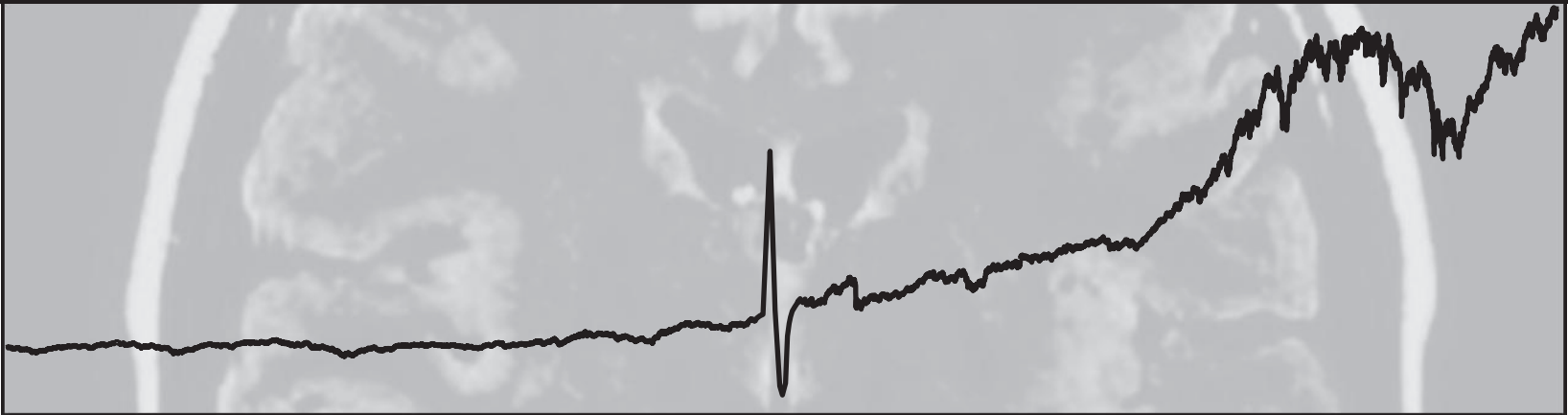


# *Meeting Program*



6TH ANNUAL MEETING

Park City, UT

SEPTEMBER 25-28, 2008



SOCIETY FOR  
NEUROECONOMICS

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# Schedule of Events for Neuroeconomics 2008, Park City, UT

## Thursday, September 25, 2008

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1:30 - 5:00 pm	Workshops in the Foundations of Neuroeconomics	
	<i>The two workshops will occur simultaneously, and you may choose which one you would like to attend.</i>	
	<u>Neuroscience for Behavioral Scientists</u>	<u>Behavioral Science for Neuroscientists</u>
	<i>Location: Kokopelli Parlor II</i>	<i>Location: Painted Horse</i>
1:30 – 3:00 pm	Workshop on human electrophysiology and decision making Greg McCarthy, Yale University	Behavioral-choice theory and the quest to link neural circuitry to core processes underlying decision making Peter Shizgal, Concordia University
3:00 – 3:30 pm	<i>Coffee Break</i>	
3:30 – 5:00 pm	What TMS can(not) prove - lessons from its applications to the visual cortex. Shin Shimoyo, California Institute of Technology	Foraging theory and the behavioral ecology of animal decision-making David Stephens, University of Minnesota
6:00 pm	<i>Reception (Cash Bar)</i>	<i>Docs at the Gondola</i>
7:00 pm	<i>Buffet Dinner &amp; Poster Madness</i>	<i>Kokopelli Parlor II</i>

## Friday, September 26, 2008

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8:00 – 8:45 am	<i>Continental Breakfast</i>		<i>Grand Ballroom Lobby</i>
8:45 – 9:00 am	Elke Weber	Welcome & Opening Remarks	
<b>Social Factors in Decision Making</b>			<i>Kokopelli Parlor II</i>
9:00 – 9:30 am	Jeff Cooper	Learning to like: social observation influences prefrontal activation for viewing others	Jeffrey C. Cooper, Tamar Kreps, Arthur Aron, Brian Knutson
9:35 – 10:05 am	Venkat Lakshminarayanan	The origins of other-regarding preferences: capuchins (Cebus apella) are sensitive to others' welfare	Venkat R. Lakshminarayanan, Laurie R. Santos
10:10 – 10:40 am	Vasily Klucharev	Neural mechanisms of social decisions	Vasily Klucharev, Kaisa Hytonen, Mark Rijpkema, Ale Smidts, Guillén Fernández
10:45 – 12:25 pm	Poster Session I & Refreshments		<i>White Pine Ballroom</i>
12:30 – 1:40 pm	<i>Lunch</i>		<i>The Canyons Pavilion</i>
	<i>Lunchtime Discussion: Standards in Neuroeconomics Courses (confirmed attendees only please)</i>		<i>The Cabin Corral</i>
<b>Individual and Lifespan Differences</b>			<i>Kokopelli Parlor II</i>
1:45 – 2:15 pm	Gregory R. Samanez-Larkin	Financial decision making across the adult life span	Gregory R. Samanez Larkin, Camelia M. Kuhnen, Brian Knutson
2:20 – 2:50 pm	Julian Jamison	The development of preferences in rat pups	Julian Jamison, Kat Saxton, Peter Aungle, Darlene Francis
2:55 – 3:25 pm	Bernd Weber	Combining panel data and genetics – proof of principle and first results	Bernd Weber, Jurgen Schupp, Martin Reuter, Christian Montag, Nico Siegel, Thomas Dohmen, Uwe Sunde, David Huffmann, Gert Wagner, Armin Falk
3:30 – 4:00 pm	Todd Hare	Neural mechanisms of self-control in decision-making	Todd A. Hare, Colin F. Camerer, Antonio Rangel
4:05 – 5:45 pm	Poster Session II & Refreshments		<i>White Pine Ballroom</i>
7:00 pm	<i>Dinner—Rocky Mountain BBQ</i>		<i>Red Pine Lodge*</i>

\*Red Pine Lodge is located mid-mountain—the Flight of the Canyons gondola will take guests to and from dinner beginning at 6:45pm. In case of inclement weather, dinner will be at The Canyons Pavilion.

## Saturday, September 27, 2008

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8:30 – 10:00 am

*Continental Breakfast*

*Grand Ballroom Lobby*

### Valuation I: Non-Risky and Multiple Attributes

*Kokopelli Parlor II*

10:00 – 10:30 am	Bernd Figner	Asymmetries in intertemporal discounting: neural systems and the directional evaluation of immediate vs future rewards	Bernd Figner, Eric J. Johnson, Grace Lai, Amy Krosch, Jason Steffener, Elke U. Weber
10:35 – 11:05 am	Brian Knutson	Neural antecedents of the endowment effect	Brian Knutson, G. Elliott Wimmer, Scott Rick, Nick G. Hollon, Drazen Prelec, George Loewenstein
11:10 – 11:40 am	Steven Kennerley	Neurons in the frontal lobe encode the value of multiple decision variables	Steve Kennerley, Aspan Dahmubed, Antonio Lara, Jonathan Wallis
11:45 – 12:15 pm	Tali Sharot	Choice shapes, and reflects, expected hedonic outcome	Tali Sharot, Benedetto De Martino, Raymond J Dolan

12:20 – 1:30 pm

*Lunch*

*The Canyons Pavilion*

### Valuation II: Risky Attributes

*Kokopelli Parlor II*

1:35 – 2:05 am	Kenway Louie	Value-based gain control: relative reward normalization in parietal cortex	Kenway Louie, Lauren Grattan, Paul Glimcher
2:10 – 2:40 pm	Vasco Galhardo	Neuroeconomy of pain: rodent gambling task impairment induced by chronic pain models	Vasco Galhardo, Miguel Pais-Vieira, Manuela Pinto, Deolinda Lima
2:45 – 3:15 pm	Kaisa Hytonen	How prior gains and losses influence our decisions under risk: an fMRI study	K. Hytonen, G. Baltussen, M.J. van den Assem, V. Klucharev, A. Smidts, G.T. Post
3:20 – 3:50 pm	Peter Bossaerts	Neurobiological foundations for "dual system" theory in decision making under uncertainty: fMRI and EEG evidence	Peter Bossaerts, Ulrik Beierholm, Cedric Anen, Helene Tzieropoulos, Steven Quartz, Rolando Grave de Peralta, Sara L. Gonzalez

*Evening free, dinner on your own*

## Sunday, September 28, 2008

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8:00 – 9:00 am

*Continental Breakfast*

*Grand Ballroom Lobby*

### Learning: From Rodent to Human

*Kokopelli Parlor II*

9:00 – 9:30 am	Paul Phillips	Predicted rewards continue to elicit dopamine release when the predictor fails to acquire incentive value	Paul E. M. Phillips, Jeremy J. Clark, Christina A. Akers, Scott B. Ng-Evans, Shelley B. Flagel, Sarah M. Clinton, Terry E. Robinson, Huda Akil
9:35 – 10:05 am	Adam Kepecs	How uncertainty boosts learning: Dynamic updating of decision strategies	A. Kepecs, N. Uchida, Z.F. Mainen
10:10 – 10:40 am	Saleem Nicola	Nucleus Accumbens dopamine and the decision to engage in reward-seeking	Saleem M. Nicola, Howard L. Fields

10:45 – 11:25 am

*Break & Hotel Check-Out*

*Grand Ballroom Lobby*

11:30 – 12:00 pm	John Pearson	Firing rates of neurons in posterior cingulate cortex predict strategy-switching in a k-armed bandit task	John Pearson, Benjamin Y. Hayden, Sridhar Raghavachari, Michael L. Platt
12:05 – 12:35 pm	Robb Rutledge	A neural representation of reward prediction error identified using an axiomatic model	Robb B. Rutledge, Mark R. Dean, Andrew Caplin, Paul W. Glimcher

**Poster Session I: Friday 10:45am – 12:25pm**

#	Section Topic	Title	Authors
1	Risky Choice	Grasping the fundamental difference between expected utility and mean-variance theories	Mathieu d'Acremont Peter Bossaerts
2	Risky Choice	Behavioral and neurobiological effects of expert messages on risky decision making	Jan B. Engelmann, C. Monica Capra, Charles Noussair, Gregory S. Berns
3	Risky Choice	Anterior cingulate cortex mediates ambiguity aversion in monkeys	Benjamin Y. Hayden, Sarah R. Heilbronner, Michael L. Platt
4	Risky Choice	Revisit "Prominent Deck B phenomenon" in the Iowa Gambling Task	Ching-Hung Lin, Yao-Chu Chiu, Yu-Kai Lin, Jing-Long Tsai
5	Risky Choice	Brain maps of Soochow Gambling Task	Ching-Hung Lin, Yao-Chu Chiu, Yu-Kai Lin, Jen-Chuen Hsieh
6	Risky Choice	Brain maps of Iowa Gambling Task: From uncertainty to certainty	Ching-Hung Lin, Yao-Chu Chiu, Chou-Ming Cheng, Tze-Chen Yeh
7	Risky Choice	Distinct neural representations of behavioral risk and reward risk	Peter N. C. Mohr, Guido Biele, Hauke R. Heekeren
8	Risky Choice	Individual differences in the Iowa Gambling Task: A computational account	Lee I Newman, Thad A. Polk, Stephanie D. Preston
9	Risky Choice	Heterogeneity in risky decision making in 6-to-7-year-old children	David Paulsen, Scott Huettel, Michael Platt, Elizabeth Brannon
10	Risky Choice	Exploring the behavioral and neurobiological foundations of three components of uncertainty	Elise Payzan, Peter Bossaerts
11	Risky Choice	Neurobiological responses in individuals making choices in uncertain environments: Ambiguity and conflict	Helen Pushkarskaya, Xun Liu, Michael Smithson, Jane E. Joseph
12	Risky Choice	Supplementary eye field reflects values of action and outcome in a gambling task	Na Young So, Veit Stuphorn
13	Risky Choice	Sleep deprivation modulates risky decision-making strategies	Vinod Venkatraman, YM Lisa Chuah, John. W. Payne, Scott Huettel, Michael WL Chee
14	Risky Choice	Strategic modulation of cognitive control in decision-making under uncertainty	Tal Yarkoni Todd S. Braver
15	Risky Choice	The effect of self-generated criterion on feedback-related negativity	Nai-Shing Yen, Yin-Fang Chang, Kuan-Ying Lin, Chang-Hao Kao, Ying-Ru Lai
16	Risky Choice	Genetic determinants of financial risk taking	Camelia M. Kuhnen, Joan Chiao
17	Valuation	rTMS over the right dorsolateral prefrontal cortex down-modulates the computation of values in decision-making	Mickael Camus, Neil Halelamien, Shinsuke Shimojo, John O'Doherty, Colin Camerer, Antonio Rangel
18	Valuation	Local differences in the neural encoding of facial and monetary rewards	John A. Clithero, David V. Smith, R. McKell Carter, Michael L. Platt, Scott A. Huettel
19	Valuation	Dissociating goal values, decision values, and prediction errors in the human brain	Todd A. Hare, John O'Doherty, Colin F. Camerer, Wolfram Schultz, Antonio Rangel
20	Valuation	Medial orbitofrontal cortex interacts with the anterior insula to compute subjective values in complex social decisions	Todd A. Hare, Colin F. Camerer, Dan Knopfle, John O'Doherty, Antonio Rangel
21	Valuation	Neurons in anterior and posterior cingulate cortex encode distinct decision variables in three different economic tasks	Sarah R. Heilbronner, Benjamin Y. Hayden, Michael L. Platt
22	Valuation	Economic value coding by single neurons in the human amygdala	Rick L. Jenison, Hiroyuki Oya, Hiroto Kawasaki, Matthew A. Howard III, Antonio Rangel
23	Valuation	Topography of social and nutritive reward coding in striatum	J.T. Klein, M.L. Platt
24	Valuation	Visual attention drives the construction and comparison of values in simple economic choice	Ian Krajbich, Carrie Armel, Antonio Rangel
25	Valuation	Neural representation of value in the absence of choice	Stephanie C. Lazzaro, Ifat Levy, Robb B. Rutledge, Paul W. Glimcher
26	Valuation	Neurally dissociating valuative and non-valuative contingency learning	O'Dhaniel Mullette-Gillman, Scott Huettel
27	Valuation	What you do know can hurt you: Environmental state cues in a dynamic decision-making task	A. Ross Otto, Arthur B. Markman, Bradley C. Love
28	Valuation	Aversive goal values are negatively encoded in the medial orbitofrontal cortex at the time of decision-making	Hilke Plassmann, John O'Doherty, Antonio Rangel
29	Valuation	The presence of framing effects in rats	Mehwish Saba Bhatti, Jaeseung Jeong
30	Valuation	Taste-independent reward-related representations in the insular cortex.	Albino J. Oliveira-Maia, Ivan E. de Araujo, Clara Monteiro, Virginia Workman, Vasco Galhardo, Sidney A. Simon, Miguel A. L. Nicolelis

