in the vSTR (Berns, McClure, Pagnoni, & Montague, 2001; McClure, Berns, & Montague, 2003) and the VTA (D’Ardenne, McClure, Nystrom, & Cohen, 2008). Collectively these results have led to the common conclusion that key dopaminergic regions (i.e., VTA and vSTR) and their targets (e.g., ventromedial prefrontal cortex, VMPFC) constitute the brain’s reward system (Figure 1). Nevertheless, the processing of reward is not limited to these regions. For example, an early primate electrophysiology study by Platt and Glimcher (Platt & Glimcher, 1999) demonstrated that activity of neurons in posterior parietal cortex was highly correlated with value of different response options. These and similar results from brain regions associated with response selection and motor output (Deaner & Platt, 2003; Dorris & Glimcher, 2004; McCoy, Crowley, Haghhighian, Dean, & Platt, 2003; McCoy & Platt, 2005) indicate that value information can modulate processing at many stages of decision making.
Figure 1: Brain regions supporting reward processing and value computation. Reward experience and evaluation evokes activation in several interconnected brain regions within the brain’s dopaminergic system. Key regions include the ventral tegmental area (VTA), the ventral striatum (vSTR), and the ventromedial prefrontal cortex (VMPFC).

1.1.2 Value: Alternative Explanations

The role of the dopaminergic system in forming and updating predictions about rewards is now well established (reviewed in Schultz, 2006). Yet, intriguing research points to other interpretations for the functions of these regions. One key focus of current research examines potentially separate signals associated with anticipation and receipt of rewards. Knutson and colleagues took the basic paradigms used in prior primate electrophysiology studies and create a novel response-time task suitable for fMRI (Knutson, Westdorp, Kaiser, & Hommer, 2000). At the beginning of each trial, participants viewed a single cue that indicated the potential monetary consequences of
that trial (e.g., a gain or loss). Then, following a short and variable delay, a target appeared. If the participant pressed a button sufficiently quickly thereafter, then the monetary reward would be delivered (or a monetary punishment would be avoided). During the period in which participants anticipated potential rewards, Knutson and colleagues observed robust striatal and medial prefrontal activation, consistent with the role of these regions in reward anticipation. This basic paradigm, called the Monetary Incentive Delay (MID) task, has become a common approach for eliciting anticipation-related activation in reward-related regions (reviewed in Knutson & Greer, 2008).

Similarly, early fMRI studies using gambling games revealed that receipt of monetary rewards evoked vSTR activation (Breiter, Aharon, Kahneman, Dale, & Shizgal; Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Elliott, Friston, & Dolan, 2000). Delgado and colleagues (Delgado et al., 2000) used a card-guessing task in which correct guesses were associated with monetary gains, but incorrect guesses were associated with monetary losses. They found that activation in the vSTR increased to winning, compared to losing trials. Some evidence indicates, however, that reward receipt evokes activation specifically in the VMPFC (Knutson, Fong, Adams, Varner, & Hommer, 2001b; Knutson, Fong, Bennett, Adams, & Homme, 2003), consistent with a role of that region in computing the expected value of a reward (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005). Considered generally, activation in VMPFC (and adjacent orbitofrontal cortex, OFC) may reflect the assessed value of rewards. Studies using single-unit
recordings indicate that the responsiveness of VMPFC neurons to rewards depends on the monkey’s satiation (Critchley & Rolls, 1996; Rolls, Sienkiewicz, & Yaxley, 1989), a conclusion that has since been replicated in human participants using fMRI (Kringelbach, O’Doherty, Rolls, & Andrews, 2003; O’Doherty, Rolls, Francis, Bowtell, McGlone, Kobal, Renner, & Ahne, 2000). (While we note that studies in primates have focused on central and lateral orbital frontal cortex neurons, for simplicity, we refer to this region as VMPFC; assessing neuronal similarities across orbital frontal cortex and VMPFC will be an important objective for future research in decision neuroscience.)

Value computations in VMPFC likely play an important role during active decision making, as considered later in this review.

While decision neuroscience research has most commonly used monetary rewards (in humans) and juice rewards (in monkeys), strong evidence indicates that reward-related responses generalize to a wide range of stimuli. Neuroimaging and single-unit experiments have observed vSTR and VMPFC activation in response to many sorts of sensory rewards, including tastes (Berns et al., 2001; O’Doherty, Rolls, Francis, Bowtell, & McGlone, 2001b; O’Doherty, Deichmann, Critchley, & Dolan, 2002; Small, Gregory, Mak, Gitelman, Mesulam, & Parrish, 2003), smells (Anderson, Christoff, Stappen, Panitz, Ghahremani, Glover, Gabrieli, & Sobel, 2003; Gottfried, O’Doherty, & Dolan, 2002), touch (Rolls, O’Doherty, Kringelbach, Francis, Bowtell, & McGlone, 2003), attractive faces (Aharon, Etcoff, Ariely, Chabris, O’Connor, & Breiter, 2001; Cloutier,

Value learning requires consideration of both positive and negative outcomes. Electrophysiological studies have identified sets of neurons within the VTA that code for either aversive or appetitive events (Brischoux, Chakraborty, Brierley, & Ungless, 2009; Joshua, Adler, Mitelman, Vaadia, & Bergman, 2008), which could potentially project into distinct regions of the striatum for separate processing of losses and gains (Seymour, Daw, Dayan, Singer, & Dolan, 2007a). Notably, aversive stimuli can also evoke activation in similar brain regions as rewarding stimuli depending on context (Becerra, Breiter, Wise, Gonzalez, & Borsook, 2001; Jensen, McIntosh, Crawley, Mikulis, Remington, & Kapur, 2003; Kim, Shimojo, & O'Doherty, 2006).
Finally, some research suggests that the dopaminergic system may signal a broader class of environmental events than just reinforcers. In particular, research points to a potential role for the striatum, at least, in the response to salient but non-rewarding events (Zink, Pagnoni, Chappelow, Martin-Skurski, & Berns, 2006; Zink, Pagnoni, Martin, Dhamala, & Berns, 2003; Zink, Pagnoni, Martin-Skurski, Chappelow, & Berns, 2004). For example, vSTR activation can be evoked by unexpected but meaningful auditory stimuli (e.g., sirens, dog barks) in the absence of any overt rewards (Zink et al., 2006). Important evidence in support of a salience perspective would come from the demonstration of valence-independent changes (e.g., increases in activation to both positive and negative cues and/or outcomes). Recent attempts to dissociate reward salience from reward valence have led to equivocal results, at least within the vSTR, with evidence both for (Cooper & Knutson, 2008) and against (Jensen, Smith, Willeit, Crawley, Mikulis, Vitcu, & Kapur, 2007; Litt, Plassmann, Shiv, & Rangel, 2011) valence-independent activation. Future studies will be necessary to reconcile these disparate perspectives.

### 1.1.3 Uncertainty

A second important decision variable is uncertainty. Considered in a psychological (Garner, 1962) or economic (Knight, 1921) context, uncertainty reflects the absence of some desired information—such as about the timing, content, value, or certainty of future rewards. Uncertainty pervades many real-world decisions, and
organisms actively seek to reduce uncertainty in many contexts. Note that uncertainty is intimately connected to reward valuation; cues about future rewards, by definition, minimize uncertainty. As shown by Fiorillo and colleagues (Fiorillo, Tobler, & Schultz, 2003), the pattern of cue- and reward- dopamine neuron activity described in the previous section scales with probability: as the probability of reward increases, cue-related activity increases but outcome-related activity decreases. The same study also indicates that uncertainty may lead to sustained activity of dopaminergic neurons during anticipation periods (Fiorillo et al., 2003). And, valuation-related activation of the striatum tracks probability in a nonlinear manner, consistent with probability weighting functions identified behaviorally (Hsu, Krajbich, Zhao, & Camerer, 2009).

When uncertainty reflects known probabilities, decisions involve risk. Studies of risky choice typically ask participants to select between outcomes with different probability of reward or with different variances of potential reward distributions. Across numerous studies, key areas involved in risky decision making include ventrolateral and orbital prefrontal cortex, anterior cingulate cortex, posterior parietal cortex, and insular cortex (Behrens, Woolrich, Walton, & Rushworth, 2007; Huettel, 2006; Huettel, Song, & McCarthy, 2005; Huettel, Stowe, Gordon, Warner, & Platt, 2006; McCoy & Platt, 2005; Preuschoff, Quartz, & Bossaerts, 2008) (Figure 2). Given the complexity of risky choice, parsing the distinct contributions of these regions remains an active area of study. One important target for current research has been anterior insular cortex.
Building upon prior research linking this region to representations of bodily states, Bechara, Damasio, and their colleagues have linked the insula (and VMPFC) to internal feedback signals that may shape behavior away from potential negative consequences (Bechara, Damasio, & Damasio, 2000; Damasio, 1996). Consistent with this idea, insular activation increases both to stimuli that signal increasing environmental risk (Huettel et al., 2005; Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003) and attempts to minimize risk (Kuhnen & Knutson, 2005). Recent work by Preuschoff and colleagues (Preuschoff et al., 2008) suggests that activation of the anterior insula represents a signal for a risk prediction error. Under their model, the anterior insula tracks unexpected changes in risk, based on new information or decision outcomes. This intriguing result may provide an important link to cognitive neuroscience studies of the role of insular cortex in cognitive control.
Figure 2: Brain regions supporting decision uncertainty. Several brain regions respond to uncertainty, or situations lacking desired information about the timing, content, value, or certainty of rewards. These include the insular cortex (Ins), anterior cingulate cortex (ACC), lateral prefrontal cortex (LPFC), and posterior parietal cortex (PPC).

A smaller set of studies have examined the effects of ambiguity, or unknown probabilities, upon decision making. Consider the following example, adapted from Ellsberg (Ellsberg, 1961). In front of you are two urns, each with 100 colored balls. The left urn has exactly 50 red balls and 50 blue balls, while the right urn has an unknown number of red balls and an unknown number of blue balls (and no other colors). You win a monetary prize if you declare a color, reach into the urn, and pull out a ball of your chosen color. What do you do? When faced with analogues of this decision in the laboratory, most individuals choose to pull a ball from the left, or risky, urn. But, examination of the decision problem reveals that the chances of winning are exactly the same in either case (i.e., 50%). When Hsu and colleagues (Hsu, Bhatt, Adolphs, Tranel, &
presented similar decision problems to participants in a fMRI session, they found that lateral orbitofrontal cortex and the amygdala exhibited significantly greater activation to decisions involving ambiguity, compared to decisions involving risk. A similar approach was used by Huettel and colleagues (Huettel et al., 2006), who observed ambiguity-related activation in different regions: the insula, the posterior parietal cortex, and the lateral prefrontal cortex, with the last of these also tracking ambiguity preferences. These disparate results may reflect distinct aspects of ambiguity-related processing. The lateral orbitofrontal cortex, in particular, has been associated with aversion to negative events (for a review, see Krningelbach & Rolls, 2004; e.g., O'Doherty, Krningelbach, Rolls, Hornak, & Andrews, 2001a). This interpretation is supported by lesion data reported by Hsu and colleagues (2005), who found that patients with orbitofrontal cortex damage exhibited decreased aversion to ambiguity (and risk). Conversely, regions of prefrontal and parietal cortex may be critical for forming representations of potentially knowable information, as recently shown by Bach and colleagues (Bach, Seymour, & Dolan, 2009).

Uncertainty can also be induced by increasing the delay before a reward is received, which leads subjects to devalue potential rewards (i.e., temporal discounting). To account for known anomalies in intertemporal choice, researchers have proposed that temporal discounting reflects two processes: an impulsive system (β) that rapidly devalues rewards that are not immediately attainable, and a patient system (δ) that
exhibits much more gradual discounting. Studies by McClure and colleagues (McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007; McClure, Laibson, Loewenstein, & Cohen, 2004) supported this two-system model, such that the β system comprises reward-related regions including the vSTR and the VMPFC, whereas the δ system includes cognitive regions like lateral parietal and lateral prefrontal cortices. Other research has cast doubt onto the β-δ model with evidence that intertemporal choices follow from activation of a single system for subjective value (Kable & Glimcher, 2007) comprising vSTR, posterior cingulate cortex, and VMPFC. Of particular relevant for resolving this debate will be paradigms that examine delay discounting as it occurs, as has been explored in a few recent studies (Gregorios-Pippas, Tobler, & Schultz, 2009; Luhmann, Chun, Yi, Lee, & Wang, 2008; McClure et al., 2007).

### 1.1.4 Social Interactions

Real-world decision making often involves social settings where individuals must not only consider the value and uncertainty of outcomes, but also incorporate information about other individuals (Sanfey, 2007). Decision neuroscience research has investigated two main classes of information about other individuals: their actions (e.g., in competitive games) and their characteristics (e.g., facial features).

Studies of social interactions often first constrain behavior using interactive games with well-defined rules and payoffs (Von Neumann & Morgenstern, 1944), and then implement psychological parameters (e.g., guilt, envy, fairness, equity) into
subsequent analyses. This general approach has provided valuable insights about the mechanisms underlying cooperation (Rilling, Gutman, Zeh, Pagnoni, Berns, & Kilts, 2002; Singer, Kiebel, Winston, Dolan, & Frith, 2004), fairness (Hsu, Anen, & Quartz, 2008; Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Tabibnia, Satpute, & Lieberman, 2008), altruism (Harbaugh et al., 2007; Moll et al., 2006; Tankersley, Stowe, & Huettel, 2007), punishment (Buckholtz, Asplund, Dux, Zald, Gore, Jones, & Marois, 2008; de Quervain, Fischbacher, Treyer, Schellhammer, Schnyder, Buck, & Fehr, 2004; Seymour, Singer, & Dolan, 2007b).

Most such studies have used fMRI to scan one individual who interacts with other participants, whether real or computer generated, outside of the scanner. For example, research by Sanfey and colleagues (Sanfey et al., 2003) using the Ultimatum Game demonstrated that activation in the anterior insula increased to others’ unfair actions, whereas activation of lateral prefrontal cortex increased when ignoring unfairness and accepting an offered reward. Another important approach has been hyperscanning, which involves scanning multiple individuals simultaneously (King-Casas, Tomlin, Anen, Camerer, Quartz, & Montague, 2005; Montague, Berns, Cohen, McClure, Pagnoni, Dhamala, Wiest, Karpov, King, & Apple, 2002). The power of this latter approach was first shown by King-Casas and colleagues, who scanned pairs of subjects while they interacted in an investment game (King-Casas et al., 2005). This game requires one player to trust the other with some of their money, whereupon if the
trust is reciprocated both players benefit. By identifying correlations between the activation patterns of two subjects’ brains, these researchers provided evidence that activation of the caudate was consistent with the development of an intention to trust. Note that while most research on social interactions has used human participants, some primate electrophysiology research has set up decision scenarios modeled on competitive games (Barraclough, Conroy, & Lee, 2004; Dorris & Glimcher, 2004). For example, Barraclough and colleagues (Barraclough et al., 2004) demonstrated that neurons in DLPFC encoded decision variables critical for strategic choice (e.g., interactions between past decisions and opponent tendencies).

Social interactions can themselves be highly rewarding (Fehr & Camerer, 2007). For example, Rilling and colleagues (2002) reported activation in reward-related regions when individuals cooperated during a repeated Prisoner’s Dilemma game (Rilling et al., 2002). Reward can also be derived from punishing others; as shown by de Quervian and colleagues (de Quervain et al., 2004), punishing a non-cooperative counterpart evokes activation in the ventral caudate. Recently, Hsu and colleagues (Hsu et al., 2008) examined fairness by allowing participants to distribute food donations to groups of Ugandan orphans. They found the striking results that the efficiency (i.e., overall amount of food) and inequity (i.e., imbalance of allocations across individuals) of food donations were tracked in distinct regions—the putamen and insula, respectively—with the tradeoff between these parameters expressed in the caudate activation. As shown by
these studies, the decision variables identified earlier in this review for individual choice behavior also modulate social interactions. Yet, despite these similarities, it remains unclear whether individual and social decisions involve similar coding at the neuronal level.

Social interactions also rely on gaining information about others’ characteristics. Particularly relevant are faces, whose complexity and informational properties make them intrinsically rewarding (Little, Jones, Waitt, Tiddeman, Feinberg, Perrett, Apicella, & Marlowe, 2008). Attractive faces reliably evoke activation in the VMPFC, as seen in a wide range of experimental paradigms (Aharon et al., 2001; Cloutier et al., 2008; O’Doherty et al., 2003; Winston et al., 2007). However, activation in ventral striatum has been only infrequently observed (Aharon et al., 2001; Cloutier et al., 2008). Moreover, recent work has demonstrated that heterosexual males will trade small amounts of money to view photographs of attractive females (Hayden, Parikh, Deaner, & Platt, 2007), paralleling previous research showing that male monkeys will sacrifice juice rewards to view images of females’ perinea (Deaner, Khera, & Platt, 2005; Klein, Deaner, & Platt, 2008). Heterosexual males will also work (i.e., exert effort) to view photographs of attractive females (Aharon et al., 2001; Hayden et al., 2007). Furthermore, it has also been found that the reward value of viewing an attractive face increases with increasing duration of presentation (Hayden et al., 2007).
How is social information integrated with non-social information to guide behavior? Some brain systems may play roles specifically in social decision making. Research in both humans (Behrens, Hunt, & Rushworth, 2009) and monkeys (Rudebeck, Buckley, Walton, & Rushworth, 2006) has demonstrated that distinct regions of the medial prefrontal cortex compute social and non-social information: the anterior cingulate sulcus tracks changes in reward expectations, whereas the anterior cingulate gyrus responds to social information. Moreover, regions involved in social cognition—particularly the temporal-parietal junction (TPJ) (Figure 3)—also contribute to decision processes (Behrens, Hunt, Woolrich, & Rushworth, 2008). However, most regions that support decision making likely do so in both individual and social contexts (see Behrens et al., 2009; Lee, 2008 for reviews). In the next section, we consider how the brain may integrate information from a variety of sources to reach decisions.

Figure 3: Brain regions supporting social cognition. Assessing the intentions of others reliably evokes activation in the temporal parietal junction (TPJ).
1.2 Value Comparison

Neuroeconomic research often seeks to understand how value computations lead to specific choices (Glimcher & Rustichini, 2004; Rangel et al., 2008; Sanfey et al., 2006). To facilitate value comparison, a variety of goods, experiences, and actions must be converted into some sort of “common currency” wherein comparisons can quickly and efficiently be made upon the same relative scale (Montague & Berns, 2002). Elucidating the specific computations that underlie a common currency representation would have important implications for valuation and decision making (Montague & King-Casas, 2007). Of note, however, relatively few decision neuroscience studies have used multiple reward modalities, as necessary for evaluating relative valuation.

Yet in recent years, there has been substantial interest in relative valuation, often in the context of economic exchanges like purchasing decisions. A common fMRI paradigm allows participants to trade money earned in the experimental setting for goods of greater or lesser value. When participants purchased inexpensive familiar objects, subjective value of those goods was correlated with activation in vSTR but not VMPFC, whereas subsequent information about prices modulated activation of VMPFC and insular cortex (Knutson, Rick, Wirnmer, Prelec, & Loewenstein, 2007). In contrast, when hungry participants placed bids on food items that could be consumed after the scanning session, activation in VMPFC was modulated by the subjective desirability of
the food items (Plassmann, O'Doherty, & Rangel, 2007). Additional recent fMRI studies have demonstrated that a similar region of VMPFC is involved in computing the value of items during trading (Hare, Camerer, & Rangel, 2009; Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008). Neurons in ventral prefrontal cortex have also been shown to code for the relative value of juice rewards, across a variety of task parameters and decision contexts (Padoa-Schioppa & Assad, 2006, 2008). These studies thus converge on the idea that VMPFC represents a critical substrate for trading money for another good or service—and potentially, a more general computation of common currency.