**Poster Session II: Friday 4:05pm – 5:45pm**

#	Section Topic	Title	Authors
1	Choice	Temporal discounting elicits a distributed network of mesolimbic and lateral cortical brain regions, which predict choice for future rewards.	Kacey Ballard, Brian Knutson
2	Choice	Real versus hypothetical rewards and gains versus losses: Investigation of the behavioral and neural differences in delay discounting	Warren K. Bickel, Jeffery A. Pitcock, Richard Yi, Edgardo J. Angtuaco
3	Choice	Activation likelihood estimate meta-analysis of monetary incentive delay (MID) task findings	Stephanie Greer and Brian Knutson
4	Choice	Fast versus accurate value-based choices involve different computational processes	Milica Milosavljevic, Alexander Huth, Antonio Rangel, Christof Koch
5	Choice	Neural signatures of choice-overload and choice set-value in the human brain.	Elena Reutskaja, Colin Camerer, Rosemarie Nagel, Richard Andersen, Axel Lindner
6	Choice	Charging neutral stimuli with motivational properties reveals mechanisms that underlie choice	Jaspinder Sagoo, Roger Carpenter
7	Choice	Neural predictors of healthy and unhealthy food choice	Jyrki Suomala, Markus Kivikangas, Jussi Numminen
8	Social	Emulations, creativity, and the brain	Jyrki Suomala
9	Social	The evolution of cooperation: Helping behavior in capuchin monkeys ( <i>Cebus apella</i> )	Jennifer L. Barnes, Laurie R. Santos
10	Social	A Neuroeconomic analysis of herding in finance	C. Burke, P. Tobler, W. Schultz and M. Baddeley
11	Social	Anonymous and public generosity: Neural evidence of different motives.	Benjamin Bushong, William T. Harbaugh, Ulrich Mayr
12	Social	Agent-based network model for the public goods game	Dongil Chung, Kyongsik Yun, Jaeseung Jeong
13	Social	Neural substrates of free-riding and cooperation during the standard public goods game	Dongil Chung, Jaeseung Jeong
14	Social	The contribution of implicit race bias to estimations of trustworthiness	Damian Stanley, Peter Sokol-Hessner, Michael Perino, Mahzarin Banaji, Liz Phelps
15	Social	Reactions to unequal payment are differently modified by medial prefrontal brain regions in women and men	Bernd Weber, Klaus Fliessbach, Peter Trautner, Marieke Schnabel, Courtney Philips, Christian Elger, Armin Falk
16	Emotion/Affect	The psychophysiological effects of emotion on decisions with high/low importance	Pei-Ling Chen, Nai-Shing Yen, Hsuan-Yu Lin, Yung-Chi Chang, Chun-Jui Liu
17	Emotion/Affect	Escape from disgust: Emotion motivates mental and physical avoidance of social targets	Lasana T. Harris, Daniela Schiller, Susan Fiske, Elizabeth Phelps
18	Emotion/Affect	Neuroeconomics in stressed rats	L.K. Jones, T. Yoon, J.J. Kim
19	Emotion/Affect	Influence of unconscious emotions on financial decision-making situation	Markus Kivikangas, Jari Kätsyri, Meeri Mäkäräinen, Mikko Sams, Niklas Ravaja
20	Emotion/Affect	Quantifying expressions of emotion in psychological games: Theory, experiments, and econometrics	Mahdi Rastad, Lusha Zhu, Jesse Spencer-Smith, Roger Koenecker, Ming Hsu
21	Methods	The neural-like assumptions and parameters in the agent-based computational economic models	Shu-Heng Chen
22	Methods	Salvaging orbito-frontal cortex: improved fMRI image reconstruction for neuroeconomics	Eric J. DeWitt, Robb B. Rutledge, Damian Stanley, Paul W. Glimcher, Souheil J. Inati
23	Methods	Interpretable classifiers for fMRI improve prediction of purchases	Logan Grosenick, Stephanie Greer, Jonathan Taylor, Brian Knutson
24	Methods	Neural computations underlying hypothetical vs. real decision making	Min Jeong Kang, Mickael Camus, Antonio Rangel, Colin Camerer
25	Methods	Virtuous decisions: exemplarity in and out of the laboratory	Michael L. Spezio, Warren Brown, Gregory Peterson, Kevin Reimer, James Van Slyke
26	Methods	The length of feedback interval and inter-trial interval effects decision-making in choice tasks	Darrell A. Worthy, W. Todd Maddox, Arthur B. Markman
27	Methods	Meal patterns of mice under systematically varying procurement and consummatory costs for food in a closed economy	Deniz Atalayer, Neil E. Rowland
28	NeuroMarketing	How fame affects the encoding of products: An fMRI-study into the effect of celebrity endorsers on neural processing	Mirre Stallen, Gitty Smit, Vasily Klucharev, Ale Smidts, Guillén Fernández
29	NeuroMarketing	The effect of retail brand frames on the evaluation of product packaging – first insights from consumer neuroscience	Marco Stoll, Mirja Hubert, Tim Eberhardt, Peter Kenning
30	NeuroMarketing	Hemispheric processing of metaphors in advertisements	Kristy Vance, Andrew Phillips, Sandra Virtue

**Thursday, September 25, 2008**  
**Workshop: Neuroscience for Behavioral Scientists**

**Session 1, 1:30 - 3:00pm**

Workshop on Human Electrophysiology and Decision Making

Gregory McCarthy

Department of Psychology, Yale University

The movement of ions across cell membranes during neuronal activity generates electrical and magnetic fields that can be recorded from suitably placed sensors located outside the head. With the use of appropriate signal processing and statistical analyses, changes in neuronal activity related to sensory, motor, and cognitive events can be measured noninvasively. The temporal resolution of these measurements – on the order of milliseconds – have attracted the interest of researchers interested in decision-making. The combination of electrophysiological and neuroimaging techniques holds the promise for describing brain activity with high spatial and temporal resolution.

In this workshop presentation, the electrogenesis of these electrical and magnetic signals will be described and the analytical methods used for their analysis will be critiqued. Particular attention will be paid to methods that attempt to describe the location within the brain of the neuronal sources contributing to these fields. Applications of the techniques to human decision-making will also be discussed.

~ Coffee Break ~

**Session 2, 3:30 - 5:00pm**

What TMS can(not) prove - lessons from its applications to the visual cortex

Shinsuke Shimojo<sup>1,2</sup>

<sup>1</sup>Division of Biology / Computation and Neural Systems, California Institute of Technology (Pasadena, CA); <sup>2</sup>JST.ERATO Shimojo Implicit Brain Function Project (Atsugi, Kanagawa, Japan)

TMS(Transcranial Magnetic Stimulation) sticks out as a unique technique in behavioral neuroscience with several distinctive characteristics. First, TMS can be applied to normal human subjects noninvasively, unlike electric stimulation via electrodes. Second, TMS has low spatial, and high temporal resolutions, which are almost opposite to those of brain imaging techniques such as fMRI. Last but not least, it is an active intervention (i.e. stimulation or suppression) technique, as opposed to the mainstream recording techniques such as EEG and brain imaging. As a result, TMS provide us with a unique opportunity to nail down causal relationship between brain activity and psychophysical performance. On the other hand, it has its own limitations, among which its inability to stimulate deeper tissues in the brain is serious.

In this talk, I will first introduce the TMS from historical and biophysical perspectives. I will also present a biophysical model that aims to simulate how each neuron reacts to the TMS stimulation. In the second part, I will summarize my own TMS studies with my collaborators, which are mainly in the visual cortices. They will nicely demonstrate the facilitatory and suppressive aspects with regard to visual awareness. Finally, I would like to discuss future directions. In particular, I would like to address issues such as; (a)TMS can potentially be combined with other techniques such as EEG, fMRI and tDCS, but why bother? and (b)what we can do with TMS (either single, dual, or repetitive) for neuroeconomics and decision making.

In conclusion, TMS seems to provide a promising new direction in neuroeconomics and cognitive neuroscience of decision making, which have been so far governed predominantly by fMRI.

**Thursday, September 25, 2008**

**Workshop: Behavioral Science for Neuroscientists**

**Session 1, 1:30 - 3:00pm**

**Behavioral-choice theory and the quest to link neural circuitry to core processes underlying decision making**

Peter Shizgal

Concordia University

Neuroeconomics is rooted in a diverse set of disciplines in the biological, social, and information sciences. Each of these disciplines strives, in idiosyncratic ways, to understand the determinants and consequences of allocation decisions. Neuroeconomics promises to play a unifying role by grounding such decisions in biological structure: the neural circuitry involved in evaluating returns, costs, and risks, in selecting goals, in determining how to achieve them, and in committing resources to their pursuit. To illustrate the challenges entailed in the neuroeconomic program and the role of behavioral-choice theory in overcoming them, I will discuss ongoing research on the role played by dopaminergic neurons in core processes underlying behavioral allocation.

The first experiments to examine the effects of manipulating dopaminergic neurotransmission on performance in a behavioral-choice paradigm were carried out in rats working for rewarding electrical brain stimulation. Although much has been learned since about the underlying neural circuitry, consensus has yet to be reached concerning the stage(s) of processing at which dopaminergic neurons intervene and how the influence of these neurons is partitioned between the investment of effort and the evaluation of returns, costs, and risks. I will review recent work that applies behavioral-choice theory towards resolving some longstanding debates concerning dopaminergic function, overcoming the ambiguity inherent in widely used measurement methods, and identifying the long-sought neurons that give rise to the rewarding effect. I will also explore how this approach could be generalized to behaviors directed at natural goal objects.

*~ Coffee Break ~*

**Session 2, 3:30 - 5:00pm**

**Foraging theory and the behavioral ecology of animal decision-making**

David Stephens

University of Minnesota

This workshop will introduce the field of behavioral ecology paying special attention to foraging behavior and decision-making. Behavioral ecologists view behavioral traits as a consequence of natural selection that must be understood in an ecological context. In short, they ask the question how does behavior X contribute to the animal's survival and reproduction (i.e. it's evolutionary fitness). Models in behavioral ecology typically resemble economic models, and rely on the mathematical techniques of optimization and game theory. Behavioral ecologists tend to divide behavior into functional categories such as reproduction behavior, social behavior, aggressive behavior and foraging behavior. This workshop will emphasize foraging behavior because there is a well-developed foundation of models in this area; it is an empirically accessible topic, and it makes many connections to other fields (comparative psychology, cognitive science, community ecology, and of course neuroeconomics). Our review of foraging theory will emphasize models and tests of models. At the same time, I hope to point out 'economically important' aspects of animal foraging behavior that may be novel to those outside the field. Classical foraging theory consists of three models that consider prey choice, patch exploitation and the effects of competitors on patch choice. Taken together these three models represent a coherent, interconnected body of theory that has served as a starting point for many developments. I discuss several of these new lines of inquiry such as food storage (caching and fattening), predator avoidance, and provisioning. Finally, I will discuss what studies of foraging behavior might tell us about how to design and interpret experimental studies of decision-making.

# Friday, September 26, 2008

## *Abstracts for Morning Session*

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### **Social Factors in Decision Making**

9:00 – 9:30 am	Jeff Cooper	Learning to like: social observation influences prefrontal activation for viewing others
9:35 – 10:05 am	Venkat Lakshminarayanan	The origins of other-regarding preferences: capuchins ( <i>Cebus apella</i> ) are sensitive to others' welfare
10:10 – 10:40 am	Vasily Klucharev	Neural mechanisms of social decisions

### ***Kokopelli Parlor II***

Jeffrey C. Cooper, Tamar Kreps, Arthur Aron, Brian Knutson
Venkat R. Lakshminarayanan, Laurie R. Santos
Vasily Klucharev, Kaisa Hytonen, Mark Rijpkema, Ale Smidts, Guillén Fernández



# Learning to like: social observation influences prefrontal activation for viewing others

Jeffrey C. Cooper<sup>1\*</sup>, Tamar Kreps<sup>1</sup>, Arthur Aron<sup>2</sup>, Brian Knutson<sup>1</sup>

<sup>1</sup>Department of Psychology, Stanford University, Stanford, CA; <sup>2</sup>Department of Psychology, Stony Brook University, Stony Brook, NY

\*Correspondence at: [jcooper@stanford.edu](mailto:jcooper@stanford.edu)

How do we learn who to like? Observing others provides an important source of information. Often, people make enduring positive and negative judgments of others based on limited observation. Little is known, though, about how the brain builds positive or negative social impressions on the basis of observation. We scanned participants with event-related fMRI in a novel social prediction task. Participants observed the outcomes round-by-round of a six-person repeated public goods game and made predictions about how much was donated on each round. Participants were not told in advance that the donation profiles of each player in the game were designed to be more or less generous. Participants were accurate at estimating each player's average donation, and formed strong impressions of each player. After observation, generous players were liked more, while selfish players were liked less. To investigate how participants' impressions changed over time, we fitted a single-parameter associative learning model to each participant's predictions, and used that model to create individualized regressors of each player's estimated generosity (average donation) over time. When participants viewed the faces of each player, activation in ventromedial prefrontal cortex correlated positively with model estimates of generosity. When receiving feedback about actual donation amounts, activation in anterior striatum and parahippocampal cortex correlated positively with unexpectedly high donations. Finally, when making predictions about donation outcomes in each round, activation in the ventromedial prefrontal cortex correlated with predicting higher rather than lower donations. This study is among the first to examine how observation changes both emotional impressions of others and neural responses to them. The effects suggest that brain networks involved in learning about rewards for ourselves are also engaged in learning about reward for other people. The effects are also consistent with the hypothesis that others we like are processed in the brain similar to other kinds of rewards.

## Acknowledgements

Funding for this project has been provided by a grant from the FINRA Investor Education Foundation (2006-07-004) and NIMH training grant 5T32MH020006-10.

## The Origins of Other-Regarding Preferences: Capuchins (*Cebus apella*) Are Sensitive to Others' Welfare

Venkat R. Lakshminarayanan<sup>1</sup>, Laurie R. Santos<sup>1</sup>

<sup>1</sup>Department of Psychology, Yale University, New Haven, CT

Humans exhibit striking regard for others in many contexts – donating blood, volunteering for military service, and even incurring costs to punish antisocial behavior [1-2]. A growing body of experimental evidence suggests that we differ from our closest primate relatives in this regard. Several studies suggest that closely-related chimpanzees lack our species' prosocial tendencies [3-4], leading some to speculate that our human other-regarding preferences stem from our reproductive status as cooperative breeders [5-6]. In contrast to this account, we provide a demonstration that the capuchin monkey (*Cebus apella*) exhibits robust prosocial behavior in spite of the fact that this species does not cooperatively breed.

In our experiment, adapted from a primate analog of the dictator game [3-4], a capuchin subject (designated as the proposer) could determine the size of the reward provided to another capuchin (the receiver). While the proposer's payoffs were the same regardless of the reward he chose for the receiver, the proposer had the option of providing the receiver with either a large reward (a marshmallow) or a low-quality reward (a celery). We then compared monkey proposers' likelihood of delivering the larger reward in a condition in which a receiver monkey was present (*test condition*) to a condition in which no receiver was present (*empty control condition*) and another in which no monkey was present and an opening allowed the subject to access rewards in the receiver's chamber (*selfish control condition*).

Monkeys gave the marshmallow (rather than the celery) at greater-than-chance levels in the test condition ( $t(6) = 3.47, p < 0.01$ ), and on the selfish control condition ( $t(6) = 5.55, p < 0.001$ ), but not on the empty control condition ( $t(6) = 1.73, p = n.s.$ ). Demonstrating that they understood the nature of the task, monkeys delivered the larger reward more often in the selfish control condition than in the empty control condition (Mean Diff.: 20.6% marshmallow pulls,  $t(6) = 4.99, p = 0.01$ ). Importantly, the proposer's personal payoff (i.e., marshmallow vs. celery) had no effect on subjects' prosocial tendencies ( $F(1,6) = 1.51, p = 0.26$ ). This result is striking given that humans exhibit diminished regard for others when actors receive relatively smaller rewards than receivers [e.g., 5], contrasting with the rates of giving we observed in capuchins.

Capuchins reliably give food to others in this analog of the dictator game, providing the first evidence that a non-cooperatively-breeding species shares human prosocial tendencies. In fact, capuchins prosociality persists even case in which a proposer's prosocial actions results in the receipt of a relatively smaller personal reward. These results raise the possibility that prosociality may be broadly shared throughout the primate order despite its conspicuous absence in apes [3-4], and thus raise the possibility that ecological factors other than cooperative breeding underlie the emergence of altruism in our species.

### Acknowledgements

This work was supported by an NSF Human Social Dynamics Grant (SES-0624190). LRS was supported by Yale University. Correspondence and requests for materials should be addressed to V.R.L. ([venkat.lakshminarayanan@yale.edu](mailto:venkat.lakshminarayanan@yale.edu)).

### References

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- [2] Henrich, J., et al., (2004). *Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-Scale Societies*, (Oxford: Oxford University Press).
- [3] Silk, J., et al. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, 437, 1357-1359.
- [4] Jensen, K., Call, J. & Tomasello, M. (2007). Chimpanzees are rational maximizers in an ultimatum game. *Science*, 318, 107-109.
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## Neural mechanisms of social decisions

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Human behavior is guided not only by subjective values or attitudes, but also by the perceived behavior of others, in particular by social norms (Cialdini and Goldstein, 2004). Despite a growing body of literature describing neural mechanisms of decision making, we know little about the mechanism underlying social influence on human decisions.

Here we utilize the cognitive neuroscience approach (Phelps and LeDoux, 2005; Schultz, 2006) to provide a useful framework for studying reinforcement learning mechanisms of conformity in decision making. Recent neuroscientific and computational models assume that goal-directed behavior requires continuous performance monitoring. Successful behavioral patterns are reinforced while errors call for adjustments of behavior. Recently, Read Montague and Terry Lohrenz (Montague and Lohrenz, 2007) hypothesized that compliance with social norms requires neural signals related both to the norm and to deviations from it. Here we show, using functional magnetic resonance imaging, that conformity is based on reinforcement learning and is predicted by the neural ‘error’ signal evoked by deviations from social norms.

The present study shows that group opinion affects one’s judgments of facial attractiveness, which play a critical role in human social interaction. A deviation from the group opinion is detected by neural activity in the rostral cingular zone (RCZ) and ventral striatum. These regions produce a neural signal similar to prediction error signal in reinforcement learning that indicates a need for social conformity: a strong conflict-related signal in the RCZ and NAc triggers adjustment of judgments in line with group opinion. Furthermore, the individual amplitude of the conflict-related signal in the ventral striatum correlated with differences in conforming behavior across subjects. Both the NAc and the RCZ receive midbrain dopaminergic innervations. Moreover, animal studies robustly demonstrated that the prediction error signal is dopamine-mediated (Schultz, 2006). Thus, dopamine-dependent synaptic plasticity is a potential cellular mechanism for long-term conforming adjustments of judgments (Schultz, 2006). Overall, our results suggest that social conformity is underlined by the neural error-monitoring activity which signals probably the most fundamental social mistake — an error of being too different from others.

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**Poster Session I: Friday 10:45am – 12:25pm**

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7	Risky Choice	Distinct neural representations of behavioral risk and reward risk	Peter N. C. Mohr, Guido Biele, Hauke R. Heekeren
8	Risky Choice	Individual differences in the Iowa Gambling Task: A computational account	Lee I Newman, Thad A. Polk, Stephanie D. Preston
9	Risky Choice	Heterogeneity in risky decision making in 6-to-7-year-old children	David Paulsen, Scott Huettel, Michael Platt, Elizabeth Brannon
10	Risky Choice	Exploring the behavioral and neurobiological foundations of three components of uncertainty	Elise Payzan, Peter Bossaerts
11	Risky Choice	Neurobiological responses in individuals making choices in uncertain environments: Ambiguity and conflict	Helen Pushkarskaya, Xun Liu, Michael Smithson, Jane E. Joseph
12	Risky Choice	Supplementary eye field reflects values of action and outcome in a gambling task	Na Young So, Veit Stuphorn
13	Risky Choice	Sleep deprivation modulates risky decision-making strategies	Vinod Venkatraman, YM Lisa Chuah, John. W. Payne, Scott Huettel, Michael WL Chee
14	Risky Choice	Strategic modulation of cognitive control in decision-making under uncertainty	Tal Yarkoni Todd S. Braver
15	Risky Choice	The effect of self-generated criterion on feedback-related negativity	Nai-Shing Yen, Yin-Fang Chang, Kuan-Ying Lin, Chang-Hao Kao, Ying-Ru Lai
16	Risky Choice	Genetic determinants of financial risk taking	Camelia M. Kuhnen, Joan Chiao
17	Valuation	rTMS over the right dorsolateral prefrontal cortex down-modulates the computation of values in decision-making	Mickael Camus, Neil Halelamien, Shinsuke Shimojo, John O'Doherty, Colin Camerer, Antonio Rangel
18	Valuation	Local differences in the neural encoding of facial and monetary rewards	John A. Clithero, David V. Smith, R. McKell Carter, Michael L. Platt, Scott A. Huettel
19	Valuation	Dissociating goal values, decision values, and prediction errors in the human brain	Todd A. Hare, John O'Doherty, Colin F. Camerer, Wolfram Schultz, Antonio Rangel
20	Valuation	Medial orbitofrontal cortex interacts with the anterior insula to compute subjective values in complex social decisions	Todd A. Hare, Colin F. Camerer, Dan Knopfle, John O'Doherty, Antonio Rangel
21	Valuation	Neurons in anterior and posterior cingulate cortex encode distinct decision variables in three different economic tasks	Sarah R. Heilbronner, Benjamin Y. Hayden, Michael L. Platt
22	Valuation	Economic value coding by single neurons in the human amygdala	Rick L. Jenison, Hiroyuki Oya, Hiroto Kawasaki, Matthew A. Howard III, Antonio Rangel
23	Valuation	Topography of social and nutritive reward coding in striatum	J.T. Klein, M.L. Platt
24	Valuation	Visual attention drives the construction and comparison of values in simple economic choice	Ian Krajbich, Carrie Armel, Antonio Rangel
25	Valuation	Neural representation of value in the absence of choice	Stephanie C. Lazzaro, Ifat Levy, Robb B. Rutledge, Paul W. Glimcher
26	Valuation	Neurally dissociating valuative and non-valuative contingency learning	O'Dhaniel Mullette-Gillman, Scott Huettel
27	Valuation	What you do know can hurt you: Environmental state cues in a dynamic decision-making task	A. Ross Otto, Arthur B. Markman, Bradley C. Love
28	Valuation	Aversive goal values are negatively encoded in the medial orbitofrontal cortex at the time of decision-making	Hilke Plassmann, John O'Doherty, Antonio Rangel
29	Valuation	The presence of framing effects in rats	Mehwish Saba Bhatti, Jaeseung Jeong
30	Valuation	Taste-independent reward-related representations in the insular cortex.	Albino J. Oliveira-Maia, Ivan E. de Araujo, Clara Monteiro, Virginia Workman, Vasco Galhardo, Sidney A. Simon, Miguel A. L. Nicolelis

# Grasping the Fundamental Difference between Expected Utility and Mean-Variance Theories

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Several papers have examined the conditions under which the behavioral predictions of Mean-Variance (MV) and Expected Utility (EU) models coincide; focusing on the shape of the utility function or subtle measures of risk such as semi-variance. There is yet a fundamental difference in the two approaches: EU requires the explicit learning of probabilities using, for instance, Bayesian updating, with the drawback that, as the number of state probabilities increases, accurate estimation of probabilities becomes impossible [1]. This learning limitation does not hold for the MV optimizer, who can simply learn the mean and variance using a reinforcement learning algorithm. We conjecture that this fundamental difference has important behavioral effects which we will explore with the proposed experimental paradigm.

In this paradigm, the outcome of each gamble is based on random drawing of a ball from a bin. Balls within each bin are distinguished by color. There may be many balls of the same color, but participants do not know how many. Like in standard lotteries, each ball is labeled with a number. This number is the same for balls of the same color and determines how much participants earn when a ball is drawn. For instance, if the red balls are labeled "5", he/she make 5 francs every time a red ball is drawn. Whenever we change the bin, we give the opportunity to try it out, before making decision whether to buy into the gamble or not. Participants can sample as much as they like. The crucial feature of the task is that occasionally, we may change the labels without changing the composition of the bin (number of balls of each color).

States (as determined by the number of colors) and payoff variance are changed independently. We hypothesize that as the number of states increases and because this increases the number of probabilities to estimate, an EU maximizer will need to sample more in order to learn the value of the bin. This is not the case for a MV optimizer, who will conversely sample more if the payoff variance increases, in order to get an accurate estimate of the mean. In addition, changes in labels require the MV optimizer to resample the bin because he/she did not keep track of the probabilities, as opposed to the EU decision-maker. Data will be collected with this paradigm and results will be evaluated in view of the hypotheses.

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# Behavioral and Neurobiological Effects of Expert Messages on Risky Decision Making

Jan B. Engelmann, C. Monica Capra, Charles Noussair, Gregory S. Berns

In the current experiment, we investigated the behavioral and neural mechanisms whereby advice from an expert affects an individual's risk attitude for money. We used fMRI to investigate two competing hypotheses about how advice influences decisions taken under risk: 1) by influencing individuals' valuation mechanisms (i.e. changing the utility function and/or probability weighting); or 2) by overriding these valuation mechanisms. Our results are consistent with the second hypothesis.

Participants (N=24) made choices between a sure win and lotteries providing ex-ante probabilities of winning (1%, 10%, 20%, 37%, 80%, 90%, 99%) for a relatively high payoff. Prior to scanning, a certainty equivalent (CE) procedure assessed the curvature of the probability weighting function,  $w(p)$ , and the level of risk aversion for each individual, using a modified version of the Parameter Estimation by Sequential Testing (PEST) procedure. This staircase procedure iteratively adjusts the value of the sure win to generate choice reversals within each probability condition, while halving the step-size after every reversal until a threshold value indicative of choice indifference is reached. To isolate the brain circuitry through which expert messages exert their effect on risk-taking behavior, fMRI was employed. Inside the scanner, participants made choices between a sure win (safe option) and a lottery (risky option) in two conditions: 1) expert messages (MES); and 2) messages were unavailable (NOM). The specific message we used in the MES condition was provided by a risk-averse satisficing expert (C.N.).