Nevertheless, many decisions may rely on more than just brain systems for value computation. Behavioral economics research has identified a variety of anomalies in preferences, including the endowment effect (Thaler, 1980) and framing effects (Tversky & Kahneman, 1981a), that may reflect context-dependent contributions from specific brain regions (reviewed in Clithero & Smith, 2009; Seymour & McClure, 2008). Recent neuroimaging studies of the endowment effect, or the tendency to overvalue goods that one already possesses, indicate that activation in the vSTR tracks value in a largely reference-dependent manner (De Martino, Kumaran, Holt, & Dolan, 2009; Knutson, Wimmer, Rick, Hollon, Prelec, & Loewenstein, 2008). Framing effects occur when the manner of representing a decision problem (e.g., describing outcomes either as losses or as gains from different points of reference) biases individuals toward one choice or another. Decisions consistent with framing effects evoke increased activation in the
amygdala, while decisions inconsistent with framing effects evoke increased activation in dorsomedial prefrontal cortex (De Martino, Kumaran, Seymour, & Dolan, 2006); the latter effect may reflect the role of this region in implementing strategies for decision making (Venkatraman, Payne, Bettman, Luce, & Huettel, 2009a).

Adaptive decision makers should also incorporate value information from decisions that are not made; i.e., from rewards that are observed, but not received, or “fictive” outcomes (Chiu, Lohrenz, & Montague, 2008; Hayden, Pearson, & Platt, 2009a; Lohrenz, McCabe, Camerer, & Montague, 2007). Building from prior neuroimaging work that suggested the vSTR responds to fictive outcomes (Chiu et al., 2008; Lohrenz et al., 2007), a recent electrophysiological recording study in monkeys indicated that single neurons in anterior cingulate cortex (ACC) track fictive outcomes (Hayden et al., 2009a). Critically, neurons representing fictive outcomes utilized a similar coding scheme as neurons that represented experienced outcomes. These studies demonstrate that at least some brain regions incorporate unobtained outcomes into value computations, which may greatly facilitate decision making in dynamic, complex environments.

1.3 Open Questions

Past decision neuroscience studies have highlighted how value computation and decision making rely on key brain systems, including the VMPFC and vSTR. Furthermore, some studies have highlighted how social cognition recruits other brain systems, including the TPJ. Yet, several significant questions remain: How are different
forms of value represented within the VMPFC? How do these value representations shape individual differences in preferences and behavior? Are similar value computations carried out in social contexts where decisions involve other people? How do brain systems involved with social cognition interact with the VMPFC to shape preferences in social decision making?

To examine these questions, my colleagues and I conducted three fMRI studies (Figure 4) that focused on the neural circuitry of social valuation. In study 1 (Chapter 2), we identify distinct value signals within ventromedial prefrontal cortex. In study 2 (Chapter 3), we extend these results to individual differences in social decision making involving donations to charity. In study 3 (Chapter 4), we capitalize upon a major strength of fMRI by examining the interactions between regions supporting value computation and regions supporting social cognition. Taken together, our results provide new mechanistic insight into the neural circuitry of social valuation—with the potential to create new models that will facilitate our understanding of disordered social decision making.
Figure 4: Overview of studies. We conducted three fMRI studies to examine the neural circuitry of social valuation.
2. Distinct Value Signals Within Anterior and Posterior Ventromedial Prefrontal Cortex

The core feature of an economic exchange is a decision to trade one good for another, based on a comparison of relative value. Economists have long recognized, however, that the value an individual ascribes to a good during decision making (i.e., their relative willingness to trade for that good) does not always map onto the reward they actually experience. Here, we show that experienced value and decision value are represented in distinct regions of ventromedial prefrontal cortex (VMPFC) during the passive consumption of rewards.

2.1 Introduction

In economic exchanges, individuals sacrifice their capital to obtain goods, presumably because the benefit of the good outweighs its cost. There has been substantial progress toward identifying the neural mechanisms of valuation (Breiter et al., 2001; Delgado et al., 2000; Knutson et al., 2001b; Knutson et al., 2003; O'Doherty et al., 2001a). Key brain regions, as identified by primate electrophysiology and human neuroimaging, include the ventral striatum (vSTR) for learning about reward contingencies (Knutson & Cooper, 2005; Schultz, 2006) and the ventromedial prefrontal cortex (VMPFC) for evaluating reward outcomes (Blair, Marsh, Morton, Vythilingam, Jones, Mondillo, Pine, Drevets, & Blair, 2006; Padoa-Schioppa & Assad, 2008).

1 This chapter uses material from a coauthored paper published in the Journal of Neuroscience (Smith et al., 2010).
Relatively less is known about how these and related brain regions interact in the course of economic exchange. Across a number of recent neuroscience studies, participants have traded money earned in the experimental setting for subsequently received goods (De Martino et al., 2009; Hare et al., 2009; Hare et al., 2008; Knutson et al., 2007; Knutson et al., 2008; Plassmann et al., 2007). When participants purchased inexpensive familiar objects, subjective value was correlated with activation in vSTR but not VMPFC, whereas price information modulated activation of VMPFC and insula (Knutson et al., 2007). In contrast, when hungry participants placed bids on food items that could be consumed after the scanning session, activation in VMPFC was modulated by the subjective desirability of the food (Plassmann et al., 2007). Thus, converging evidence indicates that VMPFC carries signals that support economic exchange, particularly in the representation of decision value. However, all neuroscience studies of economic exchange have estimated the value of goods, such as electronics, food, or money, from decisions made prior to consumption. This approach precludes separation of the neural representations of the value of a good during decision making [decision value, or goal value in the terminology of Hare and colleagues (2008)] from the value derived from its consumption (experienced value).

Social rewards, such as photographs of attractive people, provide an ideal good for disentangling neurometric measurements of experienced value and decision value. Unlike monetary rewards, the experienced value derived from images of attractive
people occurs immediately at presentation, and thus can be measured during a neuroimaging session (Aharon et al., 2001; Hayden et al., 2007; O'Doherty et al., 2003; Winston et al., 2007). Indeed, heterosexual males will trade small amounts of money or expend effort to view photographs of attractive females during experimental sessions (Hayden et al., 2007).

We hypothesized that individuals’ idiosyncratic VMPFC responses to passively experienced rewards would predict their subsequent economic exchanges. To test this hypothesis, we collected fMRI data from heterosexual male adults in a multimodal reward task offering two types of rewards: photographs of female faces varying in attractiveness and images indicating receipt of money (Figure 5A). Because of the potentially confounding effects associated with reward anticipation (Knutson et al., 2001b; Knutson et al., 2003; O'Doherty et al., 2002), participants viewed all images passively, with no response required for their delivery. In a subsequent economic exchange task, participants traded money to view novel faces; they could spend more money to view a more attractive face, or less money to view a less attractive face (Figure 5B). From the rate of exchange, we estimated each participant’s relative decision value for monetary and social rewards. Our analyses addressed three key and unanswered questions: Do distinct regions within VMPFC signal a good’s experienced value and its decision value? Second, are neural representations of decision values computed even in the absence of decision making? Third, are these representations independent of the type of reward?
2.2 Materials and Methods

2.2.1 Participants

Twenty-six self-reported heterosexual male participants completed the study (age range: 18-28y; mean age 21.8y). Data from 3 participants were excluded prior to analyses because of excessive head movement (>4mm) or experimental non-compliance, leaving 23 individuals in the final sample. Participants were given a $40 endowment, earned an additional $15 to $25 based on the passively viewed monetary stimuli, and spent an average of $4.31 to view attractive faces. All participants gave written informed consent under a protocol approved by the Institutional Review Board of Duke University Medical Center.

2.2.2 Stimuli and Tasks

In the multimodal reward task (Figure 5A), participants were presented with a succession of images drawn from two categories: photographs of U.S. currency and photographs of female faces. The currency photos ($5, $2, or $1) were either normal colors (indicating a gain) or red (indicating a loss). The face images were drawn from a large stimulus set we downloaded from a free public website (http://www.hotornot.com).
Figure 5: Experimental tasks. (A) Trial structure for the *multimodal reward task*. Male, heterosexual young adults passively viewed a randomized sequence of images of female faces and monetary rewards (2 s event duration; 2 s fixation interval). The face images varied in valence from very attractive to very unattractive, based on ratings from an independent group of participants. The monetary rewards, whose value ranged from $5 to -$5, influenced the participant’s overall payout from the experiment. To ensure task engagement, participants responded to infrequent visual targets that appeared as small yellow borders around the image. (B) Trial structure for the *economic exchange task*. Trials began with a decision phase (lasting 4 s) in which the participant was forced to spend a small amount of money to view a face. Participants could choose to spend more money to view a more attractive face or less money to view a less attractive face. Following the decision phase, there was an anticipation phase that lasted either 2 s or 4 s. Then a single face, randomly selected from the chosen attractiveness category, was displayed for 2 s. Trials were separated by a variable interval whose duration ranged from 2 s to 6 s.

Face images were cropped to show only the face and were resized to uniform dimensions. Before the main fMRI study, these photographs were rated for attractiveness (on a 10-point scale) by a separate cohort of heterosexual young-adult males (N = 16) who did not participate in subsequent studies. To remove individual bias in the use of the response scale, ratings were normalized by converting to z-scores for
each participant and then averaged across all raters. We excluded from our stimulus set 83 photographs whose variability across raters was more than two standard deviations [SDs] above the average for all photographs. Using these normalized attractive ratings, we identified four categories of attractiveness (Table 1).

Table 1: The attractiveness categories used in the present experiment. All are drawn from the distribution of normalized attractiveness ratings, with ratings here expressed as z-scores.

<table>
<thead>
<tr>
<th>Category</th>
<th>min</th>
<th>max</th>
<th>mean</th>
<th>SD</th>
<th>N of photos</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-star</td>
<td>-2.11</td>
<td>-1.05</td>
<td>-1.36</td>
<td>0.23</td>
<td>138</td>
</tr>
<tr>
<td>2-star</td>
<td>-0.68</td>
<td>-0.32</td>
<td>-0.47</td>
<td>0.06</td>
<td>174</td>
</tr>
<tr>
<td>3-star</td>
<td>0.34</td>
<td>0.69</td>
<td>0.48</td>
<td>0.07</td>
<td>157</td>
</tr>
<tr>
<td>4-star</td>
<td>1.02</td>
<td>2.48</td>
<td>1.43</td>
<td>0.28</td>
<td>130</td>
</tr>
</tbody>
</table>

Participants first participated in five 60-trial runs of the multimodal reward task. On each trial, a single image appeared at fixation for 2 s, followed by a 2-s fixation interval, providing a minimum stimulus onset asynchrony (SOA) of 4 s. Face and monetary photographs appeared equally often and in randomized order. The face stimuli were equally likely to be drawn from each of the four attractiveness categories. So that each run resulted in a net monetary gain, two-thirds of the monetary images indicated gains and one-third indicated losses. No response was required to either type of stimulus. To ensure attention to the experimental stimuli, the participants pressed a button to the occurrence of an infrequent (<5% of all trials) small yellow border around the edge of the images. At the end of the session, each participant rolled a die to select
one of the runs and received the earnings from that run as a supplement to the endowment (range: $15 to $25).

Next, participants completed an economic exchange task (Figure 5B). On each trial, participants chose between two options, each involving the sacrifice of a monetary payment (1 to 12 cents) for the opportunity to view a face from a known attractiveness category (1- to 4-stars for increasing attractiveness). Both payment and attractiveness varied randomly across trials within uniform distributions, with the constraints that the two face options always differed in attractiveness and that the more attractive face always carried the greater monetary cost. Participants thus decided whether to sacrifice a greater amount of money to view a more attractive face. After a 4-s decision window, the screen went blank for a variable anticipation interval of 2-4 s, before a face from the selected category was presented for 2 s. The intertrial interval ranged from 2-6 s.

Participants made between 75 and 150 decisions during the economic exchange task.

Both tasks were programmed using the Psychophysics Toolbox version 2.54 (Brainard, 1997). Stimuli were projected onto a screen at the back of the scanner bore, and participants viewed the stimuli through mirrored goggles. Responses were recorded using a MRI-compatible button box.

Following the main experiment, participants rated the attractiveness of the presented female faces. These post-experiment ratings were nearly identical to preliminary ratings from the independent cohort of participants that had been used for
establishing attractiveness categories (mean $r = 0.82 \pm 0.07$), indicating that our mapping of stimuli to categories was appropriate for our participant sample.

### 2.2.3 Estimating Decision Value

From our economic exchange task, we calculated two measures of decision value for each participant: the proportion of trials in which the participant sacrificed money to view a more attractive face, and the willingness to pay (WTP) for a one-star increment in attractiveness. Prior studies have calculated WTP from decisions to procure a good, usually within the context of an incentive-compatible auction (cf. Plassmann et al., 2007). Here, we identified the minimum relative cost (i.e., the price difference between the two options) that was sufficient to predict an economic exchange (i.e., a trial in which the participant chose the more expensive/attractive option). We estimated WTP using an iterative technique that determined the amount of money (stepping from 0 to 20 cents in 1-cent increments) that best predicted the actual decisions made by that subject.

### 2.2.4 Image Acquisition

Functional MRI data sensitive to blood-oxygenation-level-dependent (BOLD) contrast were acquired using a novel spiral-in SENSE sequence (acceleration factor = 2), as implemented on a 3 Tesla General Electric scanner with an 8-channel receiver. We chose this sequence in order to reduce susceptibility artifacts and recover signal in ventral frontal regions of interest (Pruessmann, Weiger, Bornert, & Boesiger, 2001; Truong & Song, 2008). Each participant performed 5 runs, each consisting of 122
volumes (TR: 2 s; TE: 27 ms; voxel dimensions: 4 x 4 x 4 mm; 30 slices; 64 x 64 matrix; FOV: 256 mm; flip angle: 60°). The first 8 volumes of each run were discarded to allow for magnetic stabilization. High-resolution anatomical images were acquired to aid in normalization and coregistration (T1-weighted 3D IR-prep GRE sequence; TR: 7.2 ms; TE: 2.9 ms; voxel dimensions: 1 x 1 x 2 mm; 256 x 224 matrix; FOV: 256 mm; flip angle: 12°).

2.2.5 FMRI Data Analysis

Analyses were conducted using the FSL analysis package (Smith, Jenkinson, Woolrich, Beckmann, Behrens, Johansen-Berg, Bannister, De Luca, Drobnjak, Flitney, Niazy, Saunders, Vickers, Zhang, De Stefano, Brady, & Matthews, 2004). We corrected for head motion by realigning the time series to the middle volume (Jenkinson, Bannister, Brady, & Smith, 2002). Non-brain material was removed using the brain extraction tool (Smith, 2002). Differences in slice acquisition time were corrected using Fourier-space phase-shifting. Spatial smoothing used a Gaussian kernel of full-width-half-maximum 6mm. The entire 4D dataset was grand-mean intensity normalized using a single multiplicative factor. To remove low frequency drift in the MR signal, we used a high-pass temporal filter (Gaussian-weighted least-squares straight line fitting, with sigma = 50s). Functional data were registered to stereotaxic space (MNI; Montreal Neurological Institute) (Jenkinson & Smith, 2001).
Before applying a general linear model (GLM), we removed noise in our preprocessed data using independent components analysis (ICA). We first conducted a probabilistic ICA using MELODIC (Beckmann & Smith, 2004). We next applied an automated technique that classified noise components using three heuristics (Smith & Huettel, 2009). First, we classified all components according to the frequency at which maximum power was observed, and we removed those within the top 10% of that classification distribution (i.e., those with power at the highest frequencies). Second, to identify components associated with transient and discontinuous changes in the MR signal (i.e., those associated with fluctuations in the scanner hardware), we calculated the maximum change for each component within a 6 s moving window and discarded those components in the top 10% of that distribution. Third, we used the motion parameter estimates (three axes of rotation and three directions of translation) from our preprocessing steps to identify the correlation of each component with head motion, removing the 10% with the greatest correlation with one or more head motion parameters. Together, these three steps removed 981 components (27.74%). We note that although the choice of a 90th percentile cutoff is arbitrary, our use of a fixed, a priori criterion and automated component removal eliminates the possibility of subjective bias in preprocessing.

Statistical analyses proceeded in three stages. First, denoised functional data were analyzed using a general linear model with local autocorrelation correction...
For each run, we set up separate statistical models for monetary and social rewards. The monetary reward model comprised six regressors that corresponded to each amount ($5, $2, $1, -$1, -$2, and -$5). The social reward model comprised four regressors representing each level of attractiveness (1-star, 2-star, 3-star, 4-star). A nuisance regressor modeled the target-detection component of the task. All regressors consisted of unit impulses convolved with a canonical hemodynamic response function. Our key contrasts involved bidirectional comparisons of high vs. low monetary value ($5 and $2 gains vs. $5 and $2 losses) and of high vs. low facial attractiveness (4-star vs. 1-star). Secondary contrasts examined the responses to all face images and to all monetary images, independently. We then combined data across runs, for each subject, using a fixed-effects model, and combined data across subjects using a mixed-effects model (Beckmann, Jenkinson, & Smith, 2003; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004). Measures of percent signal change were obtained by converting the mean parameter estimates and normalizing to the lowest reward level in each model; this provides interpretable, albeit independent, baselines for both face and monetary rewards.

Except where noted, all z-statistic (Gaussianised t) images were thresholded using clusters determined by $z > 2.3$ and a corrected cluster-significance threshold of $p < 0.05$ (Worsley, 2001). Statistical overlay images were created using MRICron (Rorden, Karnath, & Bonilha, 2007) and anatomical labels for local maxima were obtained from
the Talairach Client (Lancaster, Woldorff, Parsons, Liotti, Freitas, Rainey, Kochunov, Nickerson, Mikiten, & Fox, 2000). All coordinates in the manuscript are reported in MNI space.

2.3 Results

2.3.1 Behavioral Data

During the multimodal reward task, heterosexual male adults passively viewed two types of images, presented in a randomized sequence: photographs of female faces and photographs of currency. To ensure vigilance, participants performed a simultaneous target detection task by pressing a button to the infrequent (< 5% of all trials) appearance of a small yellow border around the image. Overall target detection accuracy was very good (mean 91% ± 2%, across participants) and was not significantly different between the two classes of images.

2.3.2 Activation in Anterior VMPFC Reflects Experienced Value

We analyzed fMRI data from the multimodal reward task using independent models for the monetary rewards and for the social rewards. Collapsing across all regressors for each reward type revealed main effects in expected regions: images of attractive faces evoked activation in the fusiform face area and lateral occipital cortex (Table 2), whereas images of monetary gains and losses evoked activation in the intraparietal sulci and cuneus, among other regions (Table 3).
Table 2: Regions exhibiting increased activation to photographs of their faces, regardless of their attractiveness, compared to monetary rewards. Coordinates of cluster maxima are in MNI space. Cluster size is provided in terms of the number of 2 mm³ voxels. Abbreviations: BA (Brodmann Area).

<table>
<thead>
<tr>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Region</th>
<th>BA</th>
<th>Z-stat</th>
<th>Cluster size</th>
</tr>
</thead>
<tbody>
<tr>
<td>48</td>
<td>-62</td>
<td>6</td>
<td>Middle Temporal Gyrus</td>
<td>BA 39</td>
<td>6.40</td>
<td>6255</td>
</tr>
<tr>
<td>-42</td>
<td>-78</td>
<td>0</td>
<td>Middle Occipital Gyrus</td>
<td>BA 19</td>
<td>5.14</td>
<td>3640</td>
</tr>
<tr>
<td>6</td>
<td>40</td>
<td>-22</td>
<td>Rectal Gyrus</td>
<td>BA 11</td>
<td>4.33</td>
<td>1397</td>
</tr>
</tbody>
</table>

Table 3: Regions exhibiting increased activation to monetary rewards, regardless of their value, compared to photographs of faces. Coordinates of cluster maxima are in MNI space. Cluster size is provided in terms of the number of 2 mm³ voxels. Abbreviations: BA (Brodmann Area).