We employed nonlinear logistic regression to extract each participant's probability weighting function from binary decisions using a modified version of Prelec's compound invariant form with additional parameters estimating the effect of the message on probability weighting. The difference in utility between the lottery and sure win (SW) was given by:  $\Phi = w(p) \times 1000^\gamma - SW^\gamma$ , where  $w(p) = \exp[-\beta (-\ln p)^{\alpha+(\delta*m)+(\lambda*t)}]$ ,  $\gamma$  is the curvature of the utility function,  $\alpha$  is the probability weighting parameter,  $p$  is the probability of winning the lottery for 1000 currency units,  $m$  is a dummy variable indicating the presence of message,  $\delta$  measures the effect of the message,  $t$  is time, and  $\lambda$  is a learning rate. The probability of choosing the sure win ( $P_{SW}$ ) was estimated as  $P_{SW} = \exp(\Phi) / [1 + \exp(\Phi)]$  using nonlinear logistic regression. This method yielded group-level parameter estimates that agree with findings from behavioral economics ( $\alpha = 0.62$  and  $\beta = 1.46$ ). Importantly, we obtained behavioral evidence demonstrating that the presence of expert advice led to a significant increase in the curvature ( $\alpha$ ) of  $w(p)$  in the direction of the advice.

To isolate networks that correlated with probability weighting during decision-making, we modeled activity during the decision phase in terms of the presence of the message (MES, NOM) and type of decision made by participants (sure win, gamble) and entered each participant's weighting function as a parametric modulator in first-level models. Significant correlations ( $P < 0.001$ ) with  $w(p)$  were obtained when subjects chose the sure win during the NOM condition in bilateral superior parietal lobe, anterior cingulate cortex, anterior insula, inferior frontal gyrus and caudate nucleus. The presence of expert messages resulted in a loss of this relationship of activity to  $w(p)$ . These findings indicate the presence of *nonlinear* probability weighting during choice in a network of structures previously implicated in risky decision-making, which was offset when information about the opinion of an expert was displayed.

# **Anterior cingulate cortex mediates ambiguity aversion in monkeys**

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People prefer risky options, in which reward probabilities are known, to ambiguous ones, in which reward probabilities are unknown. Normatively, these two forms of uncertainty – often referred to as risk and ambiguity -- should be treated equivalently by decision makers. Nonetheless, people avoid ambiguity in a wide variety of situations, paying a premium for a risky option with the same expected value. Although risk has attracted more experimental and theoretical interest, ambiguity is arguably more common in real-life situations, in part because probabilities are rarely explicitly stated. Nevertheless, the evolutionary origins and neural wellspring of ambiguity aversion remain obscure. We investigated this problem by examining the behavior of rhesus monkeys in an ambiguous decision-making task. We found that rhesus monkeys, like humans, prefer risky gambles to ambiguous ones, demonstrating that ambiguity aversion may arise from a shared cognitive heritage. We also show that neurons in the anterior cingulate cortex (ACC) signal, successively, the presence of ambiguity, choice of an ambiguous option, and the reward outcomes that follow such choices. Together, these data demonstrate that ACC mediates ambiguity aversion, and does so without recourse to human language, symbolic culture, or abstract currency.

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# Revisit “Prominent Deck B phenomenon” in the Iowa Gambling Task

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From 1994 to 2008, Bechara et al. [1, 2] demonstrated that the Iowa gambling task can successfully distinguish between normal decision makers and affective deficits. However, there have a growing number of researchers have demonstrated that normal decision makers prefer the bad deck B to the other three decks [1], including Bechara et al [2, 3]. Lin et al.[4] labeled this observable fact the “prominent deck B phenomenon”. Actually, this phenomenon directly challenged the basic findings of the Iowa gambling task for 1994. To further confirm the reproducibility of IGT in 1994, this study recruited 48 college students, including 24 males and 24 females to perform the original version of IGT this year. Each subject played the computer version of IGT twice (200 trials) to confirm their preferences of decks in IGT. This study indicated that most subjects preferred bad deck B to the other three decks confirming the findings of Bechara et al. for the year 2008 [2, 3], but conflicting with the original findings in 1994[1].

From a post-analytical perspective, deck B displayed high-frequency gain and considerable losses; namely during an average of ten trials, subjects experienced nine large gains (\$ 100) and one massive loss (\$ -1250). The Iowa group considered that normal decision makers gradually hunch the internal rule. Restated, subjects progressively inhibit their preference for deck B after encountering a few large losses (\$ -1250). (In the original study of Bechara et al.) (1994), subjects inhibited their preferences for deck B after encountering two trials of huge loss in average; nevertheless in the study conducted by Bechara et al. during 2007 and 2008, normal decision makers were unable inhibit their preferences for deck B by encountering after encountering an average of three large losses. The “prominent deck B phenomenon” truly existed in the IGT. The inconsistent findings between 1994 IGT and 2008 IGT should be able to be carefully explained by the Iowa group.

## Acknowledgements

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# Brain Maps of Soochow Gambling Task

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In an uncertain world, organisms have difficulty in predicting the future based solely on inductive reasoning. Sometimes, an unpredictable and dramatic event will require users to change their plans. Nassim Taleb stated this phenomenon as the “Black Swan” phenomenon in his recent book [1]. Recently, Chiu et al. [2, 3] have used a IGT[4]-modified task, namely the Soochow Gambling Task (SGT) to demonstrate choice patterns under uncertainty. In the SGT, decks A and B possessed frequent gains and infrequent large losses (deck A: 8 × (\$ ) 200, 2 × (\$ ) -1050; deck B: 8 × (\$ ) 100 , 2 × (\$ ) -650), in addition to a negative expected value (\$ -500) over an average of ten trials. In contrast, decks C and D possessed frequent losses and infrequent large gains (deck C: 8 × (\$ ) -200, 2 × (\$ ) 1050; deck D: 8 × (\$ ) -100 , 2 × (\$ ) 650) but exhibited a positive expected value (\$ 500) over an average of ten trials. The findings of SGT indicated that, in situations of uncertainty, most subjects were unable to inhibit their preference for the high-frequency gain choice (deck), although this choice sometimes led them to suffer heavy losses. The subjects adopted a simple strategy, namely the “gain-stay, loss-randomized” strategy to cope with unpredictability. However, few studies explored the brain correlates in response to the choice pattern during the performance of SGT. This investigation recruited 24 volunteers to participate in the SGT-fMRI scanning. The findings replicated those of Lin et al. [5] and indicated that the Insular cortex (IN) and Basal ganglia (BG) were important drivers of decision making during the anticipatory period, and that the parietal lobule (PL) and Medial Frontal Cortex (MFC) were critical in assessing outcomes during the experience (outcome appearance) period. This work implied that in the face of uncertainty, organisms may utilize the original brain mode (IN, BG) to deal with situations and that the neocortex (PL, MFC) may serve as a temporary assistant by gathering incomplete information piece by piece (trial by trials) for inductive reasoning.

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- [5] Lin CH, Chiu YC, Cheng CM, Hsieh JC: **What is the real function of medial frontal cortex under a complete uncertainty?**

# Brain Maps of Iowa Gambling Task: From Uncertainty to Certainty

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Bechara et al. [1] developed a very creative task, namely the Iowa Gambling Task (IGT) to test the choice behavior under uncertainty. Iowa group's serial finding indicated that normal participants can gradually hunch the final outcome and get the final benefit. They also suggested the somatic brain loops included that the medial frontal cortex, amygdala, insular/ somatosensory cortex and brain stem related to the emotional decision-making. However, Dunn et al. [2] performed a global review for IGT and Somatic Marker hypothesis (SMH) and indicated that there have many neurological and brain imaging studies demonstrated the variant evidences for somatic brain loops. Recently, Lin et al. [3] have demonstrated a global brain map for Iowa gambling task by separating the anticipatory and experience period. However, there is few imaging study to observe the brain response when the subjects directly refer to the explicit knowledge (internal gain-loss probability and value) to perform the IGT, namely the certainty period. Therefore, the neural correlates in response to dynamic decision processing under certainty will be important to clarify the issue of somatic loops. The present study was extended the Lin et al. study [3] and additionally examine the brain response of decision processing under certainty. The 24 volunteers were same as Lin et al. research and they performed the original IGT twice. In the second run (certainty period), the gain-loss probability and value was disclosed to subjects. At the mean time, subjects were received the functional scanning of MRI. The present result indicated that, during the certainty period, most brain regions was similar with Lin et al. finding [3] under uncertainty, namely the insular cortex was highly involved the anticipation of making decision and parietal cortex was related to the value representation after outcome appearance. However, the basal ganglia have non-significant activation during the anticipatory period of certainty. During the certainty situation, most brain activation was less than that of uncertainty. Interestingly, the medial frontal cortex (MFC) can also be observed during the subjects perceived the largest loss of deck B under certainty stage. The present finding indicated that the MFC maybe act the role of monitoring error under not only the ambiguity situation (uncertainty) but also logic-loaded condition (certainty).

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# Distinct Neural Representations of Behavioral Risk and Reward Risk

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How people deal with risk has important consequences in many decision domains. Inspired by economic and psychological research, recent studies have investigated the neural representations of risk [1,2 for review]. Different types of risk, however, can be distinguished and play different roles in decision processes. According to Huettel [3] *behavioral risk* is the uncertainty about which action should be taken while *reward risk* reflects uncertainty about possible outcomes. The goal of the present study was to identify neural circuits involved in risk processing and to differentiate neural representations of behavioral and reward risk.

Here we used a voxel-wise quantitative meta-analysis (activation likelihood estimation (ALE) [4]) of previous fMRI studies. We included results of 22 neuroimaging studies (published 2001-2008) that have explicitly examined the neural representations of risk or uncertainty. From these studies we included contrasts that (a) compared risky with safe decision situations, (b) compared high risk with low risk decisions, and (c) identified correlations with the degree of risk or uncertainty. The ALE-statistic revealed consistent risk-related activations in bilateral anterior insula (aINS), right dorsolateral prefrontal cortex (DLPFC) and medial prefrontal cortex (MPFC) ( $p < .05$ , corrected). To investigate the possible dissociation (behavioral vs. reward risk), we conducted separate ALE meta-analyses for studies that investigated only behavioral risk (8 studies, 77 foci) in the absence of reward risk and for studies on reward risk (12 studies, 76 foci) in the absence of behavioral risk, respectively. A conjunction between these two ALE meta-analyses identified a cluster in the superior part of the right aINS that responded to both behavioral and reward risk ( $p < .05$ , corrected). We also found distinct representations for reward and behavioral risk when contrasting the ALE-maps. MPFC and right DLPFC showed greater activations in response to behavioral risk whereas the aINS showed greater activations for reward risk.

In sum, our results show that the brain represents different types of risk in different brain regions. Conjoint activation in the superior part of the aINS indicates that both types of risk might be partly related.

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# Individual differences in the Iowa Gambling Task: A Computational Account

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The Iowa Gambling Task (IGT) is a well-studied experimental paradigm known to simulate both intact and impaired real-world decision making in choice tasks that involve uncertain payoffs. Prior computational studies of the IGT have led to a standard model of the task known as the expectancy valence model (Busemeyer & Stout, 2008) that is a member of the class of single-state Q-learning models well documented in the literature on computational reinforcement learning. This standard model has been used to characterize, parametrically, decision making performance in diverse populations of subjects including patients with ventromedial prefrontal lesions, patients with disorders of the basal ganglia, and individuals diagnosed with a wide range of psychopathologies such as chronic substance dependence, pathological gambling, and schizophrenia. Although the standard model has provided a useful starting point for characterizing decision making performance in the aggregate, little work has been done to investigate how well this class of models captures individual differences in decision making.

In the present work we investigated how well reinforcement learning models were able to capture individual differences in decision making in a population of forty adults who performed the IGT. We specified a set of ten candidate models that included the standard model and nine alternative models independently motivated by behavioral and neural considerations. We fit these models to individual decision data and used information-theoretic methods to select from among these candidate models those that were best supported by the data.

Although many of the candidate models reproduced the aggregate behavior of our subjects, we found that not one of the ten models was well-supported for even a majority of the subjects. In fact, the standard model was a best fit for only a third of the subjects. Notably, an alternative model that incorporated risk-sensitivity in its learning mechanism outperformed the standard model. Yet, even this model was a best fit for fewer than half of the subjects. By analyzing the support for each model at the individual level, we identified several subsets of decision makers. One subset was best fit by the standard model, suggesting that their choice behavior was driven by expected value as learned from the net payoffs experienced from each of four decks of cards. A second (and largest) subset of subjects was best fit by a risk-sensitive model suggesting that avoiding losses is an important component of reward in addition to monetary payoffs. Three other subsets were identified by models that performed poorly overall, but were the best fit for these subjects: these subsets included subjects who exhibited sensitivity to the average level of experienced rewards, to reward variance, and to the gradual decay of learned information.

Our results (i) suggest that there are significant individual differences in decision making performance in the IGT, (ii) reveal several dimensions on which decision making differs, (iii) highlight the fact that these differences are not captured by differences in parameter values of any one model that has yet been applied to the task, and (iv) caution against using parameter differences to characterize impaired IGT performance in clinical populations until more robust models are identified.

## **Heterogeneity in risky decision making in 6- to -7-year-old children**

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Studies of risky decision making in children have been relatively few in number, and fewer still are those examining individual differences[1]. The current study tested 6- to 7-year-old children in a risky decision paradigm that manipulated risk level and magnitude. Children made decisions involving a choice between one of two Sure Bet values, or between a Sure Bet and a Gamble with the goal of collecting coin tokens that could be later traded for toy prizes. The Sure Bet comparisons were included to assess sensitivity to the numerical contrasts required to assess risk in the Gamble trials. Expected value (EV) was equated for Sure Bet and Gamble options at two levels of magnitude (two and four coins) and for two levels of Risk (coefficients of variation 0.7 and 1.4)[2]. The results found that children could be classified readily into two groups: Risk Sensitive (RS) and Risk Insensitive (RI). Both groups chose the Gamble over the Sure Bet more often for larger magnitudes; i.e. when the EV was 4 coins, the RI group gambled equally as often on Low Risk and High Risk trials, but chose to gamble more often than the RS group. The RS group, however, chose to gamble more with Low Risk trials than with High Risk trials and observed a greater effect of magnitude. Children identified as risk-sensitive subsequently participated in a fMRI study to identify brain regions involved with processing differential risk and magnitude comparisons. Our results highlight variability in sensitivity to risk among children and emphasize the importance of assessing variability in strategies in the development of decision making. Behavioral and imaging results as a function of strategy will be described with an emphasis on separating the neural systems involved in quantity comparisons from those involved in assessing risk.