<table>
<thead>
<tr>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Region</th>
<th>BA</th>
<th>Z-stat</th>
<th>Cluster size</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>-72</td>
<td>34</td>
<td>Precuneus</td>
<td>BA 7</td>
<td>6.26</td>
<td>11072</td>
</tr>
<tr>
<td>40</td>
<td>-40</td>
<td>44</td>
<td>Inferior Parietal Lobule</td>
<td>BA 40</td>
<td>4.92</td>
<td>3306</td>
</tr>
<tr>
<td>32</td>
<td>4</td>
<td>64</td>
<td>Middle Frontal Gyrus</td>
<td>BA 6</td>
<td>4.95</td>
<td>3110</td>
</tr>
<tr>
<td>62</td>
<td>-46</td>
<td>-8</td>
<td>Middle Temporal Gyrus</td>
<td>BA 21</td>
<td>4.79</td>
<td>1570</td>
</tr>
<tr>
<td>-24</td>
<td>6</td>
<td>62</td>
<td>Superior Frontal Gyrus</td>
<td>BA 6</td>
<td>4.23</td>
<td>1562</td>
</tr>
<tr>
<td>-52</td>
<td>-56</td>
<td>-14</td>
<td>Middle Temporal Gyrus</td>
<td>BA 37</td>
<td>4.51</td>
<td>587</td>
</tr>
</tbody>
</table>

To identify brain regions whose activation was modulated by the experienced value of monetary rewards, we contrasted fMRI responses to large monetary gains (defined as +$5 and +$2) compared to large monetary losses (defined as -$5 and -$2). We refer to this contrast as our metric of monetary value. We found that two subregions within the VMPFC and adjacent frontopolar cortex responded significantly more to monetary gains than to losses (Figure 6A; Table 4). A confirmatory analysis modeling monetary value as a linear parametric effect revealed activation in a similar region.
within anterior VMPFC (Table 5). Moreover, a post hoc analysis that did not use a minimum cluster size for significance or a correction for multiple comparisons (as similar to prior studies using small-volume correction; (e.g., Knutson et al., 2007; Winston et al., 2007) revealed increased activation in vSTR to monetary gains compared to losses (z-stat = 2.9; MNI coordinate = x-9, y12, z-8). No regions exhibited significantly greater activation to monetary losses than to monetary gains.

Table 4: Regions exhibiting sensitivity to monetary value, defined as increased activation to large gains (+$5 & +$2) compared to large losses (-$5 & -$2). Coordinates of local maxima within clusters of activation are in MNI space. Cluster size is provided in terms of the number of 2 mm$^3$ voxels. Distinct clusters are separate by blank rows. Abbreviations: BA (Brodmann Area).

<table>
<thead>
<tr>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Region</th>
<th>BA</th>
<th>Z-stat</th>
<th>Cluster size</th>
</tr>
</thead>
<tbody>
<tr>
<td>12</td>
<td>58</td>
<td>2</td>
<td>Medial Frontal Gyrus</td>
<td>BA 10</td>
<td>3.43</td>
<td>713</td>
</tr>
<tr>
<td>-2</td>
<td>68</td>
<td>-2</td>
<td>Medial Frontal Gyrus</td>
<td>BA 10</td>
<td>3.41</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>64</td>
<td>0</td>
<td>Medial Frontal Gyrus</td>
<td>BA 10</td>
<td>3.27</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>44</td>
<td>-10</td>
<td>Medial Frontal Gyrus</td>
<td>BA 11</td>
<td>3.22</td>
<td></td>
</tr>
<tr>
<td>-2</td>
<td>62</td>
<td>-2</td>
<td>Medial Frontal Gyrus</td>
<td>BA 10</td>
<td>3.08</td>
<td></td>
</tr>
<tr>
<td>-18</td>
<td>32</td>
<td>34</td>
<td>Medial Frontal Gyrus</td>
<td>BA 9</td>
<td>3.79</td>
<td>591</td>
</tr>
<tr>
<td>-14</td>
<td>40</td>
<td>6</td>
<td>Anterior Cingulate</td>
<td>BA 32</td>
<td>3.21</td>
<td></td>
</tr>
<tr>
<td>-26</td>
<td>20</td>
<td>44</td>
<td>Middle Frontal Gyrus</td>
<td>BA 8</td>
<td>3.12</td>
<td></td>
</tr>
<tr>
<td>-24</td>
<td>24</td>
<td>52</td>
<td>Superior Frontal Gyrus</td>
<td>BA 8</td>
<td>3.00</td>
<td></td>
</tr>
<tr>
<td>-18</td>
<td>46</td>
<td>10</td>
<td>Anterior Cingulate</td>
<td>BA 32</td>
<td>2.97</td>
<td></td>
</tr>
</tbody>
</table>
Table 5: Regions whose activation increases with increasing monetary reward size. Coordinates of local maxima within clusters of activation are in MNI space. Coordinates of local maxima within clusters of activation are in MNI space. Cluster size is provided in terms of the number of 2 mm³ voxels. Abbreviations: BA (Brodmann Area).

<table>
<thead>
<tr>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Region</th>
<th>BA</th>
<th>Z-stat</th>
<th>Cluster size</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>68</td>
<td>-2</td>
<td>Medial Frontal Gyrus</td>
<td>BA 10</td>
<td>3.38</td>
<td>596</td>
</tr>
<tr>
<td>12</td>
<td>60</td>
<td>0</td>
<td>Medial Frontal Gyrus</td>
<td>BA 10</td>
<td>3.13</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>68</td>
<td>0</td>
<td>Superior Frontal Gyrus</td>
<td>BA 10</td>
<td>3.06</td>
<td></td>
</tr>
<tr>
<td>-6</td>
<td>72</td>
<td>-4</td>
<td>Medial Frontal Gyrus</td>
<td>BA 10</td>
<td>3.02</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>52</td>
<td>-10</td>
<td>Medial Frontal Gyrus</td>
<td>BA 10</td>
<td>2.94</td>
<td></td>
</tr>
</tbody>
</table>

We next identified regions whose activation was modulated by the attractiveness of social rewards, by comparing activation to images of attractive faces (from the 4-star category) to images of unattractive faces (from the 1-star category). We refer to this contrast as social value. Regions of the vSTR and VMPFC responded significantly more to attractive faces compared to unattractive faces (Figure 6A; Table 6). A confirmatory analysis modeled experienced value of the face images using a single linear effect and found significant activation in similar regions (Table 7). The inverse contrast (unattractive faces > attractive faces) did not reveal any significant activation at our statistical threshold.
Table 6: Regions exhibiting sensitivity to social value, defined as increased activation to attractive faces (those from the 4-star category) compared to unattractive faces (those from the 1-star category). Coordinates of local maxima within clusters of activation are in MNI space. Cluster size is provided in terms of the number of 2 mm³ voxels. Distinct clusters are separate by blank rows. Abbreviations: BA (Brodmann Area).

<table>
<thead>
<tr>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Region</th>
<th>BA</th>
<th>Z-stat</th>
<th>Cluster size</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>48</td>
<td>-8</td>
<td>Medial Frontal Gyrus</td>
<td>BA 10</td>
<td>3.31</td>
<td>1046</td>
</tr>
<tr>
<td>-8</td>
<td>18</td>
<td>-6</td>
<td>Caudate</td>
<td>*</td>
<td>3.23</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>38</td>
<td>-12</td>
<td>Medial Frontal Gyrus</td>
<td>BA 11</td>
<td>3.19</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>42</td>
<td>-6</td>
<td>Anterior Cingulate</td>
<td>BA 32</td>
<td>3.04</td>
<td></td>
</tr>
<tr>
<td>-18</td>
<td>18</td>
<td>0</td>
<td>Caudate</td>
<td>*</td>
<td>3.02</td>
<td></td>
</tr>
<tr>
<td>50</td>
<td>-76</td>
<td>-2</td>
<td>Middle Occipital Gyrus</td>
<td>BA 19</td>
<td>3.41</td>
<td>600</td>
</tr>
<tr>
<td>34</td>
<td>-92</td>
<td>-6</td>
<td>Middle Occipital Gyrus</td>
<td>BA 18</td>
<td>3.35</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>-82</td>
<td>8</td>
<td>Middle Occipital Gyrus</td>
<td>BA 19</td>
<td>3.32</td>
<td></td>
</tr>
<tr>
<td>54</td>
<td>-72</td>
<td>10</td>
<td>Middle Temporal Gyrus</td>
<td>BA 39</td>
<td>3.25</td>
<td></td>
</tr>
<tr>
<td>48</td>
<td>-74</td>
<td>6</td>
<td>Middle Occipital Gyrus</td>
<td>BA 19</td>
<td>3.23</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>-84</td>
<td>-2</td>
<td>Inferior Occipital Gyrus</td>
<td>BA 18</td>
<td>3.21</td>
<td></td>
</tr>
</tbody>
</table>
Table 7: Regions whose activation increases with increasing social reward size. Coordinates of local maxima within clusters of activation are in MNI space. Cluster size is provided in terms of the number of 2 mm$^3$ voxels. Distinct clusters are separate by blank rows. Abbreviations: BA (Brodmann Area).

<table>
<thead>
<tr>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Region</th>
<th>BA</th>
<th>Z-stat</th>
<th>Cluster size</th>
</tr>
</thead>
<tbody>
<tr>
<td>50</td>
<td>-76</td>
<td>-2</td>
<td>Middle Occipital Gyrus</td>
<td>BA 19</td>
<td>3.98</td>
<td>2856</td>
</tr>
<tr>
<td>36</td>
<td>-84</td>
<td>16</td>
<td>Middle Occipital Gyrus</td>
<td>BA 19</td>
<td>3.60</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>-82</td>
<td>6</td>
<td>Middle Occipital Gyrus</td>
<td>BA 19</td>
<td>3.58</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>-80</td>
<td>16</td>
<td>Cuneus</td>
<td>BA 18</td>
<td>3.56</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>-86</td>
<td>10</td>
<td>Cuneus</td>
<td>BA 18</td>
<td>3.53</td>
<td></td>
</tr>
<tr>
<td>34</td>
<td>28</td>
<td>-6</td>
<td>Inferior Frontal Gyrus</td>
<td>BA 47</td>
<td>3.60</td>
<td>1971</td>
</tr>
<tr>
<td>0</td>
<td>48</td>
<td>-8</td>
<td>Medial Frontal Gyrus</td>
<td>BA 10</td>
<td>3.36</td>
<td></td>
</tr>
<tr>
<td>-8</td>
<td>16</td>
<td>-6</td>
<td>Caudate</td>
<td>*</td>
<td>3.20</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>-16</td>
<td>-2</td>
<td>Thalamus</td>
<td>*</td>
<td>3.19</td>
<td></td>
</tr>
<tr>
<td>-16</td>
<td>16</td>
<td>2</td>
<td>Caudate</td>
<td>*</td>
<td>3.16</td>
<td></td>
</tr>
<tr>
<td>-18</td>
<td>-62</td>
<td>48</td>
<td>Precuneus</td>
<td>BA 7</td>
<td>3.57</td>
<td>640</td>
</tr>
<tr>
<td>-26</td>
<td>-50</td>
<td>48</td>
<td>Precuneus</td>
<td>BA 7</td>
<td>3.42</td>
<td></td>
</tr>
<tr>
<td>-10</td>
<td>-64</td>
<td>60</td>
<td>Precuneus</td>
<td>BA 7</td>
<td>3.24</td>
<td></td>
</tr>
<tr>
<td>-20</td>
<td>-54</td>
<td>34</td>
<td>Precuneus</td>
<td>BA 31</td>
<td>3.10</td>
<td></td>
</tr>
<tr>
<td>-20</td>
<td>-90</td>
<td>24</td>
<td>Cuneus</td>
<td>BA 18</td>
<td>3.68</td>
<td>620</td>
</tr>
<tr>
<td>-26</td>
<td>-82</td>
<td>36</td>
<td>Precuneus</td>
<td>BA 19</td>
<td>3.39</td>
<td></td>
</tr>
<tr>
<td>-26</td>
<td>-68</td>
<td>24</td>
<td>Precuneus</td>
<td>BA 7</td>
<td>3.16</td>
<td></td>
</tr>
<tr>
<td>-28</td>
<td>-70</td>
<td>20</td>
<td>Posterior Cingulate</td>
<td>BA 31</td>
<td>3.08</td>
<td></td>
</tr>
<tr>
<td>-34</td>
<td>-86</td>
<td>24</td>
<td>Superior Occipital Gyrus</td>
<td>BA 19</td>
<td>2.87</td>
<td></td>
</tr>
</tbody>
</table>
Figure 6: Neurometric measures of monetary and social experienced value. (A) To identify brain regions whose activation tracked monetary value, we contrasted large monetary gains (+$5 and +$2) minus large monetary losses (-$5 and -$2). Within anterior medial prefrontal cortex [x12, y58, z2] and adjacent frontopolar cortex [x-2, y68, z-2] there was a clear effect of the valence of monetary rewards (shown in green).

We additionally identified brain regions whose activation tracked social value by contrasting the response to faces drawn from our most-attractive category (4-star) and that to faces drawn from our least-attractive category (1-star). Activation was modulated by the valence of social rewards in the ventral striatum [vSTR; x-8, y18, z-6] and ventromedial prefrontal cortex [VMPFC; x0, y48, z-8] (shown in red). Using a conjunction analysis, we identified a small region of anterior VMPFC [aVMPFC; x0, y46, z-8] whose activation increased to increasing value for both forms of rewards (shown in yellow), and survived an additional cluster correction of 15 contiguous voxels. All areas of activation passed a cluster significance threshold of z > 2.3, with whole-brain cluster-correction at p < 0.05. (B) Interrogation of the aVMPFC region that responded to both rewards revealed that activation within this area increased with increasing monetary reward. Error bars indicate standard error of the mean (SEM). (For display purposes, error bars were calculated without correcting for normalized values.) (C) Within the aVMPFC region, activation increased with increasing attractiveness, with least response to the most unattractive faces and greatest response to the most attractive faces. Error bars indicate SEM. (For display purposes, error bars were calculated without correcting for normalized values.)
A conjunction analysis revealed that the only region exhibiting a significant response to both forms of rewards was located within the anterior VMPFC (aVMPFC; Figure 6A). Activation within this region resembled a monotonic concave function (similar to a utility curve) for both increasing monetary value (Figure B) and increasing social value (Figure 6C).

2.3.3 Activation in Posterior VMPFC Reflects Decision Value

We next tested our core hypothesis that neurometric measures of subjective value—as obtained outside the decision context—predict subsequent decision value. On each trial of the economic exchange task, subjects chose whether to sacrifice more money to view a more attractive face. We observed considerable inter-individual variability in participants’ willingness to exchange money for viewing a more-attractive image (Figure 7); the proportion of such exchanges ranged from 0.01 to 0.91 across participants (M = 0.34; SD = 0.25). We also quantified willingness to pay (WTP) for a one-star increase in attractiveness. WTP ranged from 0 to 6.4 cents/star (M = 1.41; median = 0.33) and correlated strongly with the proportion of exchanges [r = 0.74; ρ = 0.91; p < 0.001 for both tests].
Figure 7: Individual differences in exchange rate. In our economic exchange task, participants had the opportunity to exchange small amounts of money for the opportunity to view a more attractive face. This task afforded an opportunity to examine each participant's relative economic valuation of social and monetary rewards. We observed substantial inter-individual differences in participants' willingness to make these exchanges; shown in the plot is a ranking of participants (N = 23) by the proportion of time they sacrificed a larger amount of money to purchase a more attractive face.

We introduced each participant’s proportion of exchanges as a covariate in the across-participants analysis of the multimodal reward task. We emphasize that this task was conducted earlier in the experimental session, and thus we are using the prior fMRI data to predict the subsequent economic decisions. Strikingly, the difference between experienced social value and experienced monetary value [(4-star minus 1-star) minus (large gains minus large losses)] in the posterior VMPFC (pVMPFC) was a strong positive predictor of exchange rate. Those subjects who exhibited the greatest response to social value compared to monetary value within pVMPFC were most likely to sacrifice money for the opportunity to see a more attractive face (Figure 8A).
Conversely, participants with the weakest response to social value compared to monetary value within pVMPFC were least likely to sacrifice money to view a more attractive image. This relationship was robust throughout our entire range of decision preferences (Figure 8B; for proportion of economic exchanges: $r = 0.72$; for mean WTP: $r = 0.74$). No other brain region (including aVMPFC; $r_{(24)} = -0.02$, $p > 0.90$) exhibited a significant relationship between neurometric value sensitivity and exchange rate, at our correction threshold.
Figure 8: Posterior VMPFC encodes information about decision value. (A) We investigated whether neurometric representations of value (in the multimodal reward task) could predict whether a given individual was likely to subsequently trade money to view faces (in the economic exchange task). To do this, we introduced exchange rate (as a proportion of total opportunities) as a factor in an across-participants analyses. We found one region within the posterior VMPFC (pVMPFC; x6, y26, z-14) in which differential neurometric representations of value, defined as Social Value (4-star minus 1-star) minus Monetary Value (large gains minus large losses), predicted exchanges. Shown are voxels passing a significance threshold of $p < 0.001$ (uncorrected); the pVMPFC peak of activation was highly significant [$z = 3.24$]. (B) Within pVMPFC, increasing neurometric value for social compared to monetary rewards predicted increasing likelihood of economic exchanges ($r = 0.72$). That is, those individuals who had the greatest neurometric value for social compared to monetary rewards, as defined by a double subtraction of Social Value (4-star minus 1-star) minus Monetary Value (large monetary gains minus large monetary losses), readily exchanged money to view more-attractive faces. In contrast, those individuals with the least neurometric value for social compared to monetary rewards were unlikely to sacrifice that money for a better social reward. The line represents the least-squares fit to the data points; each point reflects the average response within pVMPFC for each participant.

2.4 Discussion

Our results provide new insight into the neural substrates of economic value. We found that distinct regions within VMPFC track distinct aspects of economic value:
aVMPFC tracks experienced value for both social and monetary rewards, whereas
pVMPFC tracks the relative decision value between reward categories (Figure 8).

Strikingly, information predictive of decision value was observed in pVMPFC even during the passive experience of rewards. Such a result provides strong evidence that VMPFC encodes multiple value signals that are simultaneously and obligatorily computed during experience of rewards.

Figure 9: Regions identified as pVMPFC and aVMPFC. We identified two distinct subregions of VMPFC that responded to different forms of value. Shown in red is anterior VMPFC (aVMPFC; x0, y46, z-8). This region was the sole point of overlap for monetary and social value, indicating a role for processing experienced rewards. Shown in blue is posterior VMPFC (pVMPFC; x6, y26, z-14). This region was identified in a whole-brain analysis in which we regressed relative neural value (Social > Money reward responses) against relative economic value (Social > Money; proportion of exchanges for faces).

Considerable prior neuroimaging and electrophysiological work has implicated VMPFC in the assignment of value to environmental stimuli (Kringelbach & Rolls, 2004; McClure, Li, Tomlin, Cypert, Montague, & Montague, 2004; Padoa-Schioppa & Assad, 2008). Anterior VMPFC, in particular, has been reported to encode outcome probability
in monetary decision tasks (Knutson & Cooper, 2005) and to track rewarding outcomes across different reward modalities (Knutson et al., 2003; O’Doherty et al., 2001a; O’Doherty et al., 2002). Of note, we found significant vSTR activation only to the face stimuli, not the monetary stimuli, in apparent conflict with prior work suggesting this region responds similarly for social and monetary rewards (Izuma, Saito, & Sadato, 2008). This may reflect a bias within vSTR activation toward anticipation of rewards (Knutson, Adams, Fong, & Hommer, 2001a), or it may reflect our use of strict cluster correction. When we relaxed our cluster correction threshold, which effectively simulates the small-volume correction approach common in studies of the striatum, we found robust vSTR activation to monetary rewards. Thus, aVMPFC may play an integrative role in the experience of rewarding stimuli, perhaps through indirect input from vSTR and other reward-related regions.

Yet, while activation in aVMPFC scaled with increasing experienced value for each reward category, it was unpredictive of the relative valuation of those categories, as measured in a subsequent decision-making task. Instead, information predictive of decision value was found in pVMPFC, a region that has been recently associated with willingness to pay during active decision making within a number of studies (De Martino et al., 2009; Hare et al., 2009; Hare et al., 2008; Plassmann et al., 2007). We note that our centroid of pVMPFC activation closely matches that reported in prior studies.
(Plassmann et al., 2007), which provides converging evidence for that region’s role in valuation.

However, our work differs from these prior studies in several important ways. First, we determined decision value independently for each participant, based on their relative preferences between monetary and face rewards in a separate incentive-compatible choice task. Second, the hedonic value from our face images was obtained within the scanning session, allowing us to measure experienced value—and preclude it as a confounding factor. Third, we observed activation patterns predictive of decision value even though subjects were not engaged in any decision task, eliminating the alternative possibility that pVMPFC supports decision-making processes that are correlated with value (e.g., disengagement when faced with low-value options), and not value itself. Fourth, our subjects viewed only novel images of unknown individuals, saw those images only once, and made subsequent decisions based only on category ratings (e.g., 4-star). Given these design features, our results provide compelling evidence that pVMPFC activation reflects the relative tradeoffs between two subjectively valued continua—a necessary condition for the existence of a neural common currency (Montague & Berns, 2002).

The existence of a common neurometric scale for value—whether in VMPFC (cf. Kable & Glimcher, 2007; Rangel et al., 2008) or elsewhere—would facilitate decision making by providing a means for comparison of different goods, services, and even
abstract experiences. Yet, our data also indicate that the region encoding a common currency for decision value (pVMPFC) may be distinct from those supporting experienced value (aVMPFC and vSTR). An intriguing possibility—one strongly supported by our data—is that multiple value signals exist simultaneously within ventral prefrontal cortex, each contributing to distinct aspects of experience and behavior. We speculate that neurological disorders characterized by pathological decision making (e.g., anorexia, obsessive compulsive disorder, sex addiction) could result from dysfunction of neuronal populations that code the decision value for specific types of rewards.
3. Neural Predictors of Self and Charity Framing Effects

Individuals can exhibit marked differences in their choices depending on how a decision is presented. Many real-world decisions also differ in their consequences: some decisions impact only the decision maker, but others impact many individuals. Yet, little is known about the mechanisms underlying how economic preferences change depending on the specific target of a decision. Here, we show that these preferences are rooted in idiosyncratic responses within pVMPFC.

3.1 Introduction

Decision making relies on the ability to compute the value of specific goods and commodities before comparing their values and choosing higher-valued option. Using relatively simple economic paradigms, these valuation processes have been investigated in a large corpus of decision neuroscience research (Grabenhorst & Rolls, 2011; Padoa-Schioppa, 2011; Smith & Huettel, 2010; Vlaev, Chater, Stewart, & Brown, 2011; Volkow, Wang, & Baler, 2011), with several studies highlighting the VMPFC, in particular, as a key brain region in valuation (Hare et al., 2009; Krajbich, Camerer, Ledyard, & Rangel, 2009; Lim, O'Doherty, & Rangel, 2011; Litt et al., 2011; Wunderlich, Rangel, & O'Doherty, 2010). Recent work has begun to extend this conceptualization of valuation and VMPFC activation by demonstrating that multiple value signals exist simultaneously within VMPFC, with anterior aspects of VMPFC encoding the experienced value for a good and posterior VMPFC (pVMPFC) encoding the decision value for a good (Baumgartner,
Knoch, Hotz, Eisenegger, & Fehr, 2011; Smith, Hayden, Truong, Song, Platt, & Huettel, 2010c).

Relative to these simple scenarios involving economic exchanges, other decisions are more complex, requiring the integration of multiple decision variables, including uncertainty and social interactions. This increased complexity is evident in decisions whose outcomes do not directly impact the decision maker, as in the case of charitable donations (Harbaugh et al., 2007; Hare, Camerer, Knoepfle, & Rangel, 2010; Moll et al., 2006; Zaki & Mitchell, 2011). In addition, increased complexity is apparent in decisions whose contextual presentation dramatically affects the decision maker, as in the case of framing tasks (De Martino, Harrison, Knafo, Bird, & Dolan, 2008; De Martino et al., 2006; Deppe, Schwindt, Kramer, Kugel, Plassmann, Kenning, & Ringelstein, 2005; Kahneman & Frederick, 2007; Roiser, de Martino, Tan, Kumaran, Seymour, Wood, & Dolan, 2009; Talmi, Hurlemann, Patin, & Dolan, 2010; Tversky & Kahneman, 1981b; Windmann, Kirsch, Mier, Stark, Walter, Gunturkun, & Vaitl, 2006; Zheng, Wang, & Zhu, 2010).

Across both social decisions involving other people and framing tasks, individuals can vary, often quite substantially, in their behavior and brain responses (De Martino et al., 2006; Hare et al., 2010; Roiser et al., 2009). Yet, little is known about the neural mechanisms that shape individual differences in complex decisions involving the simultaneous integration of multiple decision variables.
We predicted that individuals’ idiosyncratic pVMPFC responses would predict individual differences in preferences in decisions requiring the integration of decision variables related to uncertainty and social valuation. To evaluate this hypothesis, we recruited two samples of participants (E1: N = 232; E2: N = 65) and asked them to engage in a financial decision making task that has been previously used to study framing effects (De Martino et al., 2006) (Figure 10). Importantly, this task allowed us to manipulate both the framing of a decision and the decision target, as all trials were presented as potential monetary gains or losses that could impact the decision maker or a charity of his or her choosing. Our analyses focused on three core questions. First, do decisions framed as potential losses recruit increased dorsomedial prefrontal activation, irrespective of choice? Second, are regions supporting social cognition recruited when participants make decisions for their chosen charity relative to themselves? Third, are idiosyncratic responses within pVMPFC predictive of individual differences in relative biases between self and charity framing effects?

3.2 Materials and Methods

To evaluate the replicability of our primary findings, we conducted two independent experiments using a similar task and demographic distribution of participants. We note, with brackets, methodological and procedural differences where they exist.
3.2.1 Participants

A total of 297 participants with normal or corrected-to-normal vision completed the fMRI study, which consisted of two independent experiments with non-overlapping participant samples. Experiment 1 (our primary sample, except where noted) consisted of 232 participants (mean age: 21.7 years; range: 18-31 years; 133 females); Experiment 2 consisted of 65 participants (mean age: 24.7; range: 18-43; 32 females). Although prescreening excluded individuals with prior psychiatric or neurological illness, other individuals were excluded based on data quality concerns or equipment failure (see Preprocessing), leaving a final sample of 217 participants in Experiment 1 and 58 participants in Experiment 2. All participants gave written informed consent as part of a protocol approved by the Institutional Review Board of Duke University Medical Center.

3.2.2 Stimuli and Task

Participants engaged in three runs of a financial decision-making task (Figure 10) that has been previously used to study framing effects (e.g., De Martino et al., 2006). Each run consisted of 42 trials. On each trial, participants were shown a starting amount that varied uniformly from $8 to $42 [Experiment 2: $10, $20, $30, $40] before choosing between “sure” and “gamble” options. The sure option was framed such that the participant could keep (gain frame) or lose (loss frame) a fixed proportion of the starting amount. The gamble option did not differ according to frame and was represented by a
pie chart reflecting the probability (20%, 25%, 33%, 50%, 66%, 75%) [Experiment 2: 25%, 50%, 75%] of winning or losing the entire starting amount. The expected value was allowed to vary across the two options [Experiment 2: expected value for the sure option was always equal to or greater than the expected value for the gamble option]. On half the trials, participants played for themselves, and on the other half of the trials, they played for a charity of their choice (Animal Protection Society of Durham, Durham Literacy Center, Easter Seals UCP North Carolina, or American Red Cross: The Central North Carolina Chapter).

Stimuli were projected onto a screen at the back of the scanner bore, and participants viewed the stimuli through mirrored goggles. Tasks were programmed using the Psychophysics Toolbox version 2.54 (Brainard, 1997). At the end of the experiment, we randomly chose one trial to be carried out for payment purposes; this procedure ensures incentive compatibility across all trials.
Figure 10: Experimental task. Participants engaged in a financial decision-making task. At the beginning of each trial, an initial endowment was presented that indicated the target of the decision (self or charity; equally split). Following this cue, participants had the opportunity to choose between a gamble where they could keep or lose all of the initial endowment or a safe option where they would receive a guaranteed proportion of the initial endowment. The safe option was presented in two conditions: (A) a keep frame; and (B) a lose frame. Crucially, these two frames were mathematically identically and only differed in the presentation of the option ("keep" or "lose"). After the participants made their choice, a fixation was presented for 2.5 to 6.5 second. At the end of the experiment, we chose one trial at random to be resolved for payment purposes.

3.2.3 Image Acquisition

Neuroimaging data were collected using a General Electric MR750 3.0 Tesla scanner equipped with an 8-channel parallel imaging system [Experiment 2: standard spiral-in sequence on a General Electric 4.0 Tesla scanner with a 4-channel receiver coil]. Images sensitive to blood-oxygenation-level-dependent (BOLD) contrast were acquired
using a T2*-weighted spiral-in sensitivity encoding sequence (acceleration factor = 2),
with slices parallel to the axial plane connecting the anterior and posterior commissures
[repetition time (TR): 1580 ms; echo time (TE): 30 ms; matrix: 64 x 64; field of view
(FOV): 243 mm; voxel size: 3.8 x 3.8 x 3.8 mm; 37 axial slices acquired in an ascending
interleaved fashion; flip angle: 70°] [Experiment 2: TR: 2000 ms; voxel size: 3.75 x 3.75 x
3.80 mm; 34 axial slices; FOV: 240 mm; flip angle: 60°]. We chose these sequences to
ameliorate susceptibility artifacts in ventral frontal regions (Pruessmann et al., 2001;
Truong & Song, 2008). Prior to preprocessing these functional data, we discarded the
first eight volumes of each run to allow for magnetic stabilization [Experiment 2: six
volumes]. To facilitate coregistration and normalization of these functional data, we also
acquired whole-brain high-resolution anatomical scans (T1-weighted FSPGR sequence; TR: 7.58 ms; TE: 2.93 ms; voxel size: 1 x 1 x 1 mm; matrix: 256 x 256; FOV: 256 mm; 206
axial slices; flip angle: 12°) [Experiment 2: T1-weighted 3D SPGR sequence; TR: 12.2 ms;
TE: 5.3 ms; voxel size: 0.94 x 0.94 x 1.90 mm; FOV: 240 mm; 68 axial slices; flip angle:
20°].

3.2.4 Preprocessing

Our preprocessing routines employed tools from the FMRIB Software Library
(FSL Version 4.1.8; http://www.fmrib.ox.ac.uk/fsl/) package (Smith et al., 2004; Woolrich,
Jbabdi, Patenaude, Chappell, Makni, Behrens, Beckmann, Jenkinson, & Smith, 2009). We
first corrected for head motion by realigning the time series to the middle time point
(Jenkinson et al., 2002). We then removed non-brain material using the brain extraction tool (Smith, 2002). Next, intravolume slice-timing differences were corrected using Fourier-space phase shifting, aligning to the middle slice (Sladky, Friston, Tröstl, Cunnington, Moser, & Windischberger, 2011). Images were then spatially smoothed with a 6 mm full-width-half-maximum Gaussian kernel. To remove low-frequency drift in the temporal signal, we then subjected the functional data to a high-pass temporal filter with a 100 second cutoff (Gaussian-weighted least-squares straight line fitting, with sigma = 50 s). Finally, each 4-dimensional dataset was grand-mean intensity normalized using a single multiplicative factor. Prior to group analyses, functional data were spatially normalized to the MNI avg152 T1-weighted template (2 mm isotropic resolution) using a 12-parameter affine transformation implemented in FLIRT (Jenkinson & Smith, 2001); these transformations were later applied to the statistical images before cross-run and cross-participant analyses.

As part of our preprocessing steps, we examined three partially correlated measures of quality assurance and excluded subjects with extreme values on these metrics. First, we estimated the average signal-to-fluctuation-noise ratio (SFNR) for each subject (Friedman & Glover, 2006). Second, we computed the average volume-to-volume motion for each subject. Third, we identified outlier volumes in our functional data. We considered volume an outlier if its root-mean-square (RMS) amplitude exceeded the value of 150% of the interquartile range of RMS for all volumes in a run. Using these
three metrics, we excluded subjects where any measure metric was extreme relative to the other subjects (i.e., SFNR < 5th percentile of the distribution of SFNR values; outlier volumes > 95th percentile the distribution of outlier volumes; average volume-to-volume motion > 95th percentile). [In Experiment 2, we excluded runs containing more than 10% outlier volumes or more than 2 mm of volume-to-volume motion.]

### 3.2.5 FMRI Analysis

Neuroimaging analyses were conducted using FEAT (FMRI Expert Analysis Tool) Version 5.98 (Smith et al., 2004; Woolrich et al., 2009). Our first-level analysis (i.e., within run) utilized a general linear model with local autocorrelation correction (Woolrich et al., 2001). Each first-level model consisted of four regressors modeling each condition (loss frame: self or charity; gain frame: self or charity) independently; the duration that was modeled was extended over a period of time from the presentation of the cue to the time of choice. By allowing the amplitude of the predicted response to vary as a function of response time, we were able to control for the confounding effects related to response time (Grinband, Savitskaya, Wager, Teichert, Ferrera, & Hirsch, 2011a, 2011b). In this first-level model, we also included nuisance regressors to account for missed responses and outlier volumes. Except for the outlier volume nuisance regressors (which were unconvolved), all regressors were convolved with a canonical hemodynamic response function. We combined data across runs, for each subject, using
a fixed-effects model, and combined data across subjects using a mixed-effects model (Beckmann et al., 2003; Woolrich et al., 2004).

Statistical significance was assessed using Monte Carlo permutation-based statistical testing with 10,000 permutations (Nichols & Holmes, 2002). Additionally, we used threshold-free cluster enhancement to estimate clusters of activation (Smith & Nichols, 2009). Statistical overlay images were created using MRICron and MRICroGL (Rorden et al., 2007). All coordinates are reported in MNI space.

3.3 Results
3.3.1 Behavioral Data

Individuals who are fully rational should not change their choice behavior between the loss and keep frames, as these scenarios are mathematically equivalent. Yet, this subtle change often evokes substantial changes in behavior, which is known as a framing effect (De Martino et al., 2006; Tversky & Kahneman, 1981b). To evaluate whether we observed a framing effect in our subjects, we compared the average propensity to choose the gamble in loss frame relative to the keep frame. Consistent with a framing effect, we found that subjects, on average, increased their gambling behavior in loss frames (E1: $M = 58\%$; E2: $M = 43\%$) relative to keep frames (E1: $M = 30\%$; E2: $M = 27\%$), an effect that was significant in both experiments (Figure 11A and Figure 11B; E1: $F_{(1,216)} = 235.65, p < 0.001$; E2: $F_{(1,57)} = 63.84, p < 0.001$). Gambling behavior did not change as a function of decision target (charity vs. self; E1: $F_{(1,216)} = 0.02, p = 0.88$; E2: $F_{(1,57)} = 0.76, p$
= 0.38), though we note there was inconsistent evidence for an interaction between decision target and frame (E1: $F_{(1,216)} = 0.01$, $p = 0.90$; E2: $F_{(1,57)} = 7.73$, $p < 0.01$). We also found that individuals varied substantially in their susceptibility to the framing manipulation (Figure 11E and Figure 11F), defined as each subject’s increase in the proportion of trials choosing the gamble option in the loss frame relative to the keep frame. Although the individual differences in the framing effect were highly correlated between self and charity trials (E1: $r_{(215)} = 0.86$, $p < 0.001$; E2: $r_{(56)} = 0.69$, $p < 0.001$), we emphasize that subjects exhibited substantial biases in their relative susceptibility to the framing manipulation (Figure 11E and Figure 11F).

As a control analysis, we also compared response times across frames and decision targets. We found that subjects were slower to respond in loss frames compared to keep frames (E1: $F_{(1,216)} = 120.31$, $p < 0.001$; E2: $F_{(1,57)} = 93.98$, $p < 0.001$), suggesting increased deliberation when options are presented as potential losses. In contrast, decision target did not modulate response times (E1: $F_{(1,216)} = 3.24$, $p = 0.07$; E2: $F_{(1,57)} = 0.03$, $p = 0.86$), and decision target did not interact with frame type (E1: $F_{(1,216)} = 2.90$, $p = 0.09$; E2: $F_{(1,57)} = 0.64$, $p = 0.42$). These response-time effects, which are not generally discussed in framing experiments (De Martino et al., 2008; De Martino et al., 2006; Deppe et al., 2005), highlight the importance of including response time covariates in subsequent fMRI analyses (Grinband et al., 2011a, 2011b), as neural framing effects could be partially explained by time on task and nonspecific reaction time effects.
Figure 11: Behavioral data. (A and B) For both self (red) and charity (blue) decision targets, we observed a robust effect of frame where participants increased their willingness to gamble when the safe option was presented as a potential loss. (C and D) Relative to the keep frame, participants were substantially slower to respond during in the loss frame, but this effect was not modulated by decision target. (E and F) The magnitude of the framing effect (i.e., proportion of gamble trials chosen in loss frame minus keep frame) was highly variable across participants, with framing susceptibility in one condition predicting the other condition.
3.3.2 Loss Frame Evokes Activation in DMPFC

To examine the neural antecedents to the behavioral framing effects, we ignored subject choices and contrasted loss frame trials against keep frame trials, collapsing across both self and charity trials. Within the dorsomedial prefrontal cortex (DMPFC), we observed increased activation for loss frame trials compared to gain frame trials (Figure 12A and Figure 12B). To extend this finding, we examined the same DMPFC region in our second, independent sample. Although the neural framing effect did not directly replicate as a main effect ($F_{(1,216)} = 0.05, p = 0.82$), we note that, within DMPFC in the independent sample, we found evidence for an effect of frame that depended on decision target such that charity trials framed as losses evoked greater activation than charity trials framed as gains (Figure 12C; $F_{(1,216)} = 4.34, p < 0.05$).
Figure 12: Neural framing effects irrespective of choice. (A) To examine the neural basis of framing effects, we contrasted loss frame trials against gain frame trials. This contrast revealed activation within DMPFC. All areas of activation passed a permutation-based whole-brain corrected threshold of p < 0.05. (B) Within DMPFC, we found that loss frame trials evoked greater activation than keep frame trials. (C) In an independent sample, we observed a partial replication where charity trials framed as losses evoked greater DMPFC activation than charity trials framed as gains.