### **Acknowledgements**

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# Exploring the behavioral and neurobiological foundations of three components of uncertainty

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It has been suggested [1] that there are two levels of risk, namely “expected” and “unexpected” uncertainty. The distinction is based on the realization that there may be unforeseen changes in the stochastics of the reward generating process. Some refer to unexpected uncertainty as “jump risk” [2]. From a Bayesian point of view, however, expected uncertainty (or prediction risk [3]) itself is to be subdivided into two categories, namely, parameter estimation uncertainty and inherent reward stochasticity. Computationally, these three components of uncertainty, reward stochasticity, estimation uncertainty and jump risk, play a very different role. To date, little is known to what extent they affect behavior and brain processes. The aim of our study is to measure their impact, both behaviorally and neurobiologically.

To this end, we developed a new board game involving a natural sampling task in a multinomial environment with jumps.

Our board game was designed to provide a balanced exposure to the three components of uncertainty.

Behavioral data showed that subjects indeed managed to learn the three components. To better understand subjects’ inference, we fitted two competing algorithms to subjects’ choices. The first one implemented a simple reinforcement learning algorithm. The second one was based on standard Bayesian updating, augmented with a “forgetting heuristic,” to take into account the jumps. Preliminary model comparison analysis suggests that the Bayesian algorithm provides the best fit of the behavioral data.

Armed with these behavioral results, we have started a parametric fMRI analysis. Our Bayesian algorithm generates key quantitative parameters – an on-line estimated entropy signal capturing reward stochasticity, a parameter estimation uncertainty signal, and a jump risk signal. When paired with the BOLD signal, evolution of the values of these parameters, estimated from the behavioral data, should allow us to localize their encoding in the human brain.

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## Decision making under uncertainty: Ambiguity and Conflict.

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### Abstract

Ellsberg defined ambiguity as environment, “when there are questions of reliability and relevance of information, and particularly where there is conflicting opinions and evidence.” (Ellsberg, 1961, p. 659) Although, Budescu and Wallsten (1995) pointed out that the studies of decision making under ambiguity (for review see Camerer and Weber, 1992) had focused only on environments with imprecise probabilities, rather than on unknown probabilities. Smithson (1999) suggested considering an environment where equally reliable sources provide conflicting information about probabilities associated with known outcomes (*conflict*<sup>i</sup>) separately from environments with vague probabilities are associated with known outcomes (*ambiguity*). He also showed that conflicting unambiguous messages from two equally believable sources are less preferred than two informatively equivalent, ambiguous, but agreeing messages from the same sources and conflicting unambiguous sources are perceived as less credible than ambiguous but agreeing sources. Here, we demonstrate by functional magnetic resonance imaging (fMRI) that individuals' preferences for conflict (uncertainty with conflicting information about probabilities) and ambiguity (uncertainty with imprecise probabilities) predict activations associated with decision making in distinctive brain regions. Activation within the right inferior frontal and left parahippocampus was predicted by ambiguity preference. In contrast, activation of the right superior parietal cortex was predicted by conflict preference. Overall, our results indicate that decision making under ambiguity and conflict are supported by distinct neurobiological mechanisms and supports the hypothesis that ambiguity in Ellsberg sense needs to be differentiated into ambiguity coming from imprecise probabilities and ambiguities generated through conflict or disagreement between sources of information.

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<sup>i</sup> Smithson 1999 suggests four types of conflict environment: 1) conflict about probabilities, 2) conflict about utilities, 3) conflict about preferences, and 4) conflict about outcomes. In this paper we focus on the first type of conflict, i.e. conflict about probabilities.

## **Supplementary eye field reflects values of action and outcome in a gambling task.**

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Often, decisions have to be made despite uncertainty about the outcome of a chosen action. In those cases, an accurate assessment of the value of each available action is critical to make an optimal choice. To study how value affects decision-making under risk, we trained two macaque monkeys in a gambling task and recorded single unit activity in the supplementary eye field (SEF), a part of the medial frontal cortex.

In the gambling task, two visual cues were presented on the screen indicating either a sure or a gamble option. The sure option always delivered a certain amount of water reward, while the gamble option delivered either a small or a large amount of water with a certain probability. Visual cues were represented as colored squares. Seven different colors encoded seven different reward amounts. The proportion of the color in a square represented the probability that the corresponding reward amount was delivered. The monkey indicated his choice by making a saccade to one of the cues. The locations of the visual cues were randomized across trials to allow us to differentiate between motor-related and decision-related neuronal signals.

We found that the gamble option's winning probability and the alternative sure option's reward amount affected the monkey's choice behavior. In single cell recordings in the SEF, we found one group of neurons that reflected the value of the chosen option, at or around the onset of the saccadic eye movement to the chosen cue. A second group of neurons were active after the choice, when the monkey did not know how much reward he would receive after he picked the gamble option. Other neurons were active following the choice only when the monkey picked the sure option. Finally, a third group of neurons reflected the gamble outcome. After the gamble result was revealed, some of these cells were active when the gamble was won, while others were active when the gamble was lost. These preliminary findings suggest that the SEF represents and updates the value of behavioral options. SEF might play an intermediate role in decision-making by using this value signal to guide the selection of the corresponding motor command that will lead to the expected outcome.



# Sleep Deprivation Modulates Risky Decision-Making Strategies

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Sleep deprivation (SD) enhances risk-seeking behavior by elevating expectation of high gains and attenuating the emotional impact of losses<sup>1</sup>. Using a novel incentive-compatible decision-making task<sup>2</sup> that involved sets of five outcomes ranging from large monetary losses to large monetary gains (**Fig. 1**), we sought to explore the neural bases of effects of sleep deprivation on decision making strategies involving risk. Critically, the task was constructed so that subjects chose between two types of options: overall probability focused (OPF) and extreme value focused (XVF). Using the OPF strategy increased the overall chance of winning money compared to losing money, whereas using the XVF strategy either increased the magnitude of the extreme monetary gain (XVF-gain) or reduced the magnitude of the extreme monetary loss (XVF-loss). Prior results using normal healthy adults suggest systematic variability in the preference for these strategies. Activation in inferior parietal lobule and dorsolateral prefrontal cortex (PFC) predicted the OPF choices whereas activation in right anterior insula (aINS) and ventromedial PFC predicted XVF-loss and XVF-gain choices respectively.

Twenty-nine volunteers (14 females, mean age = 22.3 years) underwent functional neuroimaging in two sessions, following a night of normal sleep (rested wakefulness; RW) and after 24 h of sleep deprivation. Consistent with previous results, we found a significant interaction between decision-making strategies and states ( $F(1,28) = 6.702$ ,  $p = 0.015$ ): SD participants showed greater preference for XVF-gain and reduced preference for XVF-loss choices. These findings are consistent with an increase in risk-seeking behavior following SD. fMRI analysis elucidated the neural mechanisms associated with these shifts in strategy across states. Concurrent fMRI data also provided insight into differences in sensitivity to monetary outcomes between states.

## Acknowledgements

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# **Strategic modulation of cognitive control in decision-making under uncertainty**

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When making choices between certain rewards and uncertain rewards, humans tend to deviate markedly from the predictions of Expected Utility Theory (EUT), and demonstrates a robust aversion to risk. A number of behavioral economic and neuroeconomic studies have suggested that risk aversion reflects an exaggerated emotional response to the prospect of accruing losses or missing out on rewards, and conversely, that a higher cognitive system supported by frontoparietal brain regions is involved in regulating such responses and enforcing rational choice. The present study tested this model using an experimental paradigm that allowed differences in probability, magnitude, and expected value to vary relatively independently across two choices on a trial-by-trial basis.

Behaviorally, participants ( $n = 16$ ) showed a strong tendency to avoid risk. Multiple regression analysis was used to identify brain regions independently sensitive to differences in probability, magnitude, and expected value. Three findings were identified. First, group-level activation in frontoparietal regions such as ACC, DLPFC and frontal operculum increased selectively when participants made risky choices, irrespective of the relative value of those choices. Thus, these regions appeared to support inhibition of a dominant response bias rather than optimal decision-making per se. Second, activation in striatal and ventromedial PFC regions showed robust associations with trial-by-trial variations in probability and magnitude during both the evaluation and outcome phases of the task, but did not predict participants' actual choices, suggesting that emotional responses were not the proximal source of the risk aversion bias. Finally, at the level of individual differences, increases in frontoparietal regions were associated with better task performance and reduced risk aversion, consistent with high performers' subjective reports of using an expected value computation strategy. Taken together, these results suggest that that the putative tension between irrational affective systems and rational cognitive systems cannot fully explain risk averse decision-making behavior, and underscore the importance of considering individual differences in strategy use.

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# The effect of self-generated criterion on feedback-related negativity

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Feedback-related negativity (FRN) is a brain potential peak at 250-300ms after feedback. It is suggested that FRN is sensitive to relative consequences rather than actual outcomes (e.g. Holroyd, Larsen, & Cohen, 2004). That is, a positive feedback worse than expected could elicit FRN, but a negative feedback better than expected might not elicit FRN.

In previous study, a reference point is provided in a gambling task to examine the effect of expectancy on FRN. In the gambling task, participants select one of four decks each trial in order to obtain the maximum payoffs at the end of the game. After the cue of win or lose, participants could win or lose 100, 200, 300, and 400 points in each trial. They were instructed that, on the average, the former participants could win 250 points in the winning trials and lose 250 points in the losing trials. It is observed that the FRN is larger when the outcome is worse than the expected +250 in the winning trials or -250 in the losing trials. That is, the FRN is sensitive to the instructed expected value (Yen, Lai, Chang, Yeh & Chen, 2007). However, whether participants could generate a criterion by themselves in the same gambling task without instructed expected value is still unknown. The present study is aimed to answer that question.

Twelve undergraduates from National Chengchi University were recruited as participants. A 2 (valence: win or lose)  $\times$  4 (amount: 100, 200, 300 or 400)  $\times$  3 (position: Fz, Cz, Pz) repeated-measures ANOVA were performed. The main effect of valence was not observed, indicating that FRN is not sensitive to actual negative outcome. However, the interaction effect of valence  $\times$  amount was revealed. The diagram of valence and amount shows a reverse between 100 and 200 points. That is, the FRN seems greater at win 100, lose 200, 300 and 400 than at lose 100, win 200, 300 and 400. In order to further check whether there is a criterion that is self-generated by participants between 100 and 200. A 2 (expected valence: better or worse than 150)  $\times$  3 (position: Fz, Cz, Pz) repeated-measures ANOVA were performed. The significant main effect of expected valence suggested that the feedbacks were evaluated by the criterion: 150. To sum up this present study, the FRN is elicited by feedbacks that are worse than expected; even the expectation is not provided from environment, participants can self-generate one!

**Keyword:** feedback-related negativity, self-generated expectancy, feedback evaluation

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# **Genetic Determinants of Financial Risk Taking**

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We identify genetic markers for the propensity to take financial risks in an experimental setting, and for the instability of risk preferences. Several genes previously linked to emotional behavior and addiction (5HTTLPR, D2DR and D4DR) are found to also correlate with risk taking in investment decisions. We find that the 5HTTLPR ss allele carriers are more risk averse than those carrying the sl or ll alleles of the gene. D4DR 7-repeat allele carriers are more risk seeking than individuals without the 7-repeat allele. Individuals with the D2DR A1/A1 genotype have more stable risk preferences than those with A1/A2 or A2/A2 genotype, while those with D4DR 4-repeat allele have less stable preferences than people who do not have the 4-repeat allele. These findings contribute to the emerging literature on the genetic determinants of economic behavior.

# **rTMS over the right dorsolateral prefrontal cortex down-modulates the computation of values in decision-making**

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Several studies have shown that activity in the orbitofrontal cortex (OFC) and the right dorsolateral prefrontal cortex (rDLPFC) correlates with the values assigned to items at the time of decision-making<sup>1,2</sup>. The role of the rDLPFC in the valuation process is unknown. In particular, it is not known whether the rDLPFC plays a causal role in decision-making, or if it implements computations that are correlated with valuations, but that do not participate in the valuation process itself. We addressed this question by using repetitive transcranial magnetic stimulation (rTMS) while subjects were involved in an economic valuation task. Our results suggest that rDLPFC plays a causal role in the computation of values: compared to a control condition, applying rTMS to the rDLPFC causes a decrease in the average values assigned to items as well as a decrease of the sensitivity of the values to their underlying appetitive traits.

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## **Local Differences in the Neural Encoding of Facial and Monetary Rewards**

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Humans find both money and attractive faces rewarding. Money, however, is a secondary reward that must later be traded for other goods, whereas the viewing an attractive face can be immediately experienced by their recipients. A core goal of neuroeconomics is to better understand, by way of neural data, how different reward categories are processed, valued, and compared. Data was collected using event-related fMRI to identify brain responses of heterosexual males to female faces and money. Subjects passively received human faces of varying levels of attractiveness and monetary rewards of varying positive and negative amounts. Attractiveness of the face stimuli was calibrated based on normative data from an independent behavioral study. We examined whether the receipt of faces of varying levels of attractiveness and the receipt of varying levels of monetary rewards similarly recruit neural systems implicated in the valuation and choice of rewards. To test this hypothesis, we analyzed functional magnetic resonance imaging (fMRI) data with both a standard regression analysis and a pattern classification technique (support vector machines, SVM) to decode the different types of rewards being presented to subjects.