3.3.3 Decisions Involving Charity Recruit Social Cognition Regions

Decisions targets involving charities are inherently social, potentially recruiting brain systems involved with social cognition. We evaluated this prediction by contrasting charity trials against self trials, ignoring decisions to gamble. Within the temporal-parietal junction (TPJ) and middle temporal gyrus (mTG), we observed increased activation for charity trials compared to self trials (Figure 13A and Figure 13B). We next sought to extend this finding by examining TPJ activation in an independent sample. We found strong evidence for a direct replication of this effect.
within our independent sample (Figure 13C; \( F_{(1,57)} = 18.84, p < 0.001 \)), adding confidence to our claims regarding TPJ and charitable donations—and perhaps more generally, social cognition.

Figure 13: Brain activation associated with playing for charity compared to self. (A) To examine how different decision targets are processed, we contrasted charity trials against self trials. This contrast revealed activation within middle temporal gyrus (mTG) and temporal-parietal junction (TPJ). All areas of activation passed a permutation-based whole-brain corrected threshold of \( p < 0.05 \). (B) Within TPJ, we found that charity trials evoked greater activation than self trials. (C) In an independent sample, we replicated our TPJ effect, observing increased activation for charity trials relative to self trials.

3.3.4 Posterior VMPFC Predicts Relative Framing Biases

Our previous work indicated that decision value signals within posterior VMPFC predict subsequent preferences (Libedinsky, Smith, Teng, Namburi, Chen,
Huettel, & Chee, 2011; Smith et al., 2010c). Here, we evaluated whether signals within posterior VMPFC (Figure 14A) predict other implicit preferences: relative differences between self and charity framing effects. To test this hypothesis, we first extracted the normalized effect size within posterior VMPFC for the interaction contrast [pVMPFC effect size: (Self Loss – Self Gain) – (Charity Loss – Charity Gain)], for each subject. We then combined these neural data across both experiments, forming a sample with 275 participants. Next, we regressed these neural effects onto the behavioral Self minus Charity Framing effects [proportion of gambles: (Self Loss – Self Gain) – (Charity Loss – Charity Gain)]. We found a (weakly) positive relationship between the neural and behavioral self minus charity framing effects (Figure 14B; \( r_{(273)} = 0.11, p = 0.06 \)), suggesting posterior VMPFC mediates relative biases between self and charity framing effects.
3.4 Discussion

Decision making is rife with individual differences. In the most basic sense, these individual differences in decision making are evident in people’s willingness to purchase goods and commodities, preferences that can be predicted by idiosyncratic responses within VMPFC (Hare et al., 2008; Levy & Glimcher, 2011; Plassmann et al., 2007; Smith et al., 2010c). Here, we asked whether similar neural mechanisms predict individual differences in decisions involving greater complexity compared to simple purchasing. To do this, we designed a modified framing task whose outcomes could
affect the decision maker or a charity of their choosing. This task elicited a host of individual differences: subjects were highly variable in their susceptibility to the framing manipulation, an effect that depended on the decision target. Strikingly, we show that idiosyncratic VMPFC responses predicted individual differences in differential framing effects between self and charity decision targets.

Our VMPFC results are consistent with previous framing studies that have found that VMPFC activation tracks individual differences in framing susceptibility (De Martino et al., 2006). Yet, while our analyses were conducted irrespective of the actual choices made by each subject, previous framing studies have examined the neural underpinnings of framing by comparing brain responses across different choices. For example, De Martino and colleagues (2006) contrasted trials in which the subject chose the gamble option vs. the safe option in the loss frame relative to the keep frame \((\text{Gamble}_\text{Loss} - \text{Safe}_\text{Loss}) - (\text{Gamble}_\text{Keep} - \text{Safe}_\text{Loss})\). The only brain region that exhibited a neural framing effect was the amygdala, whose activation increased when subjects chose in a manner consistent with framing effect. Extending these findings, Roiser and colleagues found that genetic variation at the serotonin transporter-linked polymorphic region (5-HTTLPR) modulated amygdala activation associated with framing effects (Roiser et al., 2009).

Although amygdala activation is noticeably absent from our data, we emphasize that this is most likely due to our focus on the valuation phase of the task, which
preceded the actual choice made by the subject. Instead, our neural framing effects point
to the dorsomedial prefrontal cortex (DMPFC), which has been previously implicated in
a host of behaviors, particularly strategic conflict (Venkatraman et al., 2009a;
Venkatraman, Rosati, Taren, & Huettel, 2009b). As DMPFC activation has also been
associated with time on task and nonspecific effects of attention (Brown, 2011; Grinband
et al., 2011a, 2011b; Yeung, Cohen, & Botvinick, 2011), we emphasize that our analyses
attempted to control for differential response time across framing conditions by
modeling these effects within a multiple regression framework. Furthermore, recent
studies have highlighted how neuronal responses within frontal cortex can be
dissociated from attention and arousal (reviewed in Wallis & Rich, 2011). Future studies
could further disambiguate the effects of frame (and valuation) and time on task by
conducting trial-specific analyses (Mumford, Turner, Ashby, & Poldrack, 2011),
contrasting trials with similar response times.

Our task also differs from previous framing studies by incorporating different
decision targets. When subjects played for their charity relative to themselves, we
observed increased activation within TPJ, posterior cingulate, and mTG. These regions
are frequently implicated in situations that ask people to mentalize (i.e., utilize theory of
mind) (Adolphs, 2009; Amodio & Frith, 2006; Blakemore, 2008; Frank Van, 2009;
Lieberman, 2007; Mar, 2011; Saxe, 2006; Zebrowitz, 2006). Similar to other tasks
involving the comparison of social and monetary goods (Izuma et al., 2008; Izuma, Saito,
Sadato, 2009; Lin, Adolphs, & Rangel, 2011; Smith et al., 2010c), we conjecture that, in our task, subject choices—and hence framing effects—involves a tradeoff of the relative value between these reward categories, whose computations may occur outside of regions involved with social cognition.

As idiosyncratic responses within pVMPFC predicted the differential biases between self and charity framing effects, our results may endorse the idea that VMPFC integrates the value of different goods and actions (Montague & Berns, 2002; Montague & King-Casas, 2007), potentially shaping individual differences in preferences and behavior. Nevertheless, our results—especially the involvement of regions implicated in social cognition during social decision making—also raise the question of how other brain systems might interact with VMPFC during social valuation. Characterizing the neural circuitry of social valuation will require an interdisciplinary approach, utilizing animal work (Cohen, Haesler, Vong, Lowell, & Uchida, 2012; Wallis, 2012; Xia, Driscoll, Wilbrecht, Margolis, Fields, & Hjelmstad, 2011), brain manipulation techniques (Borchers, Himmelbach, Logothetis, & Karnath, 2012; Rorden & Karnath, 2004; Smith & Clithero, 2009), and network analyses in fMRI (Cole, Smith, & Beckmann, 2010; Leech, Braga, & Sharp, 2012; Leech, Kamourieh, Beckmann, & Sharp, 2011; Sharp, Beckmann, Greenwood, Kinnunen, Bonnelle, De Boisseyzon, Powell, Counsell, Patel, & Leech, 2011; Smith, Fox, Miller, Glahn, Fox, Mackay, Filippini, Watkins, Toro, Laird, & Beckmann, 2009; Smith, Miller, Salimi-Khorshidi, Webster, Beckmann, Nichols, Ramsey, &
Woolrich, 2011c). We speculate that this circuit-level approach will advance our understanding of social valuation and lead to an improved understanding of dysfunctional social valuation processes observed in autism (Calderoni, Retico, Biagi, Tancredi, Muratori, & Tosetti, 2012; Izuma, Matsumoto, Camerer, & Adolphs, 2011; Lombardo, Chakrabarti, Bullmore, & Baron-Cohen, 2011; Menon, 2011; Shih, Keehn, Oram, Leyden, Keown, & Muller, 2011), schizophrenia (Gold, Waltz, Prentice, Morris, & Heerey, 2008; Gradin, Kumar, Waiter, Ahearn, Stickle, Milders, Reid, Hall, & Steele, 2011; Lincoln, Mehl, Kesting, & Rief, 2011; Menon, 2011; Meyer-Lindenberg, 2010), and anorexia nervosa (Kaye, Fudge, & Paulus, 2009; Wagner, Aizenstein, Venkatraman, Fudge, May, Mazurkewicz, Frank, Bailer, Fischer, & Nguyen, 2007; Watson, Werling, Zucker, & Platt, 2010; Zucker, Losh, Bulik, Labar, Piven, & Pelphrey, 2007).
4. Social Cognition Regions Modulate Value Regions in a Preference-Specific Manner

Many brain-imaging studies implicate the ventromedial prefrontal cortex (VMPFC) in the valuation and comparison of different goods. Yet, little is known about how other brain regions interact with VMPFC during valuation. In this study, we found a network of regions involved with social cognition—including temporal-parietal junction (TPJ), frontal pole, posterior cingulate gyrus, and middle temporal gyrus—whose functional connectivity with posterior VMPFC (pVMPFC) increases with increasing social reward valuation.

4.1 Introduction

Valuation—the process of computing and then comparing the subjective value of choice options—has been studied extensively in decision neuroscience research. A consistent finding, across several human neuroimaging and animal electrophysiology studies, has been the association of ventromedial prefrontal cortex (VMPFC) activation with varied rewards, including money (Knutson et al., 2003; O’Doherty et al., 2001a), juice (Kringelbach et al., 2003; O’Doherty et al., 2001b; O’Doherty et al., 2002), and images of food (Hare et al., 2009; Hare et al., 2008; Plassmann et al., 2007; Plassmann, O’Doherty, Shiv, & Rangel, 2008). Yet, recent studies have also demonstrated that VMPFC, among other regions, responds to rewards whose value is derived from their social context, particularly social interactions (Fehr & Camerer, 2007). These studies have
provided valuable insights into the neural mechanisms underlying cooperation (Li, Xiao, Houser, & Montague, 2009; Rilling et al., 2002; Singer et al., 2004; Yoshida, Seymour, Friston, & Dolan, 2010; Zaki & Mitchell, 2011), fairness (Güroflü, van den Bos, Rombouts, & Crone, 2010; Hsu et al., 2008; Knoch et al., 2006; Rilling & Sanfey, 2011; Sanfey et al., 2003; Tabibnia et al., 2008; Wright, Symmonds, Fleming, & Dolan, 2011), altruism (Harbaugh et al., 2007; Moll et al., 2006; Tankersley et al., 2007), and punishment (Buckholtz et al., 2008; de Quervain et al., 2004; Elliott, Agnew, & Deakin, 2010; Seymour et al., 2007b). Social interactions are crucially dependent on social cognitive processes that facilitate gaining information about others’ characteristics and intentions. These social cognitive processes rely on key brain areas, including the temporal-parietal junction (TPJ), medial prefrontal cortex (MPFC), and posterior cingulate (PCC) (Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012; Mar, 2011; Nosek, Hawkins, & Frazier, 2011; Rilling & Sanfey, 2011; Saxe, 2006).

Extending these findings, Hare and colleagues recently examined how social cognition regions and value regions interact during decision making (Hare et al., 2010). They first presented subjects with a series of charitable organizations and asked them to rate each charity’s deservingness (of monetary donation) and closeness (to the rater). Next, subjects underwent fMRI scanning while deciding how much money to donate to each charity. Consistent with other valuation studies (Hare et al., 2009; Smith et al., 2010c), Hare and colleagues found a region of posterior VMPFC whose activation
correlated with the subjective value of charitable donations. Using a functional
connectivity analysis (Friston, Buechel, Fink, Morris, Rolls, & Dolan, 1997), they also
found that this VMPFC region received input from the TPJ, endorsing the idea that
regions involved with social cognition interact with regions supporting value
computation during social valuation. Though striking, these results leave open the
possibility that value regions do not receive additional information regarding the value
of social stimuli from social cognition regions.

We hypothesized that social valuation depends on a synergistic relationship
between VMPFC and regions involved with social cognition, where the ability to predict
social valuation would be enhanced by the inclusion of regions exhibiting increased
functional connectivity with VMPFC during social valuation. To test this hypothesis, we
designed a social valuation task where subjects valued social images (i.e., attractive
faces) on each trial (Figure 15A). Following the fMRI session, participants engaged in an
economic exchange task (Smith et al., 2010c) that allowed us to assess each subject’s
idiosyncratic value for the social images (Figure 15B). Our analyses focused on three
unanswered questions. First, do regions supporting social cognition interact with
posterior VMPFC in a preference-specific fashion? Second, do regions supporting social
cognition add significant explanatory power for social valuation, over and beyond value
regions alone? Third, does the interaction between regions implicated in social cognition

and those implicated value computation increase the ability to predict social valuations, over and beyond either set of regions in isolation?

4.2 Materials and Methods

4.2.1 Participants

Twenty self-reported heterosexual males with normal or corrected-to-normal vision completed the study (mean age: 23 years, range: 18-30 years). We excluded four of these individuals prior to data analyses: three for excessive head movement (> 2mm) and one because of equipment failure, leaving a final sample of 16 participants. Prescreening excluded individuals with prior psychiatric or neurological illness. All participants provided written informed consent as part of a protocol approved by the Institutional Review Board of Duke University Medical Center.

4.2.2 Stimuli and Tasks

In the scanner, participants engaged in two 36-trial runs of a social reward evaluation task (Figure 15A). Social rewards were images of female faces, drawn equally from two distinct attractiveness categories (medium-high and medium-low) determined by a previous study (Smith et al., 2010c). (Due to technical error, three participants only received images from the medium-high category; however, these three participants were indistinguishable from the other thirteen participants on all behavioral measures.) On each trial, a single social reward image was shown for 2 s and then followed by variable fixation period (1 to 5 s). After the fixation period, an 8-point ratings scale was shown for
3 s while participants expressed their attractiveness rating using an MRI-compatible button box. To control for motor anticipation, the scale ordering was randomly flipped from trial to trial. Trials were separated by a variable intertrial interval (ITI) of 4 to 8 s. Participants also performed a simple incentive-compatible reward task, but those results have been published elsewhere (Clithero, Smith, Carter, & Huettel, 2011) and, aside from general payment procedures, will not be discussed further here. Stimuli were projected onto a screen at the back of the scanner bore, and participants viewed the stimuli through mirrored goggles.
Figure 15: Experimental tasks. (A) Trial structure for the ratings task. Male, heterosexual young adults viewed a randomized sequence of images of female faces and provided, for each image, an attractiveness rating using an 8-point scale. To control for motor anticipation, the ordering of the 8-point scale was randomly flipped across trials; on some trials, the highest rating was the left-most option, and on other trials, the highest rating was the right-most option (as shown in the example). (B) Trial structure for the economic exchange task. Each trial began with a choice phase (lasting 4 s) in which the participant was forced to spend a small amount of money to view a face. Participants could choose to spend more money to view a more attractive face (denoted with increasing stars) or less money to view a less attractive face. After a variable delay period, a single face, randomly selected from the chosen attractiveness category, was displayed for 2 s.

Following the scanner session, participants performed an economic exchange task (Figure 13B) employed in previous studies (Clithero et al., 2011; Smith et al., 2010c). On each trial, participants chose whether to spend more money to view a novel high
attractiveness face or less money to view a novel low attractiveness face. Monetary cost ranged from 1 to 12 cents while attractiveness spanned four distinct categories (1- to 4-stars for increasing attractiveness). Both cost and attractiveness varied randomly across trials within uniform distributions, with the constraints that the two face options always differed in attractiveness and that the more attractive face always carried the greater monetary cost. After a 4 s decision window, the screen went blank for a variable fixation interval of 2 to 4 s before a face from the chosen category was presented for 2 s. Participants made 48 decisions during the economic exchange task.

Tasks were programmed using the Psychophysics Toolbox version 2.54 (Brainard, 1997). Cash payment was identical to our earlier work (Clithero et al., 2011). In brief, participants rolled dice to determine the reward task run (results not considered here) whose cumulative total would be added to the base payment of $50. Participants received an average of $16 for their bonus reward, and spent an average of $2.12 to view new faces in the economic exchange task, resulting in a total mean payment of approximately $66 (range $53 to $92). Participants were provided full information regarding the payment mechanism prior to the scanning session.

Prior to analyses, we normalized each participant’s attractiveness ratings by converting the raw ratings from a 1 to 8 scale into a 0 to 1 scale (minimum to maximum). We then grouped the normalized ratings by quintiles, representing the lowest quintile with a 1 and the highest quintile with a 5. This normalization procedure controls for
individual response bias and facilitates comparison across participants. Aside from one participant who only used four numbers in their ratings, all participants could be mapped to the normalized 1 to 5 scale. We note that this participant was otherwise indistinguishable from the remainder of our sample on all behavioral measures.

4.2.3 Image Acquisition

Neuroimaging data were acquired on a 3 Tesla General Electric scanner with an 8-channel parallel imaging system. Images sensitive to blood-oxygenation-level-dependent (BOLD) contrast were acquired using a T2*-weighted gradient-echo echo-planar imaging (EPI) sequence, with slices parallel to the axial plane connecting the anterior and posterior commissures [repetition time (TR): 2000 ms; echo time (TE): 27 ms; matrix: 64 x 64; field of view (FOV): 240 mm; voxel size: 3.75 x 3.75 x 3.8 mm; 34 axial slices; flip angle: 60 degrees]. Prior to analysis, the first seven volumes of each run were discarded to allow for magnetic stabilization. We also acquired whole-brain high-resolution anatomical scans to aide in normalization and coregistration (T1-weighted FSPGR sequence; TR: 7.3 ms; TE: 2.9 ms; matrix: 256 x 256; FOV: 256 mm; voxel size: 0.93 x 0.93 x 1.9 mm; 68 axial slices; flip angle: 12 degrees).

4.2.4 Preprocessing

Preprocessing used tools from the FMRIB Software Library (FSL Version 4.1.5; http://www.fmrib.ox.ac.uk/fsl/) package (Smith et al., 2004; Woolrich et al., 2009). We first corrected for head motion by realigning the time series to the middle volume
Non-brain material was then removed using the brain extraction tool (Smith, 2002). We corrected for intravolume slice-timing differences using Fourier-space phase shifting, aligning to the middle slice (Sladky et al., 2011). Spatial smoothing employed a Gaussian kernel of full-width-half-maximum 6 mm. The entire 4D dataset was grand-mean intensity normalized using a single multiplicative factor. To remove low frequency drift in the MR signal, we used a high-pass temporal filter with a 100 second cutoff (Gaussian-weighted least-squares straight line fitting, with \( \sigma = 50 \) s). Functional data were spatially normalized to the MNI avg152 T1-weighted template (2 mm isotropic resolution) using a 12-parameter affine transformation implemented in FLIRT (Jenkinson & Smith, 2001); these transformations were later applied to the statistical images before cross-run and cross-participant analyses.

As part of our preprocessing, we also identified outlier volumes in our functional data. A volume was considered an outlier if its root-mean-square (RMS) amplitude exceeded the value of 150% of the interquartile range of RMS for all volumes in a run. We excluded runs in which more than 12% of the time series was corrupted by outliers; this threshold corresponded to the 95th percentile of a distribution containing the proportion of outlier volumes across all runs of data in our sample.

### 4.2.5 FMRI Analyses

Neuroimaging analyses were conducted using FEAT (FMRI Expert Analysis Tool) Version 5.98 (Smith et al., 2004; Woolrich et al., 2009). First, we constructed a
parametric model to examine brain regions whose activation increased as a function of increasing attractiveness ratings. Our first-level analysis (i.e., within run) utilized a general linear model with local autocorrelation correction (Woolrich et al., 2001). Each first-level model consisted of four regressors modeling the presentation of the face stimulus and the ratings screen that followed the face. The regressor for the face stimulus was parametrically modulated by a series of polynomial expansions (1st and 2nd order) of the normalized participant-specific attractiveness ratings for each trial (Buchel, Holmes, Rees, & Friston, 1998). The 2nd-order expansion increases confidence in attributing response profiles; e.g., if only a 1st-order term were used, underlying relationships that were in fact quadratic could be misinterpreted as linear (Buchel et al., 1998; Winston et al., 2007). We examined the response profile in regions showing parametric effects by estimating an independent categorical model where responses levels were modeled separately. In both models, we included nuisance regressors to account for response time differences across ratings, missed ratings, and outlier volumes. Except for the outlier volume nuisance regressors (which were unconvolved), all regressors were convolved with a canonical hemodynamic response function. We combined data across runs, for each subject, using a fixed-effects model, and combined data across subjects using a mixed-effects model (Beckmann et al., 2003; Woolrich et al., 2004).
Next, we constructed a psychophysiological interaction (PPI) analysis (Friston et al., 1997) to identify voxels whose functional connectivity with pVMPFC, a canonical valuation region (Hare et al., 2009; Smith et al., 2010c), increases as a function of increasing attractiveness ratings. Our PPI model utilized the same regressors as the parametric model, but also included, for each participant, the average time course within 5mm (radius) region of interest centered on pVMPFC. This physiological regressor was multiplied by the 1st-order parametric term to form the PPI regressor. We combined data across runs, for each subject, using a fixed-effects model, and combined data across subjects using a mixed-effects model (Beckmann et al., 2003; Woolrich et al., 2004).

All z-statistic (Gaussianized t) images were thresholded using an initial cluster-forming threshold of $z > 2.3$ followed by a corrected cluster-significance threshold of $p < 0.05$ (Worsley, 2001). Importantly, we note that all activation clusters survived additional correction for outliers (Woolrich, 2008). Statistical overlay images were created using MRICron and MRicroGL (Rorden et al., 2007). Probabilistic anatomical labels for local maxima were obtained using the Harvard-Oxford Cortical and Subcortical atlases; all coordinates are reported in MNI space.

### 4.2.6 Trial-to-Trial Analysis

To examine trial-to-trial effects, we constructed a trial-by-trial model by modeling each image presentation separately. This model was similar to the other
models, but, importantly, each face presentation was modeled separately—thus capturing trial-specific processes and interactions (Bland, Mushtaq, & Smith, 2011; Pernet, Sajda, & Rousselet, 2011). We then extracted, for each trial, the median percent signal change within key regions of interest (ROI) identified from the parametric and PPI models. For each ROI, we first normalized the median parameter estimates by converting to z-scores and then excluded outliers (i.e., trials falling outside of the 2.5th or 97.5th percentiles). The resulting values were then submitted to a hierarchical regression analysis performed in Stata 12.0 (StataCorp).

4.3 Results

4.3.1 Ratings and Choice Behavior

Our behavioral analyses focused on two issues. First, we examined whether our scanner participants’ attractiveness ratings were consistent with our independent sample (Smith et al., 2010c). To do this, we compared the difference in the average normalized ratings between the two categories (medium-high and medium-low) defined by our independent sample. This analysis revealed that participants rated the high-value images significantly higher than the low-value images (high-value mean: 3.44; low-value mean: 2.10; range of differences: 0.39 to 2.31; paired $t_{(12)} = 10.47$, $p < 0.001$), indicating that our participants’ ratings were highly comparable to the ratings from our independent sample (Smith et al., 2010c). Second, we examined whether response time measures were related to trial-to-trial ratings or exchange rate. We found that the average
response time across all trials was unrelated to exchange rate ($r_{(14)} = 0.01$, n.s.). Further, for each participant, the trial-to-trial ratings were, on average, uncorrelated with the trial-to-trial response times (mean $r = 0.04$, SD: 0.16; range: -0.22 to 0.29), indicating that response times were largely independent of valuation measures.

### 4.3.2 Parametric Effects of Attractiveness

To identify brain regions whose activation tracked attractiveness ratings, we examined the main effect of the 1st-order (linear) term in our parametric model. This analysis revealed that activation in several key regions, including the ACC, anterior VMPFC, and caudate, increased with increasing attractiveness, with least response to low attractiveness faces and greatest response to high attractiveness faces (Figure 16A; see Table 8 for complete listing of activation coordinates). Within the ACC region (Figure 16B), the response was supra-linear across the normalized levels of attractiveness ratings; however, this nonlinear trend was not significant. Regions exhibiting a significant nonlinear (quadratic, the 2nd order term in our parametric model) relationship with attractiveness ratings included the anterior insula and MPFC (see Table 9 for complete listing of activation coordinates); activation in these regions followed a U-shaped pattern, with least response to medium attractiveness faces and greatest response to high and low attractiveness faces. No brain regions exhibited a significant negative relationship with the linear or quadratic predictor at our statistical threshold.
Figure 16: Brain regions tracking increasing attractiveness judgments. (A) To identify brain regions whose activation tracked attractiveness judgments, we constructed parametric model based on each participant’s ratings and examined regions exhibiting a linear relationship with ratings. Brain regions tracking attractiveness ratings included the ACC (x,y,z = 6,18,34), right caudate (x,y,z = 8,12,8), and parts of visual cortex (x,y,z = -4,-100,4; x,y,z = -28,-82,2). All areas of activation passed an initial cluster-forming threshold of z=2.3, with whole-brain cluster correction at p=0.05. (B) Interrogation of the ACC region revealed a quasi-linear trend of activation, with higher activation predicting higher ratings and lower activation predicting lower activation. Error bars reflect SEM.
Table 8: Regions whose activation increases with increasing social reward (see Figure 16). Coordinates of local maxima within the five clusters of activation are in MNI space. Probabilistic labels reflect the probability (or likelihood) that a coordinate belongs to a given region. For clarity, we only show labels whose likelihood exceeds 5%. Abbreviations: WM (white matter); sLOC (lateral occipital cortex, superior division); iLOC (lateral occipital cortex, inferior division); ACC (anterior cingulate cortex); OFG (occipital fusiform gyrus); SFG (superior frontal gyrus); TOFC (temporal occipital fusiform cortex).

<table>
<thead>
<tr>
<th>Probabilistic Anatomical Label</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z-stat</th>
<th>Cluster Volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occipital Pole (62%), WM (6%)</td>
<td>-4</td>
<td>-100</td>
<td>4</td>
<td>3.51</td>
<td>13000 mm$^3$ (p &lt; 0.001)</td>
</tr>
<tr>
<td>WM (62%), Occipital Pole (25%), iLOC (6%), OFG (5%)</td>
<td>24</td>
<td>-90</td>
<td>0</td>
<td>3.25</td>
<td></td>
</tr>
<tr>
<td>Occipital Pole (35%)</td>
<td>-2</td>
<td>-100</td>
<td>-6</td>
<td>3.17</td>
<td></td>
</tr>
<tr>
<td>Cuneal Cortex (25%), sLOC (5%)</td>
<td>-14</td>
<td>-82</td>
<td>28</td>
<td>3.17</td>
<td></td>
</tr>
<tr>
<td>Occipital Pole (65%)</td>
<td>16</td>
<td>-96</td>
<td>-2</td>
<td>3.1</td>
<td></td>
</tr>
<tr>
<td>ACC (61%), Paracingulate Gyrus (25%)</td>
<td>6</td>
<td>18</td>
<td>34</td>
<td>3.8</td>
<td>12680 mm$^3$ (p &lt; 0.001)</td>
</tr>
<tr>
<td>Juxtapositional Lobule Cortex (33%), SFG (12%)</td>
<td>0</td>
<td>8</td>
<td>60</td>
<td>3.43</td>
<td></td>
</tr>
<tr>
<td>SFG (37%), Juxtapositional Lobule Cortex (20%)</td>
<td>6</td>
<td>10</td>
<td>70</td>
<td>3.36</td>
<td></td>
</tr>
<tr>
<td>Juxtapositional Lobule Cortex (72%), ACC (5%)</td>
<td>-2</td>
<td>0</td>
<td>52</td>
<td>3.18</td>
<td></td>
</tr>
<tr>
<td>ACC (64%), Juxtapositional Lobule Cortex (21%)</td>
<td>-2</td>
<td>4</td>
<td>42</td>
<td>3.15</td>
<td></td>
</tr>
<tr>
<td>WM (98%)</td>
<td>28</td>
<td>-16</td>
<td>30</td>
<td>3.26</td>
<td>5832 mm$^3$ (p &lt; 0.01)</td>
</tr>
<tr>
<td>WM (96%)</td>
<td>22</td>
<td>-16</td>
<td>24</td>
<td>3.22</td>
<td></td>
</tr>
<tr>
<td>WM (99%)</td>
<td>20</td>
<td>-20</td>
<td>32</td>
<td>2.96</td>
<td></td>
</tr>
<tr>
<td>Right Lateral Ventricle (81%)</td>
<td>2</td>
<td>2</td>
<td>16</td>
<td>2.95</td>
<td></td>
</tr>
<tr>
<td>Left Lateral Ventricle (51%), Right Lateral Ventricle (27%)</td>
<td>0</td>
<td>10</td>
<td>10</td>
<td>2.94</td>
<td></td>
</tr>
<tr>
<td>WM (49%), Lingual Gyrus (43%)</td>
<td>14</td>
<td>-68</td>
<td>-2</td>
<td>3.17</td>
<td>3808 mm$^3$ (p &lt; 0.05)</td>
</tr>
<tr>
<td>Lingual Gyrus (55%), WM (40%)</td>
<td>14</td>
<td>-56</td>
<td>-2</td>
<td>2.97</td>
<td></td>
</tr>
<tr>
<td>OFG (47%), WM (29%), Lingual Gyrus</td>
<td>28</td>
<td>-64</td>
<td>-10</td>
<td>2.94</td>
<td></td>
</tr>
</tbody>
</table>
Table 9: Regions whose activation follows a nonlinear, U-shaped pattern in response to social reward. Coordinates of local maxima within the two clusters of activation are in MNI space. Probabilistic labels reflect the probability (or likelihood) that a coordinate belongs to a given region. For clarity, we only show labels whose likelihood exceeds 5%. Abbreviations: WM (white matter); OFC (Frontal Orbital Cortex); IFG (Inferior Frontal Gyrus, pars triangularis); MPFC (Frontal Medial Cortex); ParaCG (Paracingulate Gyrus); F Operculum (Frontal Operculum Cortex), ACC (anterior cingulate cortex).

<table>
<thead>
<tr>
<th>Probabilistic Anatomical Label</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z-stat</th>
<th>Cluster Volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>WM (61%), OFG (29%), iLOC (5%)</td>
<td>36</td>
<td>-66</td>
<td>-10</td>
<td>2.89</td>
<td></td>
</tr>
<tr>
<td>WM (44%), Intralcalcarine Cortex (39%), Lingual Gyrus (14%)</td>
<td>14</td>
<td>-64</td>
<td>4</td>
<td>2.88</td>
<td></td>
</tr>
<tr>
<td>WM (34%), iLOC (33%), Occipital Pole (5%)</td>
<td>-28</td>
<td>-88</td>
<td>0</td>
<td>3.19</td>
<td>3456 mm³ (p &lt; 0.05)</td>
</tr>
<tr>
<td>WM (72%), iLOC (9%)</td>
<td>-28</td>
<td>-82</td>
<td>2</td>
<td>3.17</td>
<td></td>
</tr>
<tr>
<td>Occipital Pole (67%), WM (8%)</td>
<td>-12</td>
<td>-100</td>
<td>18</td>
<td>2.84</td>
<td></td>
</tr>
<tr>
<td>Occipital Pole (51%), WM (24%)</td>
<td>-24</td>
<td>-96</td>
<td>4</td>
<td>2.82</td>
<td></td>
</tr>
<tr>
<td>WM (44%), Occipital Pole (19%), sLOC (16%)</td>
<td>-18</td>
<td>-90</td>
<td>16</td>
<td>2.76</td>
<td></td>
</tr>
</tbody>
</table>
4.3.3 Increased Functional Connectivity with Posterior VMPFC Predicts Social Valuation

We next tested our core prediction that pVMPFC interacts with regions associated with social cognition during the valuation of social rewards. To do this, we conducted a PPI analysis using the participant-specific pVMPFC activation and attractiveness ratings. Importantly, we also introduced each participant’s exchange rate as covariate in the group level model (average: 0.42; range: 0.1 to 0.8). Therefore, this analysis highlights regions whose functional coupling with pVMPFC is modulated by both an individual attractiveness ratings and their willingness to exchange money for faces. Strikingly, we found a network of putative social cognition regions—including TPJ, frontal pole, PCC, and middle TG (mid TG)—whose functional connectivity with pVMPFC increases with increasing social reward valuation (Figure 17; Table 10).
Figure 17: Functional connectivity between pVMPFC and regions involved in social cognition predicts social valuations. We employed a PPI analysis to identify regions whose functional connectivity with posterior VMPFC increases as a function of both increasing attractiveness ratings and increasing willingness to exchange money for faces. Shown on the left is a depiction of our seed region, posterior VMPFC, which represents a canonical valuation region. The middle panel shows a schematic of the trial-to-trial modulator (subjective attractiveness) and the participant covariate (proportion of exchanges). Shown on the right are areas whose connectivity with posterior VMPFC increases with increasing attractiveness ratings and increasing willingness to trade money for faces. These regions included the frontal pole (x,y,z = 4,70,-4), TPJ (x,y,z = -40,-60,32), middle temporal gyrus (x,y,z = -66,-32,-6), and posterior cingulate (x,y,z = -2,-46,20). All areas of activation passed an initial cluster-forming threshold of $z=2.3$, with whole-brain cluster correction at $p=0.05$. 
Table 10: Regions whose functional connectivity with pVMPFC increases as a function of increasing attractiveness ratings and increasing economic exchanges (see Fig. 17). Coordinates of local maxima within the four clusters of activation are in MNI space. Probabilistic labels reflect the probability (or likelihood) that a coordinate belongs to a given region. For clarity, we only show labels whose likelihood exceeds 5%. Abbreviations: pMTG (middle temporal gyrus, posterior division); pSTG (superior temporal gyrus, posterior division); WM (white matter); aMTG (middle temporal gyrus, anterior division); sLOC (lateral occipital cortex, superior division); iLOC (lateral occipital cortex, inferior division); ACC (anterior cingulate cortex); PCC (posterior cingulate cortex).

<table>
<thead>
<tr>
<th>Probabilistic Anatomical Label</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z-stat</th>
<th>Cluster Volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>pMTG (75%), pSTG (9%)</td>
<td>-66</td>
<td>-32</td>
<td>-6</td>
<td>3.35</td>
<td>4168 mm³</td>
</tr>
<tr>
<td>pSTG (63%), pMTG (12%), WM (11%)</td>
<td>-64</td>
<td>-28</td>
<td>2</td>
<td>3.26</td>
<td></td>
</tr>
<tr>
<td>WM (28%), pMTG (22%), MTG temporooccipital part (16%)</td>
<td>-56</td>
<td>-42</td>
<td>-6</td>
<td>3.17</td>
<td></td>
</tr>
<tr>
<td>pMTG (9%)</td>
<td>-72</td>
<td>-34</td>
<td>-4</td>
<td>3.09</td>
<td></td>
</tr>
<tr>
<td>pMTG (26%), aMTG (24%), WM (22%)</td>
<td>-56</td>
<td>-10</td>
<td>-20</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>WM (36%), sLOC (21%), Angular Gyrus (8%), iLOC (7%)</td>
<td>-38</td>
<td>-62</td>
<td>18</td>
<td>3.37</td>
<td>4128 mm³ (p &lt; 0.05)</td>
</tr>
<tr>
<td>WM (30%), sLOC (23%), Angular Gyrus (21%)</td>
<td>-42</td>
<td>-60</td>
<td>36</td>
<td>3.14</td>
<td></td>
</tr>
<tr>
<td>WM (39%), Angular Gyrus (23%), sLOC (15%)</td>
<td>-40</td>
<td>-60</td>
<td>32</td>
<td>3.07</td>
<td></td>
</tr>
<tr>
<td>WM (39%), sLOC (34%)</td>
<td>-36</td>
<td>-68</td>
<td>34</td>
<td>2.95</td>
<td></td>
</tr>
<tr>
<td>WM (62%), Angular Gyrus (18%)</td>
<td>-36</td>
<td>-60</td>
<td>26</td>
<td>2.95</td>
<td></td>
</tr>
<tr>
<td>PCC (8%), Posterior Parahippocampal Gyrus (5%)</td>
<td>-6</td>
<td>-42</td>
<td>0</td>
<td>3.36</td>
<td>3704 mm³</td>
</tr>
<tr>
<td>WM (40%), Precuneous Cortex (30%)</td>
<td>-16</td>
<td>-54</td>
<td>10</td>
<td>3.27</td>
<td></td>
</tr>
<tr>
<td>PCC (56%), Precuneous Cortex (13%), WM (10%)</td>
<td>-10</td>
<td>-48</td>
<td>4</td>
<td>3.03</td>
<td></td>
</tr>
<tr>
<td>PCC (81%)</td>
<td>-2</td>
<td>-46</td>
<td>20</td>
<td>2.92</td>
<td></td>
</tr>
<tr>
<td>WM (73%), PCC (19%), Precuneous Cortex (6%)</td>
<td>8</td>
<td>-46</td>
<td>18</td>
<td>2.91</td>
<td></td>
</tr>
<tr>
<td>Frontal Medial Cortex (71%), Frontal Pole (13%)</td>
<td>2</td>
<td>52</td>
<td>-12</td>
<td>3.5</td>
<td>3464 mm³ (p &lt; 0.05)</td>
</tr>
<tr>
<td>Frontal Pole (67%)</td>
<td>4</td>
<td>70</td>
<td>4</td>
<td>3.25</td>
<td></td>
</tr>
<tr>
<td>Probabilistic Anatomical Label</td>
<td>x</td>
<td>y</td>
<td>z</td>
<td>Z-stat</td>
<td>Cluster Volume</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>----</td>
<td>----</td>
<td>----</td>
<td>--------</td>
<td>----------------</td>
</tr>
<tr>
<td>Frontal Pole (57%)</td>
<td>4</td>
<td>70</td>
<td>-4</td>
<td>3.08</td>
<td></td>
</tr>
<tr>
<td>Frontal Pole (45%)</td>
<td>-2</td>
<td>68</td>
<td>4</td>
<td>3.03</td>
<td></td>
</tr>
<tr>
<td>Frontal Pole (47%)</td>
<td>0</td>
<td>66</td>
<td>-8</td>
<td>2.99</td>
<td></td>
</tr>
</tbody>
</table>

Our functional connectivity analysis, while consistent with prior work (Hare et al., 2010), does not in itself test a key prediction regarding the relationship between valuation regions (e.g., Figures 8 and 14) and regions supporting social cognition (e.g., Figure 13): that activation of social cognition regions provides additive power for predicting the subjective value of social stimuli. We therefore constructed a 4-level hierarchical regression on the trial-to-trial attractiveness ratings. Our first level controlled for nuisance predictors, including response time, run number, trial number, and participant identity. Our second level focused on valuation regions and introduced the trial-by-trial parameter estimates from aVMPFC and pVMPFC (Smith et al., 2010c) and each of the five regions whose activation increased with increasing attractiveness. Our third level focused on regions exhibiting connectivity with pVMPFC during social valuation—i.e., regions potentially supporting social cognition—and introduced the trial-by-trial parameter estimates from each of the four regions whose functional connectivity with pVMPFC increased with increasing social valuation. The final level of our model introduced the interaction terms between pVMPFC and each of the four PPI regions.
Strikingly, our hierarchical model demonstrated that regions supporting social cognition explained significantly more variability in ratings data than regions supporting valuation (Table 11). Chief among these regions was MTG, which exhibited a strong negative relationship with ratings data. The only other significant factor in the full model was the ACC, which was a strong positive predictor of ratings data. Overall, the full model accounted for 16% of the variability in the normalized ratings data (see Table 12 for complete regression statistics).