We found that the face stimuli evoked activation in ventral striatum that scaled with subjective value of attractiveness. Conversely, cues indicating receipt of money evoked activation in ventromedial prefrontal cortex (vmPFC) that scaled with objective value. In a later market situation, participants then decided whether to purchase brief presentations of attractive faces, spending their earned money to purchase rewards that are non-hypothetical and consumed immediately. The magnitude of vmPFC activation to monetary rewards predicted their propensity to trade those rewards for the opportunity to view a more attractive face.

Using SVM, we analyzed data from regions of interest that have previously been implicated in decision making and reward processing. SVM provides access to local patterns of activation, which allowed us to uncover fine-grained differences in the encoding of faces versus money, of monetary gains versus monetary losses, and of faces varying in attractiveness. The large number of facial stimuli presented to each subject also allowed us to construct measures of both neural and behavioral similarity across faces.

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# **Dissociating goal values, decision values, and prediction errors in the human brain**

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To make sound economic decisions, the brain needs to compute several different value-related signals. These include goal values that measure the predicted reward that results from the outcome generated by each of the actions under consideration, decision values that measure the net value of taking the different actions, and prediction errors that measure deviations from individuals' previous reward expectations. We used functional magnetic resonance imaging and a novel decision-making paradigm to dissociate the neural basis of these three computations. Our results show that they are supported by different neural substrates: goal values are correlated with activity in the medial orbitofrontal cortex, decision values are correlated with activity in the central orbitofrontal cortex, and prediction errors are correlated with activity in the ventral striatum.

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# Medial orbitofrontal cortex interacts with the anterior insula to compute subjective values in complex social decisions

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Subjective value computations are a critical component of decision-making. Although much is known about how the brain assigns values to options in situations involving simple decisions (such as foods or monetary prizes), little is known about how these values are computed in more complex decision-making situations such as those that arise in the social domain. We addressed this question using functional magnetic resonance imaging (fMRI) to look for areas that parametrically encode the subjective value of real voluntary donations to different charities. Our results show that activity in the medial orbitofrontal cortex (mOFC) reflects the computation of subjective goal value in such complex social decision-making situations. Furthermore, the area of the mOFC that we identify shows considerable overlap with regions that have been shown to encode the subjective value of simple choices (1-3), suggesting that a common valuation system is at work in this area.

The reward experienced by the individual who donates to charity is thought to be derived, at least in part, from the knowledge that her actions benefit another. This process is likely to involve neural circuits that predict and interpret the feelings or emotional states of others (i.e. empathy). Recent neuroimaging studies have shown that the anterior insula is involved in empathic responses (4-6). Although the anterior insula did not reflect subjective value computations during charitable giving, it was more active during voluntary donation decisions. A functional connectivity analysis (PPI) showed that activity in mOFC was positively correlated with activity in the right anterior insula during voluntary donation trials. These results suggest that empathy-related processes in the anterior insula may influence the computation of subjective value in the mOFC during complex social decisions.

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## Neurons in anterior and posterior cingulate cortex encode distinct decision variables in three different economic tasks

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Keywords: posterior cingulate cortex, anterior cingulate cortex, decision making, reward, subjective value

One of the central goals of neuroeconomics is to discover how different parts of the brain contribute to distinct types of economic decisions. It has been widely posited that subjective value serves as a common currency for making all types of economic decisions and is represented in multiple brain regions. Previous studies of cingulate cortex have suggested that it may be broadly important for decision making, perhaps by encoding subjective value. To test this idea, we recorded from single neurons in both posterior and anterior cingulate cortex (CGp and ACC, respectively) while rhesus macaques (*Macaca mulatta*) performed three different economic tasks. The pattern of behavioral preferences in these tasks allowed us to disambiguate subjective value from other decision parameters. Although firing rates of neurons in both regions were strongly modulated by decisions about risky, delayed, and social rewards, we found clear evidence that posterior cingulate cortex does not signal subjective value, and anterior cingulate cortex does so only weakly. Instead, firing rates of single neurons in CGp were positively correlated with subjective value in a risky decision making task, but were negatively correlated with subjective value in a delay discounting task and a social decision task. These observations suggest that a single brain area can be important for encoding multiple economic variables without combining them into a single coherent representation of subjective value.

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# Economic value coding by single neurons in the human amygdala

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In value-based decision making, a value needs to be assigned to the different actions under consideration at the time of choice. To make effective decisions values must be commensurate with the benefits generated by the decision. There are potentially a number of areas in the brain implicated in the computation of economic valuation. One candidate structure is the amygdala complex (Baxter and Murray, 2002; Holland and Gallagher, 2004; Paton et al., 2006; Murray, 2007). In terms of structure and function, the amygdala serves as a central hub of information passing from several cortical and thalamic structures making the amygdala an ideal locus for value computation.

We investigated the neural basis of a value computation by recording single unit activity in the human amygdala while patient-participants bid for the right to eat different foods in a Becker-DeGroot-Marshall (BDM) auction. While relevant functional imaging data is accumulating in this area, there have been few measures of temporally-rich single-neuron responses recorded directly from anatomically identified regions of the human cerebral cortex and amygdala. We recorded from microcontacts on an electrode implanted directly in the amygdala nuclei for which we have high resolution MRI to precisely identify where the microcontact is positioned. Furthermore, we have used electrical stimulation at the electrode contacts to investigate the causal relationship between amygdala activity and behavioral choice.

Building the bridge between economic variables and brain activity at the level of single neurons requires the development of advanced methodologies that efficiently extract information from spiking activity of the neuron. A neuron communicates with other neurons by the timing of action potentials (spikes). Mathematically, these processes are referred to as point processes because the dependent variable is a point in time (or space) and not a measure of continuous signal amplitude. We have modeled the spiking activity using a generalized linear model (GLM) that integrates the bidding used in the BDM mechanism. This model allowed us to evaluate the weighting of the bidding covariate in fitting the GLM.

Our results support the hypothesis that components of valuation in the amygdala are communicated to higher-level structures, possibly the orbitofrontal cortex, for further processing used in the computation of decision making values. The modulation of bid choices as a consequence of electrical stimulation further implicates the role of the amygdala in the computation of value.

# **Topography of social and nutritive reward coding in striatum.**

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For social animals like primates, adaptive decision making frequently requires comparing the value of interacting with or gathering information about conspecifics against the value of acquiring the food and fluid necessary to sustain healthy metabolism. In order to make decisions between actions leading to such disparate outcomes, we hypothesize the brain must first represent value for different types of decision options separately. Then, this information must be converted into a common, outcome-independent currency in which the value of potential actions can be directly compared prior to executing the most desirable action. Based on prior electrophysiological and neuroimaging evidence, we further hypothesize that distinct regions of the striatum contribute differentially to the stages of this process. To test these hypotheses, we recorded the activity of striatal neurons in male rhesus macaques while they performed a passive visual conditioning task with fluid or social image outcomes and a pay-per-view task in which decisions are based on both fluid and social image outcomes. Preliminary results support our hypotheses. We observed three classes of outcome related neurons: those encoding either social or fluid outcome independently, and neurons encoding both. These classes were differentially distributed across the ventromedial to dorsolateral extent of the striatum.

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# Visual Attention Drives the Construction and Comparison of Values in Simple Economic Choice

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Binary Choice between pairs of familiar consumption items is one of the simplest forms of economic choice. Economic and psychological models of decision-making assume that the brain makes these choices by first computing a value for both items and then comparing the values to select the best option. The exact processes used to carry out these operations are unknown. We propose a new model of how the brain makes binary choices. The model is a variant of the race-to-barrier models of perceptual decision-making with an important modification: visual attention guides the path of integration of the value signal. The model makes several novel stark predictions about the relationship between visual attention and choices, and about the performance of the decision-making process. Among others, it predicts that there is a first-fixation bias (the first seen item is more likely to be chosen), an exposure bias (items seen longer are more likely to be chosen), and a left-bias (for Westerners, items placed on the left visual field are more likely to be chosen). We test the critical assumptions of the model, as well as its predictions, using eye-tracking in a real choice task in which hungry subjects choose between snacks. The stimuli are presented on the screen using high-resolution pictures of the food. We find support for the key components of the model as well as for all of the decision-making biases listed above.

## **Neural representation of value in the absence of choice**

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Previous studies have shown that activity in the medial prefrontal cortex (MPFC) is correlated with the value of an item when a subject is making a choice. Does activity in the MPFC also encode value when there is no choice being made? We hypothesize that the same neural circuits are involved in choice and non-choice valuation. To test this hypothesis we measured brain activity in the MPFC to items passively viewed while inside the scanner to predict choices made between those items outside the scanner.

We scanned 7 subjects and used fMRI to measure the BOLD signal while subjects passively viewed images of 20 different items. The items, which all had a commercial value of about \$20, consisted of DVDs, CDs, books, posters, stationery and lotteries. On each of 440 trials, subjects were presented with an image of an item for 2 s, followed by an 8 s fixation period. Subjects were instructed to think about how much an item was worth to them in a dollar amount when they saw the image. On 20 random trials, subjects had 1.5 s to choose between an item and an amount of money. They were told that at the end of the experiment, one of these trials would be randomly selected and the subject would receive their choice. Immediately following the scan, subjects made choices between all possible pairs of the items they had seen while inside the scanner. They were told that one behavioral choice trial would be randomly selected and they would receive whichever item they chose on that trial.

We sampled activation from a region of interest (ROI) in the MPFC that showed higher activation to winning \$2 compared to losing \$2 in a separate localizer task. We measured the response in the ROI to each item, excluding the 20 choice trials, and created a “neural preference ranking” from this signal. We found that we could predict subjects’ choices with an average of 70% accuracy from the neural preference rankings measured in the MPFC. This suggests that activity in the MPFC represents the value of an item whether or not an actual choice is being made.

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# Neurally Dissociating Valuative and Non-Valuative Contingency Learning

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Action-outcome models of contingency learning have been shown to be highly predictive of many decision-making behaviors across a wide range of species. However, there exist numerous behaviors that are not currently explained by such models, such as satiety, where the valuation of a physical effect changes over time, and observational learning, in which the observer gains information about the physical effects of an action without full access to its value. We suggest that dissociating the outcome into two independent components – the physical **Effect (non-valuative component)** and the **Valuation** – will facilitate future investigations into the neural basis of valuation, goal-directed behavior, and decision making.

To identify brain regions that are involved in the learning of valuative and non-valuative contingencies, independently, we developed a novel reward-learning task. Subjects performed a two-alternative forced-choice task in which both the mappings of actions (button presses) to effects (visual object presented) and the mappings of actions to values (how much money they collected) were independently changed. Different versions of this task were employed across subjects to contrast the learning of different types of effects (spatial v. identity), control the behavioral relevance of the contingency shifts, and facilitate isolation of neural components engaging in general action-effect learning.

While subjects were engaged in these tasks, we collected functional magnetic resonance imaging (fMRI) data using an inverse spiral pulse sequence in a 4T scanner. We queried our neural data through the FSL 4.0 GLM. Major model factors were the dissociable timing of different learning event types and the reward prediction error at each learning event. A major question we will address is how brain areas previously shown to be engaged in valuative contingency learning respond during non-valuative contingency learning.

Behaviorally within our tasks, subjects used the same decision-making criteria or strategies post effect or value changes, i.e., subjects engaged in the same task across different contingency change types. Neurally, we find common and differential neural activations by contingency change type. Our analyses will focus on striatal and frontal areas, which have previously been suggested to be involved in processing valuative contingency changes.

## **What you do know can hurt you:**

### **Environmental state cues in a dynamic decision-making task**

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Traditionally, computational models of reinforcement learning tasks (e.g. the  $n$ -arm bandit) utilize decision rules that use expected values of actions as inputs. In these models, the reward history for each action informs expected action values. We propose two distinct and complementary systems for action valuation that provide input to the decision process: one valuation system that is driven by expectations of reward and another system driven by changes in environmental state cues. In an experiment investigating the use of these action valuation systems, participants made repeated selections in a two-alternative forced choice task in which the rewards associated with each action varied depending on recent response history. In this task, optimal responding is defined by maximization of total overall reward. In one condition, the reward schedules were structured so that following state cues would lead to optimal responding, while in another condition, the reward schedules were structured so that optimal responding required following only reward expectancies. One-half participants were also presented with an environmental state cue that reflected recent response history and predicted immediate reward.

We found that in the absence of state cues, participants' response patterns reflected the use of an action valuation system driven by reward expectancy. Conversely, in the presence of state cues, response patterns reflected the use of an action valuation system driven by environmental state changes. Additionally, we analyzed the data by fitting reinforcement learning models to each participant, parametrizing the degree to which the two action valuation systems guided the model's decision rule. The results suggest that the use of the two action valuation systems is flexible and is governed by the properties of the task environment.

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**Aversive goal values are negatively encoded in the medial orbitofrontal cortex at the time of decision-making**

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An essential part of goal-directed choice is the assignment of goal values (GV) to different options under consideration at the time of decision-making. This computation is done when choosing among both, appetitive and aversive items. Although dissociations between appetitive and aversive components of value signals have been shown in other domains (e.g., outcome valuation), it is not known if the brain uses a common system to assign GVs in appetitive and aversive situations, or separate ones.

A-priori, there are good behavioral and neuroscientific reasons to take seriously the hypothesis that there might be two goal valuation systems, one for appetitive decisions, and one for aversive ones. First, neural dissociations between appetitive and aversive value signals have been found in the computation of other decision-related signals such as “outcome values”, “anticipatory values”, and “prediction errors”. Second, given that neurons have a limited dynamic range, their ability to make fine distinctions between the values of stimuli would be enhanced if there were dedicated systems for appetitive and aversive valuation. Finally, a sizable amount of behavioral evidence in economics and psychology suggests that the valuation functions in the appetitive domain (gains) have different properties from those in the aversive domain (losses).