Table 11: Hierarchal regression results. To examine the incremental contribution of additional regions of interest, we performed a hierarchal regression analysis with four sequential levels: confound terms (Block 1); value terms (Block 2); functional connectivity terms (Block 3); regional interaction terms (Block 4). We found that a model incorporating the functional connectivity regions was significantly better at predicting trial-to-trial social valuations compared to value-region-only model.

<table>
<thead>
<tr>
<th>Block</th>
<th>F-stat</th>
<th>Block DF</th>
<th>Block Residual</th>
<th>R^2</th>
<th>Change in R^2</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.15</td>
<td>18</td>
<td>692</td>
<td>0.0884</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>2.73</td>
<td>9</td>
<td>683</td>
<td>0.1219</td>
<td>0.0336</td>
<td>0.0039</td>
</tr>
<tr>
<td>3</td>
<td>3.52</td>
<td>8</td>
<td>675</td>
<td>0.157</td>
<td>0.0351</td>
<td>0.0005</td>
</tr>
<tr>
<td>4</td>
<td>1.23</td>
<td>8</td>
<td>667</td>
<td>0.1691</td>
<td>0.0121</td>
<td>0.2769</td>
</tr>
</tbody>
</table>

Table 12: Complete regression statistics. For completeness, here we show the complete regression model with all four blocks and all terms.

<table>
<thead>
<tr>
<th>Block Number</th>
<th>Factor</th>
<th>Beta</th>
<th>Robust Std Error</th>
<th>t-stat</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Response Time</td>
<td>0.071</td>
<td>0.061</td>
<td>1.17</td>
<td>0.242</td>
</tr>
<tr>
<td>1</td>
<td>Trial Number</td>
<td>-0.004</td>
<td>0.002</td>
<td>-1.78</td>
<td>0.075</td>
</tr>
<tr>
<td>1</td>
<td>Run Number</td>
<td>0.030</td>
<td>0.054</td>
<td>0.55</td>
<td>0.585</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject00</td>
<td>-0.321</td>
<td>0.151</td>
<td>-2.13</td>
<td>0.034</td>
</tr>
<tr>
<td>Block Number</td>
<td>Factor</td>
<td>Beta</td>
<td>Robust Std Error</td>
<td>t-stat</td>
<td>p-value</td>
</tr>
<tr>
<td>--------------</td>
<td>--------------------------</td>
<td>-------</td>
<td>------------------</td>
<td>--------</td>
<td>---------</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject01</td>
<td>-0.310</td>
<td>0.178</td>
<td>-1.75</td>
<td>0.081</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject02</td>
<td>-0.430</td>
<td>0.126</td>
<td>-3.42</td>
<td>0.001</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject03</td>
<td>-0.238</td>
<td>0.129</td>
<td>-1.84</td>
<td>0.066</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject04</td>
<td>-0.451</td>
<td>0.160</td>
<td>-2.81</td>
<td>0.005</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject05</td>
<td>-0.094</td>
<td>0.137</td>
<td>-0.69</td>
<td>0.490</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject06</td>
<td>-0.251</td>
<td>0.147</td>
<td>-1.71</td>
<td>0.088</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject07</td>
<td>-0.364</td>
<td>0.161</td>
<td>-2.27</td>
<td>0.024</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject08</td>
<td>-0.449</td>
<td>0.137</td>
<td>-3.27</td>
<td>0.001</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject09</td>
<td>-0.631</td>
<td>0.133</td>
<td>-4.74</td>
<td>0.000</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject10</td>
<td>-0.076</td>
<td>0.139</td>
<td>-0.55</td>
<td>0.585</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject11</td>
<td>-0.292</td>
<td>0.192</td>
<td>-1.52</td>
<td>0.129</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject12</td>
<td>-0.651</td>
<td>0.149</td>
<td>-4.38</td>
<td>0.000</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject13</td>
<td>-0.134</td>
<td>0.156</td>
<td>-0.86</td>
<td>0.391</td>
</tr>
<tr>
<td>1</td>
<td>dummy_subject14</td>
<td>-0.346</td>
<td>0.132</td>
<td>-2.62</td>
<td>0.009</td>
</tr>
<tr>
<td>2</td>
<td>aVMPFC</td>
<td>0.088</td>
<td>0.053</td>
<td>1.67</td>
<td>0.096</td>
</tr>
<tr>
<td>2</td>
<td>pVMPFC</td>
<td>0.021</td>
<td>0.038</td>
<td>0.56</td>
<td>0.576</td>
</tr>
<tr>
<td>2</td>
<td>linear_ACC</td>
<td>0.107</td>
<td>0.036</td>
<td>3.02</td>
<td>0.003</td>
</tr>
<tr>
<td>2</td>
<td>linear_VC1</td>
<td>0.066</td>
<td>0.033</td>
<td>1.98</td>
<td>0.048</td>
</tr>
<tr>
<td>2</td>
<td>linear_VC2</td>
<td>0.023</td>
<td>0.038</td>
<td>0.60</td>
<td>0.546</td>
</tr>
<tr>
<td>2</td>
<td>linear_VC3</td>
<td>0.058</td>
<td>0.033</td>
<td>1.75</td>
<td>0.080</td>
</tr>
<tr>
<td>2</td>
<td>linear_WM</td>
<td>0.027</td>
<td>0.032</td>
<td>0.85</td>
<td>0.395</td>
</tr>
<tr>
<td>2</td>
<td>exchanges*aVMPFC</td>
<td>-0.140</td>
<td>0.082</td>
<td>-1.71</td>
<td>0.088</td>
</tr>
<tr>
<td>2</td>
<td>exchanges*pVMPFC</td>
<td>0.080</td>
<td>0.066</td>
<td>1.21</td>
<td>0.227</td>
</tr>
<tr>
<td>3</td>
<td>ppi_RSP</td>
<td>0.045</td>
<td>0.037</td>
<td>1.21</td>
<td>0.229</td>
</tr>
<tr>
<td>3</td>
<td>ppi_TPI</td>
<td>-0.070</td>
<td>0.034</td>
<td>-2.05</td>
<td>0.041</td>
</tr>
<tr>
<td>3</td>
<td>ppi_VMPFC</td>
<td>-0.080</td>
<td>0.050</td>
<td>-1.60</td>
<td>0.111</td>
</tr>
<tr>
<td>3</td>
<td>ppi_MTG</td>
<td>-0.112</td>
<td>0.035</td>
<td>-3.21</td>
<td>0.001</td>
</tr>
<tr>
<td>3</td>
<td>exchanges*ppi_RSP</td>
<td>0.008</td>
<td>0.064</td>
<td>0.12</td>
<td>0.903</td>
</tr>
<tr>
<td>3</td>
<td>exchanges*ppi_TPI</td>
<td>-0.095</td>
<td>0.063</td>
<td>-1.51</td>
<td>0.131</td>
</tr>
<tr>
<td>3</td>
<td>exchanges*ppi_VMPFC</td>
<td>0.016</td>
<td>0.078</td>
<td>0.21</td>
<td>0.832</td>
</tr>
<tr>
<td>3</td>
<td>exchanges*ppi_MTG</td>
<td>0.042</td>
<td>0.065</td>
<td>0.64</td>
<td>0.522</td>
</tr>
<tr>
<td>4</td>
<td>ppi_RSP*pVMPFC</td>
<td>-0.017</td>
<td>0.044</td>
<td>-0.39</td>
<td>0.697</td>
</tr>
<tr>
<td>4</td>
<td>ppi_TPI*pVMPFC</td>
<td>-0.035</td>
<td>0.041</td>
<td>-0.86</td>
<td>0.390</td>
</tr>
<tr>
<td>4</td>
<td>ppi_VMPFC*pVMPFC</td>
<td>0.042</td>
<td>0.049</td>
<td>0.86</td>
<td>0.391</td>
</tr>
<tr>
<td>4</td>
<td>ppi_MTG*pVMPFC</td>
<td>0.009</td>
<td>0.044</td>
<td>0.20</td>
<td>0.839</td>
</tr>
<tr>
<td>4</td>
<td>exchanges<em>ppi_RSP</em>pVMPFC</td>
<td>-0.050</td>
<td>0.083</td>
<td>-0.60</td>
<td>0.547</td>
</tr>
<tr>
<td>4</td>
<td>exchanges<em>ppi_TPI</em>pVMPFC</td>
<td>0.070</td>
<td>0.074</td>
<td>0.95</td>
<td>0.342</td>
</tr>
<tr>
<td>4</td>
<td>exchanges<em>ppi_VMPFC</em>pVMPFC</td>
<td>0.086</td>
<td>0.081</td>
<td>1.06</td>
<td>0.288</td>
</tr>
<tr>
<td>4</td>
<td>exchanges<em>ppi_MTG</em>pVMPFC</td>
<td>0.125</td>
<td>0.077</td>
<td>1.62</td>
<td>0.105</td>
</tr>
<tr>
<td></td>
<td>constant</td>
<td>0.143</td>
<td>0.169</td>
<td>0.84</td>
<td>0.399</td>
</tr>
</tbody>
</table>
4.4 Discussion

As value comparisons represent a crucial component of all decisions, research in decision neuroscience has heavily targeted the neural underpinnings of value computation. A key region for value computation, as identified by electrophysiological work in animals (Burke, Franz, Miller, & Schoenbaum, 2008; Padoa-Schioppa, 2009; Padoa-Schioppa & Assad, 2006, 2008) and functional neuroimaging in humans (Lebreton, Jorge, Michel, Thirion, & Pessiglione, 2009; Levy & Glimcher, 2011; Levy, Lazzaro, Rutledge, & Glimcher, 2011), is the ventromedial prefrontal cortex (VMPFC). We investigated whether and how this value region interacts with other neural systems during the course of valuation. Supporting our predictions, we found that, during social valuation, VMPFC interacted with brain regions implicated in social cognition. Importantly, we also found that these additional regions significantly enhanced our ability to predict trial-to-trial variations in social valuation.

Our results endorse the idea that value computations do not occur within a single brain region in isolation. Instead, our data support the view that value computations rely on distributed neural circuitry whose precise constituents depend upon the classes of decisions and valuations. For other rewards and decisions, VMPFC could interact with other brain systems. Consistent with this view, Hare and colleagues (2009) found that, during dietary decisions involving self control, activation within
DLPFC increased when subjects exerted self control and that this activation correlated with activation levels within VMPFC (Hare et al., 2009). Similarly, Park and colleagues (2011) found that decisions involving tradeoffs of monetary reward (positive values) and physical pain (negative values) are related to correlations between VMPFC and amygdala activation. For social valuations, our data demonstrate that VMPFC interacts with social cognition regions, particularly the TPJ and mTG.

These social cognition regions are frequently implicated in situations that ask people to mentalize (i.e., utilize theory of mind) (Adolphs, 2009; Amodio & Frith, 2006; Blakemore, 2008; Frank Van, 2009; Lieberman, 2007; Mar, 2011; Saxe, 2006; Zebrowitz, 2006). In our task, subjects view images of faces, which entails far more than simply assessing physical features, as subjects are likely concurrently evaluating the social category, identity, emotion, psychological disposition of each face (Zebrowitz, 2006). This evaluative process is highly reliant on social cognition (Zebrowitz, 2006), leading to increased activation within the medial prefrontal cortex and TPJ (Amodio & Frith, 2006; Frank Van, 2009; Mar, 2011). Therefore, we conclude that the interactions between pVMPFC and TPJ are rooted in social-evaluative processes for face stimuli.

Alternatively, activation within the TPJ region could reflect increases in attention (but see Young, Dodell-Feder, & Saxe, 2010), as this region has been broadly associated with reflexive attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Smith, Davis, Niu, Healy, Bonilha, Fridriksson, Morgan, & Rorden, 2010b; Thiel, Zilles, & Fink,
2004) and disorders of attention, such as spatial neglect (Corbetta & Shulman, 2011; Husain & Rorden, 2003; Karnath & Rorden, 2011). Moreover, attention and reward are notoriously difficult to disambiguate (Maunsell, 2004) and likely interact during the course of valuation and decision making (Kennerley & Wallis, 2009; Krebs, Boehler, Egner, & Woldorff, 2011; Krebs, Heipertz, Schuetze, & Duzel, 2011). Recognizing these concerns, we emphasize that our analyses controlled for response time differences across valuations, and, importantly, we included both linear and quadratic regressors in our statistical models. We argue that the quadratic regressor would capture neural responses that vary according to reflexive attention (or salience). Instead, our core results and analyses focus on regions whose activation (or connectivity with pVMPFC) increases as a function of increasing value. Yet, as the range of affective value for our social images may be limited to a subset of the full range of positive and negative value, future studies will have to employ social stimuli whose affective value spans a greater range, with highly positive and highly negative stimuli compared to an affectively neutral baseline condition (Said, Haxby, & Todorov, 2011; Said & Todorov, 2011; Todorov, Said, Oosterhof, & Engell, 2011).

By examining the neural circuitry of social valuation, our results illustrate the neural construction of social preferences, endorsing the idea that value regions interact with social cognition regions during social valuation. This approach—examining interactions between brain regions—has great potential for uncovering the circuitry
mediating individual differences in complex behaviors and preference. We speculate that our circuit-level approach will deepen our understanding of social valuation, potentially leading to improved models of pathological social decision making, as observed in autism (Calderoni et al., 2012; Izuma et al., 2011; Lombardo et al., 2011; Menon, 2011; Shih et al., 2011) and anorexia nervosa (Kaye et al., 2009; Wagner et al., 2007; Watson et al., 2010; Zucker et al., 2007). Nevertheless, we also emphasize that explicating the neural circuitry of social valuation will require an interdisciplinary approach, utilizing animal work (Cohen et al., 2012; Wallis, 2012; Xia et al., 2011), brain manipulation techniques (Borchers et al., 2012; Rorden & Karnath, 2004; Smith & Clithero, 2009), and network analyses in fMRI (Cole et al., 2010; Leech et al., 2012; Leech et al., 2011; Sharp et al., 2011; Smith et al., 2009; Smith et al., 2011c). Moving forward, decision neuroscience must build upon these ideas and approaches, constructing biological plausible models of interpersonal choice.
5. Moving Beyond Value Systems: Linking Circuits and Behavior

My colleagues and I have shown that social valuation relies on distributed neural circuitry, with posterior ventromedial prefrontal cortex situated as an integral hub for value computation (Chapter 2), which potentially mediates individual differences in complex decision scenarios (Chapter 3). Importantly, our data also indicate that regions involved with social cognition significantly enhance the ability of VMPFC value regions to predict social valuations (Chapter 4). Together, these results demonstrate that the computation of social value relies on distributed neural circuitry, including regions involved in assessing value and social cognition. Future research on social valuation must build upon this emerging theme and continue to link circuits and behavior.

5.1 Value Computations Rely on Interacting Brain Systems

Our work highlights how the computation of social value relies on interacting brain systems (Chapter 4). Specifically, we showed that functional connectivity between posterior VMPFC and regions linked to social cognition is increased during social valuation, an effect that was dependent on individual differences in willingness to pay for social images (Smith, Clithero, Boltuck, & Huettel, 2010a). In a similar vein, other researchers have begun to highlight how value computations within VMPFC frequently interact with other neural systems (Evans, Fleming, Dolan, & Averbeck, 2011; Hare et al., 2009; Park, Kahnt, Rieskamp, & Heekeren, 2011). For example, Hare and colleagues
(2009) predicted that dietary decisions involving self control would involve modulation of the VMPFC value signal by dorsolateral prefrontal cortex (DLPFC). They found that activation within DLPFC increased when subjects exercised self control in dietary choices, and, importantly, this activation correlated with activation levels within VMPFC at the time of choice (Hare et al., 2009). In another example of how value computations within VMPFC interact on other neural systems, Park and colleagues (2011) employed a task that asked subjects to accept or reject choice options that were combinations of monetary reward (positive values) and physical pain (negative values). They investigated how these value signals interact during the course of decision making. Using a functional connectivity analysis, they found that value-dependent changes in valuation are related to correlations between VMPFC and amygdala activation. These functional connectivity studies—combined with our own data (Chapter 4)—highlight the emerging trend within decision neuroscience to study the underlying circuitry of value computations.

Studies of functional connectivity can reveal key insights into how distal brain regions interact to shape behavior and preferences. Nevertheless, it should be noted that—save for some noteworthy exceptions (e.g., Sharp et al., 2011)—studies involving functional connectivity are generally blind to the underlying anatomical connectivity and cellular diversity within and across brain regions. And, although significant progress has been made in characterizing the human connectome (Milham, 2012; Saygin,
future work in this area will need to consider recent efforts in optogenetics that have highlighted the cellular diversity and connections within the ventral tegmentum area (Cohen et al., 2012; Xia et al., 2011), a key node for learning and predicting rewards. Despite these important caveats, I speculate that fMRI experiments will continue to feature prominently in studies investigating the neural circuitry of social valuation, as this technique affords an opportunity to gather copious amounts of neural data rich in spatio-temporal resolution.

5.2 Exploiting the Strengths of FMRI

It is axiomatic that the brain functions as a dynamic system with complex interactions that take place over both relatively small (e.g., within the inferior parietal lobule, Andersen, Asanuma, Essick, & Siegel, 1990) and large spatial scales (e.g., across the posterior cingulate gyrus and medial orbital prefrontal cortex, Carmichael & Price, 1995). Measuring these circuits poses a significant challenge in systems neuroscience (Lichtman & Denk, 2011). Although fMRI is unable to measure neuronal activity directly (Logothetis, 2008; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Logothetis & Wandell, 2004), posing some interpretative challenges (Klingner, Ebenau, Hasler, Brodoehl, Gˇrlich, & Witte, 2011; Magri, Schridde, Murayama, Panzeri, & Logothetis, 2012; Scheeringa, Fries, Petersson, Oostenveld, Grothe, Norris, Hagoort, & Bastiaansen,
2011), I believe that this method can, in principle, serve as an important tool for capturing complex interactions within and across brain regions.

### 5.2.1 Multivariate Pattern Analyses Extract Information Within Brain Regions

With the ability to obtain simultaneous measurements from tens of thousands of locations every second, fMRI methods are uniquely situated to obtain rich spatiotemporal information regarding brain function. Unfortunately, though, the vast majority of fMRI papers are focused on mass univariate techniques that fail to consider the dynamic interactions between spatial locations, even at the small spatial scale of a single brain region. Specifically, standard analytical techniques in fMRI consider each voxel separately; and this is done after proximal brain regions are averaged together via spatial smoothing (which helps reduce noise and improve functional consistency across subjects). Averaging together adjacent brain regions (voxels) clearly limits (if not distorts) the information gleaned from functional neuroimaging data. Consider a toy example with three conditions (e.g., “decision making”, “working memory”, and “attention”) (Table 13). Despite distinct spatial patterns of responses, standard analytical techniques would be unable to disambiguate these conditions, leading a researcher to erroneously conclude that (average) activation within a given region (e.g., dorsolateral prefrontal cortex) reflects any of these processes.
Table 13: Cognitive processes can be misrepresented by focusing on average levels of activation within a given brain regions (e.g., dorsolateral prefrontal cortex). Across 27 spatial locations (i.e., a cubical region of interest), hypothetical activation levels are shown across three cognitive processes. Importantly, although the average activation and variance of activation is mathematically equivalent across all three cognitive processes, each process evokes a distinct pattern of activation.

<table>
<thead>
<tr>
<th>Spatial Location</th>
<th>Hypothetical Activation for Cognitive Process</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Attention</td>
</tr>
<tr>
<td>x y z</td>
<td></td>
</tr>
<tr>
<td>1 1 1</td>
<td>5</td>
</tr>
<tr>
<td>2 2 2</td>
<td>10</td>
</tr>
<tr>
<td>3 3 3</td>
<td>5</td>
</tr>
<tr>
<td>4 4 4</td>
<td>10</td>
</tr>
<tr>
<td>5 5 5</td>
<td>5</td>
</tr>
<tr>
<td>6 6 6</td>
<td>10</td>
</tr>
<tr>
<td>7 7 7</td>
<td>5</td>
</tr>
<tr>
<td>8 8 8</td>
<td>10</td>
</tr>
<tr>
<td>9 9 9</td>
<td>5</td>
</tr>
<tr>
<td>1 9 9</td>
<td>10</td>
</tr>
<tr>
<td>2 8 8</td>
<td>5</td>
</tr>
<tr>
<td>3 7 7</td>
<td>10</td>
</tr>
<tr>
<td>4 6 6</td>
<td>5</td>
</tr>
<tr>
<td>5 5 5</td>
<td>10</td>
</tr>
<tr>
<td>6 4 4</td>
<td>5</td>
</tr>
<tr>
<td>7 3 3</td>
<td>10</td>
</tr>
<tr>
<td>8 2 2</td>
<td>5</td>
</tr>
<tr>
<td>9 1 1</td>
<td>10</td>
</tr>
<tr>
<td>1 9 1</td>
<td>5</td>
</tr>
<tr>
<td>2 8 2</td>
<td>10</td>
</tr>
<tr>
<td>3 7 3</td>
<td>5</td>
</tr>
<tr>
<td>4 6 4</td>
<td>10</td>
</tr>
<tr>
<td>5 5 5</td>
<td>5</td>
</tr>
<tr>
<td>6 4 6</td>
<td>10</td>
</tr>
<tr>
<td>7 3 7</td>
<td>5</td>
</tr>
<tr>
<td>8 2 8</td>
<td>10</td>
</tr>
<tr>
<td>9 1 9</td>
<td>5</td>
</tr>
</tbody>
</table>

Mean: 7.4          Mean: 7.4          Mean: 7.4
SD: 2.5            SD: 2.5            SD: 2.5
To discriminate distinct patterns of activations, researchers have employed multivariate pattern analysis (MVPA), which considers the joint spatial pattern across a set of voxels (Kriegeskorte, 2011; Norman, Polyn, Detre, & Haxby, 2006). In a seminal example of MVPA, Haxby and colleagues (2001) made two striking observations regarding the ventral temporal cortex: first, they observed distinct patterns of activation for different object categories that were not simply due to a single maximally responsive region; second, they demonstrated that the representation of faces and objects are widely distributed and overlapping (Haxby, Gobbini, Furey, Ishai, Schouten, & Pietrini, 2001). MVPA has continued to provide key insights into the underlying neural mechanisms of perception and action, with landmark studies demonstrating that responses within visual cortex can be used to predict subtle features regarding the visual stimuli that are not even consciously detected (Haynes & Rees, 2005; Kamitani & Tong, 2005). As the approach of MVPA is fundamentally different from standard fMRI analysis—predicting behavior from brain data, rather than predicting actual brain responses from hypothesized brain-behavior relationships—some researchers have argued that this technique provides a formal mechanism for validating reverse inference (Poldrack, 2010, 2011; Poldrack, Halchenko, & Hanson, 2009; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011), which plagues current neuroimaging work (Poldrack, 2006).
Pattern-analytic approaches have also been extended to quantify the representational content within and across brain regions under different psychological states using a technique called representational similarity analyses (Kriegeskorte, 2009; Kriegeskorte, Mur, & Bandettini, 2008; Mur, Bandettini, & Kriegeskorte, 2009). In essence, this technique estimates the population code within a region for a given stimulus, allowing researchers to compare the dissimilarity of neural coding across conditions, brain regions, and even stimulus presentations (Kriegeskorte, 2009). Applying this technique, researchers have made significant advances in our understanding of how episodic memories are formed (Xue, Dong, Chen, Lu, Mumford, & Poldrack, 2010) as well as the mechanisms supporting associative learning across time (Visser, Scholte, & Kindt, 2011).

Leveraging information across a joint spatial pattern of voxels is undoubtedly a principled and effective method for capitalizing on fMRI’s spatial resolution. Augmenting this strength, recent advances in fMRI technology have made it increasingly easy to acquire fMRI data at higher spatial resolutions, providing up to an order of magnitude of additional information for a multivariate pattern analysis (e.g., typical standard resolution: 4 x 4 x 4 mm, or 64 mm³; typical high resolution: 1.85 x 1.85 x 1.85 mm, or 6.33 mm³). Although increased spatial information may be contaminated with vascular signals (Thompson, Correia, & Cusack, 2011), high-resolution fMRI coupled with MVPA has already yielded key insights into the functional topography of
face representation within fusiform face area (Hanson & Schmidt, 2011) and odor representation and preference within the pyriform cortex (Howard, Plailly, Grueschow, Haynes, & Gottfried, 2009). Furthermore, high-resolution fMRI could also be coupled with representational-similarity analysis (Kriegeskorte, 2009; Kriegeskorte et al., 2008; Mur et al., 2009), targeting the neural representation of distinct reward categories and preferences within the ventral striatum and ventromedial prefrontal cortex (Smith, Clithero, Revill, Rorden, & Huettel, 2011b). Nevertheless, I acknowledge that MVPA is not a panacea, carrying its own limitations and interpretive challenges (Etzel, Valchev, & Keysers, 2011; Kleinschmidt, 2007; Kriegeskorte & Bandettini, 2007; Smith, Kosillo, & Williams, 2011a). Despite these limitations, this technique—and the overarching goal of leveraging the information contained in distributed patterns of brain activation—has the potential to revolutionize our understanding of how the brain represents complex actions and behaviors, including decision making and social valuation.

5.2.2 Multivariate Network Analyses Extract Information Across Brain Regions

Although comparing patterns of activation within a brain region has produced valuable insights into the mechanisms underlying valuation (Baucom, Wedell, Wang, Blitzer, & Shinkareva, 2012; Clithero et al., 2011; Hampton & O'Doherty, 2007), it is also important to consider interregional interactions. Early neuroimaging studies have quantified interregional interactions by relying heavily upon model-driven approaches that necessitate choosing a particular brain region (i.e., a “seed” region) and then
evaluating how activation in other regions (i.e., “target” regions) correlate with the seed region (Friston, Frith, Liddle, & Frackowiak, 1993; Tomasi & Volkow, 2011a; Tomasi & Volkow, 2011b). (Notably, these approaches are often extended by examining how the correlation between seed and target regions changes as a function of psychological state (Friston, 2005; Friston et al., 1997; Friston, Harrison, & Penny, 2003).) This simple approach of examining how activation in one region relates to activation in another region has yielded remarkable insights into functional topography of cognitive control (Taren, Venkatraman, & Huettel, 2011) as well as valuation (Hare et al., 2010; Hare et al., 2009; Park et al., 2011).

Yet, seed-based approaches to functional connectivity—whether focused on resting-state data or task-based data—face substantial criticism (Cole et al., 2010; Olivier, 2011; Roebroeck, Formisano, & Goebel, 2011a, 2011b; Valdes-Sosa, Roebroeck, Daunizeau, & Friston, 2011). For these approaches to be valid, the seed region must be carefully selected, ensuring that it accurately represents the functional node of interest (Smith et al., 2011c). As another concern, some studies have recently suggested that a canonical finding of anticorrelated networks—default-mode network and cognitive control network (Fox, Snyder, Vincent, Corbetta, Van Essen, & Raichle, 2005)—may reflect an analytical artifact related to regressing out the global signal (Murphy, Birn, Handwerker, Jones, & Bandettini, 2009). Other studies have highlighted a more pernicious effect, where head motion can dramatically distort functional connectivity
patterns, leading researchers to make erroneous claims regarding the functional connectivity within and across groups of individuals (Jansen, White, Mullinger, Liddle, Gowland, Francis, Bowtell, & Liddle, 2012; Power, Barnes, Snyder, Schlaggar, & Petersen, 2012; Satterthwaite, Wolf, Loughead, Ruparel, Elliott, Hakonarson, Gur, & Gur, 2012).

Recent advances in functional connectivity analyses promise to overcome these challenges by employing a truly multivariate approach: spatial independent components analysis (Beckmann, DeLuca, Devlin, & Smith, 2005; Remes, Starck, Nikkinen, Ollila, Beckmann, Tervonen, Kiviniemi, & Silven, 2011). This model-free approach capitalizes on coherent temporal fluctuations characterizing spatially independent brain networks, decomposing the neuroimaging data into sets of spatial networks that can reflect either signal (i.e., a plausible neural network) or noise (i.e., a motion artifact presenting as a distinct “ring” around the cortex (Tohka, Foerde, Aron, Tom, Toga, & Poldrack, 2008)). To evaluate individual differences in connectivity with key networks of interest, researchers have employed a dual-regression analytical approach (Bonnelle, Leech, Kinnunen, Ham, Beckmann, De Boissezon, Greenwood, & Sharp, 2011; Filippini, MacIntosh, Hough, Goodwin, Frisoni, Smith, Matthews, Beckmann, & Mackay, 2009; Leech et al., 2012; Leech et al., 2011; Sharp et al., 2011; Zuo, Kelly, Adelstein, Klein, Castellanos, & Milham, 2010). This novel analytical approach proceeds in two independent stages. First, spatial maps identified with the independent
components analyses are regressed onto each participant’s functional data (spatial regression), resulting in a T (time points) x C (components) set of beta coefficients that characterize, in each subject, the temporal dynamics for each spatial network.

Importantly, this spatial regression estimates the temporal dynamics for each spatial network while controlling for the influence of other consistent spatial patterns—some of which may reflect artifacts, such as head motion and physiological noise (Tohka et al., 2008). As part of the second step of the dual regression, the resulting temporal dynamics that describe each network, in each subject, are regressed onto each subject’s functional data (temporal regression). This temporal regression produces a set of spatial maps that quantify, within each subject, each voxel’s connectivity with each network identified with the group ICA. Completing the dual-regression analysis, these subject-specific maps are then statistically compared using Monte Carlo based permutation testing (Nichols & Holmes, 2002).

Using ICA and dual regression, several recent studies have targeted the default-mode network (DMN) (e.g., Filippini et al., 2009). This particular network—which consists of lateral inferior parietal regions near the TPJ, posterior cingulate, and VMPFC—has received considerable attention across both human (Andrews-Hanna, Reidler, Huang, & Buckner, 2010; Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Fox et al., 2005; Koyama, Di Martino, Zuo, Kelly, Mennes, Jutagir, Castellanos, & Milham, 2011; Qin & Northoff, 2011; Raichle, 2009, 2010; Raichle,
MacLeod, Snyder, Powers, Gusnard, & Shulman, 2001) and monkey studies (Hayden, Smith, & Platt, 2009b; Hutchison, Leung, Mirsattari, Gati, Menon, & Everling, 2011; Mantini, Gerits, Nelissen, Durand, Joly, Simone, Sawamura, Wardak, Orban, Buckner, & Vanduffel, 2011; Pearson, Heilbronner, Barack, Hayden, & Platt, 2011; Vincent, Patel, Fox, Snyder, Baker, Van Essen, Zempel, Snyder, Corbetta, & Raichle, 2007). Yet, the function of DMN (as well as other networks)—particularly as it relates to individual differences in behavior (Mennes, Zuo, Kelly, Di Martino, Zang, Biswal, Castellanos, & Milham, 2011) and psychological states (Laird, Fox, Eickhoff, Turner, Ray, McKay, Glahn, Beckmann, Smith, & Fox, 2011; Pfefferbaum, Chanraud, Pitel, Muller-Oehring, Shankaranarayanan, Alsop, Rohlfing, & Sullivan, 2011)—remains debated. Addressing these questions, dual-regression analyses have advanced our understanding of DMN by characterizing its implementation in cognitive control (Leech et al., 2011), its relationship to the behavioral deficits following traumatic brain injury (Bonnelle et al., 2011; Sharp et al., 2011), and its relationship with other neural networks across different psychological states (Leech et al., 2012). Future studies along these same lines could fractionate the DMN further, elucidating the relationship between the value regions and social cognition regions that make up its constituent parts (Buckner, Andrews-Hanna, & Schacter, 2008).
5.3 Future Studies

Drawing concepts from neuroscience, psychology, and economics, decision neuroscience represents an interdisciplinary field. My future work in decision neuroscience will build upon my studies on social valuation, deepening our understanding of the neurobiology of interpersonal choice. I will investigate the neural circuitry of social valuation by using multivariate-analytic methods combined with experimental designs that manipulate valuation, exploit dynamic social interactions, and characterize individual differences.

5.3.1 Manipulating Valuation Processes

Although the overwhelming majority of decision neuroscience studies have investigated valuation by observing its neural and behavioral correlates, very few studies have directly manipulated valuation processes. Valuation can be manipulated in variety of ways—from directly altering brain function (Camus, Halelamien, Plassmann, Shimojo, O'Doherty, Camerer, & Rangel, 2009; Libedinsky et al., 2011; Smith & Clithero, 2009) to imposing subtle variations in valuation context. For example, decision making—and by extension valuation—can be hugely dependent on context. From subtle variations in the presentation of choice information (e.g., “loss” or “gain”) to waiting a longer or shorter amount of time to receive a reward, there are infinite ways in which context can vary in each decision problem. In Chapter 3, using a classic example of this phenomenon—the framing effect—we showed how individuals’ preferences change
depending on whether monetary and social gambles are presented as a potential loss or gain (Smith, Venkatraman, Carter, Clithero, Skene, Platt, & Huettel, 2010d). My colleagues and I are also investigating how waiting for a reward shapes its valuation and its neural processing in regions implicated in valuation (e.g., VMPFC). My future work will characterize valuation mechanisms by manipulating them—an approach that will aid in building biologically plausible models of choice with the potential for immediate clinical impact.

5.3.2 Exploiting Dynamic Social Interactions

Social decisions involve other agents (either directly or indirectly), creating vast heterogeneity in decision complexity and structure. To examine social decisions, game theorists have developed elegant computational models (Fehr & Camerer, 2007). These models, when used in conjunction with tools from neuroscience, can provide powerful insight into the neurobiological mechanisms governing social decisions (Rilling, King-Casas, & Sanfey, 2008; Rilling & Sanfey, 2011). In my future work, I will employ game-theoretical models to investigate social decisions in tasks that emphasize interpersonal interactions. Armed with this approach and the analytical tools required to fully exploit the multivariate nature of neuroimaging data, I plan to characterize the neural construction of value signals in dynamic social decisions. Importantly, this work may provide insight into aberrant social decision making, a hallmark of several disorders, including autism and anorexia nervosa.
5.3.3 Characterizing Individual Differences

Individuals exhibit marked differences in their preferences and choices. These individual differences fall on a wide spectrum, ranging from normal to pathological. Therefore, characterizing the biological bases of individual differences in valuation is a cardinal goal for decision neuroscience. Although my initial studies have indicated that VMPFC tracks individual differences in relative decision value between reward categories, these studies do not address why VMPFC (among other regions) functions differently in different people. In some of our ongoing work, we have attempted to address this question by examining, in a large sample (N = 230), the relationship between personality variables, genetics, and brain data. However, it is important to emphasize that the mechanistic insight into the processes governing individual differences in behavior and valuation need not employ large samples of subjects and genetic data; we can also probe individual differences by using strategies that modulate them in specific ways (e.g., conditioning paradigms). Moving toward this model represents an important first step in creating decision neuroscience research programs that can have real clinical and policy implications.

5.4 Summary and Conclusions

My work has focused on the neural circuitry of social valuation. My colleagues and I first showed how posterior ventromedial prefrontal cortex (pVMPFC) computes the decision value between social and monetary goods (Chapter 2, Smith et al., 2010c).
Next, we extended these findings to complex social decisions and found that idiosyncratic responses within pVMPFC predicted differential biases between self and charity framing effects (Chapter 3, Smith et al., 2010d). In our final study, we demonstrated that value signals within pVMPFC interact with regions linked to social cognition during social valuation (Chapter 4, Smith et al., 2010a). Moving forward, decision neuroscience faces significant challenges, both conceptual and methodological (Clithero, Tankersley, & Huettel, 2008; Smith & Huettel, 2010). Chief among these challenges will be moving beyond the conceptualization of simple value systems that work in isolation, without interacting with other brain systems. I speculate that advanced methods in fMRI—particularly those employing multivariate pattern analyses and multivariate network analyses—will be uniquely situated to provide innovative insights into the neural circuitry that shape our social preferences and behavior. Characterizing this circuitry has the potential to advance our understanding of psychiatric disorders (Lincoln et al., 2011; Menon, 2011; Montague, Dolan, Friston, & Dayan, 2012), particularly schizophrenia (Gold et al., 2008; Gradin et al., 2011; Meyer-Lindenberg, 2010), depression (Elliott, Lythe, Lee, McKie, Juhasz, Thomas, Downey, Deakin, & Anderson, 2012), anorexic nervosa (Kaye et al., 2009; Wagner et al., 2007; Watson et al., 2010; Zucker et al., 2007), and autism (Izuma et al., 2011; Moran, Young, Saxe, Lee, O'Young, Mavros, & Gabrieli, 2011; Shih et al., 2011).
References


126


Biography

I am a cognitive neuroscientist with extensive training in functional magnetic resonance imaging (fMRI). I was born on September 30th, 1984 in Aiken, South Carolina. I graduated from the University of South Carolina (USC) in the spring of 2006 with a Bachelors of Science in Experimental Psychology (with a cognate in statistics). While at USC, I worked on fMRI projects focusing on spatial attention (Smith, Davis, Niu, Healy, Bonilha, Fridriksson, Morgan, & Rorden, 2010) and language (Almor, Smith, Bonilha, Fridriksson, & Rorden, 2007). I then moved to Duke University in the fall of 2006 to embark on my doctoral training. As part of my initial training at Duke, I immersed myself in three lab rotations, each employing cognitive neuroscience methods tailored to specific questions: event-related potentials to assess rapid attentional modulations of visual cortex (Appelbaum, Smith, Boehler, Chen, & Woldorff, 2011); single-unit electrophysiology in macaques to examine neuronal underpinnings to the enigmatic default-mode network (Hayden, Smith, & Platt, 2010; Hayden, Smith, & Platt, 2009); and fMRI to examine individual differences in human decision making and valuation (Smith, Hayden, Truong, Song, Platt, & Huettel, 2010). Following these rotations, I joined Dr. Scott Huettel’s lab in 2007 and shifted my focus to decision neuroscience. Since joining Dr. Huettel’s lab, I have published 13 peer-reviewed articles (4 first author; see below), with my initial study, “Distinct Value Signals in Anterior and Posterior Ventromedial Prefrontal Cortex” (Smith et al., 2010, Journal of Neuroscience), providing a springboard.
for subsequent research and grants related to the neural circuitry of social valuation.

From 2009 to 2012, my work was supported through a National Research Service Award from the National Institute for Mental Health (F31-086248; “Neurobiological Underpinnings of Decision Making”). In the fall of 2012, I will begin my postdoctoral training with Dr. Mauricio Delgado at Rutgers University.

**Honors and Awards**

- 2010: Travel Award, Organization for Human Brain Mapping Conference
- 2009-2012: National Research Service Award, NIMH
- 2009: Summer Institute in Cognitive Neuroscience Fellow, UC - Santa Barbara
- 2008: CIT Flexible Learning Space Fellow, Duke University
- 2007: Travel Award, Organization for Human Brain Mapping Conference

**Peer-reviewed Publications**