In this study we used human fMRI to look for areas that might encode for aversive goal values. In particular, we scanned satiated subjects' brains (N=19) using fMRI while they repeatedly placed real bids for the right to avoid eating different disliked foods (e.g. baby foods, canned meat) in a Becker-DeGroot-Marshak (BDM) auction. A key feature of the design was that the bids entered by the subjects generated good measures of the aversive goal values in every trial. We could then use the bids to look for brain areas that parametrically correlate with the aversive goal values. Another important feature of the design was the presence of two kinds of trials: free bid trials and forced bid trials. These two trial types were identical except that whereas subjects were free to select the amount of their bid in the free trials, they were required to bid a certain amount in the forced trials. This allowed us to separate areas that encode for goal values from areas that encode for other correlated computations (e.g., anticipatory disgust).

We found that activity in the mOFC, the rDLPFC, and parts of the posterior insula were parametrically correlated with a trial-by-trial measure of aversive goal values. Importantly, the nature of the encoding entailed a negative correlation between neural activity and goal values: the more disliked the item, the lower the recorded BOLD signal. Taking advantage of a previous closely related study on the realm of appetitive goal values we were also able to investigate whether the aversive goal values were encoded by the same areas as appetitive values, or by different ones. We found a remarkable degree of overlap between the areas encoding for appetitive and aversive goal values: activity in the bilateral mOFC and the right DLPFC correlated positively with appetitive goal values in the previous study and negatively with aversive goal values in the current study. These results provide neuroscientific evidence for a single goal valuation system that applies both to appetitive stimuli (such as financial gains, liked foods and mates) AND aversive stimuli (such as financial losses, undesirable foods, and dangers).



# **The Presence of Framing Effects in Rats**

Mehwish Saba Bhatti, Jaeseung Jeong

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Prospect theory [1] has now been widely used to explain behavior irrationalities that could not be explained with traditional theories of choice. Reference dependence is one of the major features of human decision making that has been shown to influence choice when decision makers are faced with alternatives. The aim of the study is to find how rats respond to two different alternatives when these alternatives are presented transparently and when framed. We have improved the design of the standard T-maze used for rats by introducing some changes in the T-maze. These changes allowed us not to use any stimuli other than the natural stimuli associated with the chocolate-ball cereals we have used in our experiment as primary reward. The experimental procedure is adapted [2] and necessary changes have been introduced for rats. Our results suggest that for a very strict budget of only 7 trials the rats can differentiate between the two different alternatives presented to them as two different amounts of food. We have also showed that when the alternative as framed as a choice between two sure payoffs of the same magnitude but difference in the amount of reward actually presented for that alternative; rats exhibit reference dependent behavior by avoiding the arm that frames loss. We conclude on our results that rats are also sensitive to how alternatives are presented to them. Our results also show that rats try to maximize their outcomes not only on their final states but also on the basis of whether outcomes are presented as loss or gain from a reference point.

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## Taste-independent reward-related representation in the insular cortex

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The insula represents rewarding stimuli but is undetermined if these are not mere primary chemosensory responses. Here we tested the insula's participation in the development of preferences for sucrose in sweet-blind *Trpm5*<sup>-/-</sup> mice. We show that sucrose consumption induced *c-fos* expression in the dorsal gustatory insula and that, as taste-independent preferences for sucrose developed, neuronal adaptations occurred in this area, in terms of changes in spike distribution, population activity levels and single-neuron stimulus-specificity. Furthermore, bilateral insular lesions including the gustatory cortex abolished the development of conditioned preferences for sucrose. Thus, cortical gustatory regions have a role in processing food reward that is not limited to chemosensory processing.

# Friday, September 26, 2008

## *Abstracts for Afternoon Session*

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### **Individual and Lifespan Differences**

1:45 – 2:15 pm	Gregory R. Samanez-Larkin	Financial decision making across the adult life span
2:20 – 2:50 pm	Julian Jamison	The development of preferences in rat pups
2:55 – 3:25 pm	Bernd Weber	Combining panel data and genetics – proof of principle and first results
3:30 – 4:00 pm	Todd Hare	Neural mechanisms of self-control in decision-making

### ***Kokopelli Parlor II***

Gregory R. Samanez Larkin, Camelia M. Kuhnen, Brian Knutson
Julian Jamison, Kat Saxton, Peter Aungle, Darlene Francis
Bernd Weber, Jurgen Schupp, Martin Reuter, Christian Montag, Nico Siegel, Thomas Dohmen, Uwe Sunde, David Huffmann, Gert Wagner, Armin Falk
Todd A. Hare, Colin F. Camerer, Antonio Rangel

# Financial Decision Making Across the Adult Life Span

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As the proportion of older adults continues to grow rapidly here in the US and across the globe, aging adults may be required to make increasingly more independent health-related and financial decisions. Thus, it is increasingly imperative to better understand the impact of age-related psychological changes on decision making. Although preferences, goals, and emotions heavily influence everyday choices, many decisions (such as choosing a stock in which to invest) involve high level cognitive processing [1-2]. A large body of work reveals a preservation of the processing of emotional stimuli, but a steady decline in cognitive processing capacity over the adult life span [3]. Even highly affective decisions may be overwhelmed by cognitive demands. In the present study, we used an incentive-compatible investment task [4] to assess age differences in risky financial decision making in a community-recruited, representative, adult life span sample. The present investment task requires the dynamic assessment of both reward value and risk. Prior research has demonstrated that the both value and risk learning rely on fronto-striatal networks in the brain. Behavioral results reveal that older adults make more errors when making financial decisions. However, these errors are not due to excessive risk aversion, as stereotypes might suggest, but rather are the result of incorrect reward predictions. The relationship between age and these errors is mediated by performance on the Halstead-Reitan Trail-Making Test, a neuropsychological measure associated with fronto-striatal dopamine function [5]. Neuroimaging analyses reveal that anticipatory BOLD signal activation in the nucleus accumbens predicts these mistakes. The present results suggest that it is not the absence of a ventral striatal signal with increasing age, but the presence of incorrect reward predictions in the nucleus accumbens that contribute to the selection of losing stocks (the assets in the task with an increasingly negative expected value over time). The findings have important implications for financial investing over the life course.

## Acknowledgements

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# The Development of Preferences in Rat Pups

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Standard economic theory takes individual preferences as given and fixed over the course of the lifetime. It is not always clear where preferences come from (genes, environment, active learning, imitation, etc.) nor by when in time they are implicitly assumed to be fixed: birth? age 18? Here we take an empirical approach to one dimension of this question, using rats in part because their course of development is feasible to study within a reasonable time frame. In particular, we consider the effect of stressing pregnant females on the time and risk preferences of their offspring. [Many different stressors, such as temperature and caloric disruption, can be used. For simplicity and congruence with the literature, we chose to use restraint – the subjects are rendered immobile for 30 minutes per day, which does no direct physical harm but is extremely distressing to them.]

In our experiment, pregnant females were first randomized to treatment (stress) or control. In theory, we could then also have randomized their pups (either before or after weaning) as to which mother raised them. This would allow any differential outcomes to be identified as occurring during gestation vs. being induced after birth. However, because this was only an initial investigation, and because in their natural environment the two effects are [almost] always confounded, we left all pups with their mothers. At ‘adolescence’ (roughly 30-40 days), the pups were trained and then tested on various measures of risk and time preference, using food as an incentivizing reward. For example, they discovered via forced choice that one arm of a T-maze led to a safe immediate reward and the other arm led to an uncertain (or, in the time task, a certain but delayed) reward. They were then allowed to choose which arm they preferred in a sequence of future free choice trials.

One can imagine two possible effects of a pup ‘learning’ in utero that the external environment is more difficult than average: either taking fewer risks (because the situation is harsher), or taking more risks (because the chances of survival are lower and hence it is necessary to be further out toward the tail of the distribution). In a range of tasks, especially concerning behavior when confronted with unknown risky environments (e.g. exploring an open area with food available but permeated with fox scent; or the number of head pokes when evaluating an elevated maze), we find evidence for the latter interpretation. That is, pups of the stressed mothers were more risk-taking ( $p < 0.05$  on multiple tasks). We found no statistically significant differences in time preference / impulsivity, although the treatment group was on the whole more likely to choose the immediate (smaller) reward.

Finally, one additional advantage of using rats as subjects is that we can study anatomical brain differences (post mortem) between the treatment and control groups. This analysis is currently ongoing, but initial results are intriguing. Using autoradiography techniques, we find that the prenatally stressed group exhibits significantly higher levels of serotonin transporter binding sites in the amygdala ( $p = 0.01$ ) and especially in the hippocampus ( $p < 0.0001$ ). No differences were found in dopamine transporter binding.

We believe that an approach such as this one yields natural, if speculative, implications for human behavior, both at the level of individual development and of social policy. For instance, understanding the intergenerational transfer of socioeconomic or racial stress is highly relevant for the role and scope of present-day interventions. In particular, it may not be the case that simply providing an even playing field from birth onward is sufficient to serve the goals of equity.

## Combining panel data and genetics – proof of principle and first results

Bernd Weber<sup>1,2</sup>, Jürgen Schupp<sup>3,4</sup>, Martin Reuter<sup>5</sup>, Christian Montag<sup>5</sup>, Nico Siegel<sup>6</sup>, Thomas Dohmen<sup>7</sup>, Uwe Sunde<sup>8</sup>, David Huffmann<sup>9</sup>, Gert Wagner<sup>3,10</sup>, Armin Falk<sup>11</sup>

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The combined analysis of reliable and valid behavioral phenotypes and genetic information allows us to better understand the influence of genetic polymorphisms on individual personality traits and social behavior. The incorporation of genetic material into a representative longitudinal social science survey is performed for the first time in Germany and has also worldwide been performed very sparsely, if at all.

We used the third wave of a special sample of the German socioeconomic panel (SOEP) which was drawn to test innovative measurements to pilot our method and acquire genetic material to analyze the relationship between genetic polymorphisms in important neurotransmitter systems and behavioral traits. We finally obtained sufficient genetic material from 220 subjects (male: 101; age range: 20-87; mean age: 51±17 years). These subjects participated in the “innovation sample” of the SOEP since 2005 and a second wave in 2007, providing us with information on a wide range of socioeconomic status variables, personality traits, health-related habits and behavior in economic experiments. The great advantage of a longitudinal study is that the repeated measurements of personal characteristics provide a more reliable measurement of the phenotypes than a cross-section “snapshot measure”. In addition, information on persons who did not agree to deliver their genetic material for this study is available to investigate factors influencing the selection procedure and a possible selection bias due to panel attrition.

First genetic polymorphisms with hypothesized impact on behavioral traits have been analyzed and show genotype distributions which are in line with previous population based studies (e.g. *COMT Val158Met* polymorphism: Val/Val:n=48; Val/Met:n=103; Met/Met:n=56; and do not differ from the Hardy-Weinberg equilibrium:  $\chi^2=0.0023$ , n.s.).

Preliminary results show expected relations to survey data, as an association of *patience* with the *DRD2-Taq Ia polymorphism*, with A1-allele carriers reporting significantly higher subjective patience in comparison to non-A1-allele-carriers ( $p<0.01$ ) or of the *COMT Val158Met* polymorphism with smoking status: The prevalence of smokers dependent on the genotype is: Val/Val: 37.5%, Val/Met: 30.1%, Met/Met: 17.9% ( $p<0.05$ ).

This study shows the suitability of the combination of survey data with the acquisition of “biomarkers”, especially genetic material. The sample of 220 subjects will allow us to investigate in more detail the influence of a variety of genetic polymorphisms on individual differences in behavior.

# **Neural mechanisms of self-control in decision-making.**

Todd A. Hare, Colin F. Camerer, and Antonio Rangel

Humanities and Social Sciences, California Institute of Technology

Self-control problems in value-based decision-making are at the core of a large number of social and public policy problems, and play an important role in diseases and public health concerns such as addiction and obesity. Despite decades of research, we still lack answers to many basic questions regarding self-control and decision-making. For example, it is unknown what is it about the brain's decision-making circuitry that leads to temptation or how self-control is implemented to override this temptation.

To address these questions, we used fMRI to examine the neural correlates of self-control during a 'real life' decision-making task. We recruited individuals who were dieting to lose weight and first had them rate a variety of food items for both their taste and health values. After rating the food items, the subjects decided whether or not to eat each of the food items at the end of the experiment. At the end of the experiment, one decision trial was randomly selected and the subject's choice on that trial was implemented. Individuals who were not actively monitoring their diet were also included as a comparison group.

Behavioral analysis of the subjects' choices confirmed that the majority of the dieting subjects exhibited self-control (i.e. choose not to eat items they ranked as unhealthy). A small number of dieting subjects failed to exhibit self-control and were thus included with the comparison group that did not exhibit self-control during the decision-making phase.

The imaging results showed that across both groups activity in the mOFC, a region previously shown to be involved in the encoding of appetitive goal values, was positively correlated with a stronger desire to eat the food items. At the time of decision-making, activity in mOFC for the non-self-controlling subjects was correlated with their taste ratings, but not their health ratings consistent with their behavioral choices. Medial OFC activity also increased with the decision weight in the self-control group. However, subjects in the self-control group made decisions based on the healthiness of the foods, and showed mOFC activity that reflected both health and taste ratings in the decision session. In addition, the self-control group showed greater activity than the non-self-control group in the left lateral prefrontal cortex on trials where self-control was exercised. An analysis of psychophysiological interactions indicated that lateral prefrontal regions might modulate activity in mOFC. These results suggest that lateral prefrontal regions influence mOFC value computations during the exertion of self-control in decision-making. Furthermore, differences in self-regulatory abilities across individuals might be due to differences in the ability to modulate mOFC value computations.

## **Acknowledgements**

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**Poster Session II: Friday 4:05pm – 5:45pm**

#	Section Topic	Title	Authors
1	Choice	Temporal discounting elicits a distributed network of mesolimbic and lateral cortical brain regions, which predict choice for future rewards.	Kacey Ballard, Brian Knutson
2	Choice	Real versus hypothetical rewards and gains versus losses: Investigation of the behavioral and neural differences in delay discounting	Warren K. Bickel, Jeffery A. Pitcock, Richard Yi, Edgardo J. Angtuaco
3	Choice	Activation likelihood estimate meta-analysis of monetary incentive delay (MID) task findings	Stephanie Greer and Brian Knutson
4	Choice	Fast versus accurate value-based choices involve different computational processes	Milica Milosavljevic, Alexander Huth, Antonio Rangel, Christof Koch
5	Choice	Neural signatures of choice-overload and choice set-value in the human brain.	Elena Reutskaja, Colin Camerer, Rosemarie Nagel, Richard Andersen, Axel Lindner
6	Choice	Charging neutral stimuli with motivational properties reveals mechanisms that underlie choice	Jaspinder Sagoo, Roger Carpenter
7	Choice	Neural predictors of healthy and unhealthy food choice	Jyrki Suomala, Markus Kivikangas, Jussi Numminen
8	Social	Emulations, creativity, and the brain	Jyrki Suomala
9	Social	The evolution of cooperation: Helping behavior in capuchin monkeys ( <i>Cebus apella</i> )	Jennifer L. Barnes, Laurie R. Santos
10	Social	A Neuroeconomic analysis of herding in finance	C. Burke, P. Tobler, W. Schultz and M. Baddeley
11	Social	Anonymous and public generosity: Neural evidence of different motives.	Benjamin Bushong, William T. Harbaugh, Ulrich Mayr
12	Social	Agent-based network model for the public goods game	Dongil Chung, Kyongsik Yun, Jaeseung Jeong
13	Social	Neural substrates of free-riding and cooperation during the standard public goods game	Dongil Chung, Jaeseung Jeong
14	Social	The contribution of implicit race bias to estimations of trustworthiness	Damian Stanley, Peter Sokol-Hessner, Michael Perino, Mahzarin Banaji, Liz Phelps
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22	Methods	Salvaging orbito-frontal cortex: improved fMRI image reconstruction for neuroeconomics	Eric J. DeWitt, Robb B. Rutledge, Damian Stanley, Paul W. Glimcher, Souheil J. Inati
23	Methods	Interpretable classifiers for fMRI improve prediction of purchases	Logan Grosenick, Stephanie Greer, Jonathan Taylor, Brian Knutson
24	Methods	Neural computations underlying hypothetical vs. real decision making	Min Jeong Kang, Mickael Camus, Antonio Rangel, Colin Camerer
25	Methods	Virtuous decisions: exemplarity in and out of the laboratory	Michael L. Spezio, Warren Brown, Gregory Peterson, Kevin Reimer, James Van Slyke
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30	NeuroMarketing	Hemispheric processing of metaphors in advertisements	Kristy Vance, Andrew Phillips, Sandra Virtue



# **Temporal discounting elicits a distributed network of mesolimbic and lateral cortical brain regions, which predict choice for future rewards.**

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In “temporal discounting,” individuals prefer smaller immediate rewards to larger delayed rewards, implying a trade-off between the magnitude and delay of future rewards. Prior functional magnetic resonance imaging (fMRI) studies have documented greater mesolimbic activation when people consider choices involving immediate rewards versus future rewards [1], and have also related mesolimbic activation to the discounted value of future rewards [2]. However, researchers have not yet determined how neural responses to the magnitude and delay of rewards are related to subsequent choice or individual differences in discounting behavior. We scanned 16 subjects (8 female) with fMRI (GE 1.5 T scanner, voxel size = 4 mm cubic, TR = 2000 msec, spiral in/out pulse sequence) as they engaged in a temporal-discounting task. A novel task design separated presentation of information related to the immediate reward, magnitude of the future reward, delay of the future reward, and choice. We found that while ventral striatal (including the nucleus accumbens, NAcc) and mesial prefrontal cortical (MPFC) activation positively correlated the magnitude of future rewards, dorsolateral prefrontal cortex (DLPFC) and posterior parietal cortex (PPC) activation negatively correlated with the delay of future rewards. Further, more impulsive individuals showed decreased NAcc sensitivity to the magnitude of future rewards and increased MPFC, DLPFC, and PPC sensitivity to the delay of future rewards. These findings indicate that mesolimbic dopamine regions show greater sensitivity to future reward magnitude while lateral cortical regions show greater sensitivity to future reward delay, potentially reconciling different accounts of the neural basis of temporal discounting.

## **Acknowledgements**

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# Real versus Hypothetical Rewards and Gains versus Losses: Investigation of the Behavioral and Neural Differences in Delay Discounting

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**Objective:** Valuation of future rewards requires consideration of possible fictive outcomes. Whether that valuation involves differential brain activity when those possible outcomes are real or hypothetical is unknown as no imaging study has yet to compare these conditions. This study addresses this gap in knowledge by comparing both the behavioral measures and the neural correlates of intertemporal choice for real and hypothetical money rewards. We also compare the neural correlates and valuation between hypothetical monetary gains and losses, which have been posited to involve different mechanisms. **Method:** A total of 30 adult humans participated in a behavioral and imaging session. In the behavioral session participants were presented choices between immediately available and delayed monetary gains (both a hypothetical and real \$100) and between immediate and delayed monetary loss (hypothetical \$100) to determine their indifference points. In the imaging session participants were presented with a selection of the same choices from the three discounting procedures inside a Siemens 3T scanner while whole brain echo planar images were acquired. In the real money gains condition, one of the choices made by the participant was randomly selected and their choice provided for both the behavioral and imaging sessions. **Results:** Repeated measures ANOVA of estimated levels of within-subject discounting showed no significant difference between conditions. Random effects imaging results of each condition independently were comparable to findings of previous imaging studies of delay discounting and included areas both limbic in nature as well as areas associated with executive functioning. These findings suggest that both limbic and relevant cortex area can be observed in hypothetical tasks. Paired *t* test results between the gains conditions (real versus hypothetical) and hypothetical conditions (gains versus losses) revealed limited numbers of voxels in regions not typically found to be associated with this deliberative process. **Conclusion:** Results from the independent random effects analysis of each condition produced robust activations in both limbic and executive functioning areas previously noted in published neuroimaging studies across all three discounting conditions. These findings challenge the notion of greater limbic response to real reward outcomes compared to hypothetical ones based upon a hedonic reaction to the former in contrast to the latter. Lack of significant signal change comparing gains to losses may indicate a generalization of the deliberative process of discounting without regard to a reward or loss outcome.

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## **Activation likelihood estimate meta-analysis of monetary incentive delay (MID) task findings**

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The monetary incentive delay (MID) task was specifically designed to isolate anticipation and outcome phases of processing both gain and loss incentives (Knutson et al., 2000). Over the past decade, several investigators have combined the MID task with event-related fMRI to probe different aspects of incentive processing. We conducted an activation likelihood estimate (ALE) meta-analysis (Laird et al., 2005) of twenty studies that employed the MID task (or similar tasks) to characterize regions consistently activated by gain versus nongain anticipation, gain versus nongain outcomes, loss versus nonloss anticipation, and loss versus nonloss outcomes. The difference between the gain anticipation and loss anticipation contrasts revealed increased activation of the nucleus accumbens (NAcc) and decreased activation in some regions of the anterior insula (but increases in others). The difference between the gain anticipation and gain outcome contrasts also revealed increased activation of the NAcc but decreased activation of the mesial prefrontal cortex (MPFC). These findings are consistent with initial reports that gain anticipation elicits more NAcc activation than loss anticipation, but that gain outcomes elicit more MPFC activation than gain anticipation. The results also suggest neural markers for anticipatory affect.

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## **Fast versus Accurate Value-Based Choices Involve Different Computational Processes**

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Recently, theoretical models from economics have been combined with experimental findings and techniques from psychology and neurobiology to better understand the computational processes used to make value-based choices. The literature on perceptual decision making has proposed and tested a class of integrator/race-to-barrier models that fit well the psychometric and neural data in this class of tasks. It has yet to be determined whether the models of perceptual decision making can also account for the psychometric data of simple value-based choice. Two experiments were conducted to examine this possibility. Both experiments utilized a 2-alternative-forced-choice task, where participant were asked to make a real choice between two food items by making a saccade toward the preferred item. In one experiment ('fast choices') subjects were asked to make a decision as quickly as possible. In the other ('slow choices') subjects were asked to maximize the accuracy of their choices. The results indicate that the standard diffusion models account well for the psychometric data in the 'slow choice' case, where accuracy is emphasized, but that a new version of the model, which is developed in the current paper, is required to account for the psychometric data in the case of 'fast choices', where speed is emphasized.

## Neural signatures of choice-overload and choice set-value in the human brain.

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Whereas classical economics argues that more choice is always beneficial, recent studies indicate that large choice sets can be demotivating and lead to "choice paralysis"[2, 3]. We investigated the neural bases of these phenomena by providing twenty subjects with increasing numbers of choice alternatives (N=6, 12 or 24 items) while measuring time-resolved brain activity using event-related fMRI. Subjects faced different-sized choice sets of landscape photographs from which they had to choose their most preferred one. One of these choices was then used to produce a consumer product with an imprint of the respective photograph (e.g. a mug, a T-shirt etc.). Subjects generally rated the smaller sets as having too few items and the larger sets as having too many, i.e. subjective value of the choice set was an inverted U-shaped function of the number of choice alternatives. All said choosing from the larger sets was more difficult. Preparatory fMRI-activity (i.e. activity which preceded the actual choice) increased with such perceived choice difficulty in the anterior cingulate and dorsal premotor cortex. Areas exhibiting fMRI-activity which was rather correlated with the subjective value of the choice set were mapped within posterior parietal cortex, which is known to respond in monkeys and humans to value [5] and choice behavior [1, 4]. Yet, large choice sets can also be pleasing when they include a highly-preferred item. This was implied by increased levels of fMRI-activity within the striatum in comparison to trials where all the available alternatives were similarly preferred. This pattern of fMRI-activity provides the first insight into how the brain combines the quality of choices from a set with the difficulty of making these choices into a signal that can be interpreted as the value of a choice set. Specifically, posterior parietal cortex seems to represent such subjective set-value and thus might play a major role in decision processes.

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# Charging neutral stimuli with motivational properties reveals mechanisms that underly choice

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Reaction time reflects decision time, and recent studies focusing on the stochastic nature of reaction times have revealed much about neural mechanisms that underpin human decisions. One model that has proved successful in this area is LATER<sup>1</sup>. Derived from Bayesian principles, it accurately explains latency distributions under the broadest range of conditions such as variations in expectation, urgency, information supply, and competitive racing<sup>2</sup>.

And yet, notwithstanding its scope, what LATER currently lacks is a motivational component: its decisions are based on the probability of the hypotheses rather than on their expected values. Nevertheless, recent neurophysiological experiments have demonstrated that the effects of reward on latency distribution can be related to corresponding alterations in LATER parameters.

However, a problem with many such experiments is that if such effects are studied using stimuli that are directly motivational, it is difficult to avoid the confounding effects of low-level visual attributes such as luminance and contrast, that are known to generate powerful effects on latency<sup>3</sup>. Here, we employ a novel method of indirect association to demonstrate the effect of varying motivational properties by measuring targets that are inherently latency neutral. We show that reaction times shorten towards stimuli that are associated with increased reward, the changes in the distributions indicating that rewards alter the rate of rise of the LATER decision signal, which may thus represent expected utility. Additionally, we reveal a well-defined pattern of asymmetric errors, attributable to competition between racing LATER units.

Neuroeconomists analyse choice behaviour by performing experiments that involve evaluating alternatives in perceptual and cognitive tasks. More recent techniques have made it possible to correlate abstract models of information processing with neuronal data extracted from human imaging and animal recordings. We conclude that loading neutral stimuli with motivational properties can significantly enhance investigations which rely on the comparison of targets carrying intrinsically dissimilar values.

## Acknowledgements

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# NEURAL PREDICTORS OF HEALTHY AND UNHEALTHY FOOD CHOICE

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Risk behavior to food, is an enormous challenge and cost for the public health. For example in Finland, men's and women's obesity has increased with 75% and 34% during the last two decades and currently only 33% and 48% of men and women are normal weights, respectively. Consequently there is an imminent need for research concentrating to investigate why someone would make a choice of consuming while knowing that this choice will later entail receipt of a negative consequence or outcome, and in the most severe scale, why do people get addicted to food and other stimulants?

However, despite of the importance of knowing what causes this risk behavior in eating, it is not enough to investigate the reasons and backgrounds leading to malign behavior. As it is not enough to develop an efficient way to prevent global warming if nobody employs it, similarly, it is extremely important to know how to correctly communicate to the people the information which promotes national health. Only after knowing the reasons and communicating the effectively to citizens generates the true possibility to increase national health.

Insights from the field of neuroeconomics allow us to understand why people behave injuriously, identify potential neurophysiological mechanisms that result in obese behavior, and give us the required tools for communicating the desired message to them. The phenomenon of food consumption is described from the viewpoints of temporal discounting, the framing effect and the Somatic Making Hypothesis. By applying a neurophysiological approach, the study will try to clarify whether subjective goals – i.e. food as a emotionally competent stimuli – inherit the properties of the value function as defined in Prospect Theory.

In order to answer research questions, we modify Knutson et al.'s (2007) SHOP task to address food choice issues, by replacing products with different categories of food pictures that could be presented participants having their brains scanned, and replacing price with nutritional (e.g., number of calories) information. In addition, some of the experiments, gain-framed and lost-framed will be presented. While many fMRI studies have examined how people react to images of food, or while anticipating receiving rewards, it is critical to examine how people decide whether or not to consume when faced with information about the health consequences of that consumption.

In conclusion, this approach to the subject matter are full of promise, and deserve appropriate scientific attention, and by testing of the approach our field may develop both preventative and intervention treatment programs that may lead us to more fully resolve this serious public health problem. . In the fall of 2008 the presented theory will be tested in a fMRI study at AMI center in Helsinki School of Technology.

# Emulations, Creativity, and the Brain

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A fundamental problem in neuroeconomics is understanding the relationship between the brain and behaviour. To solve this fundamental question, we have to begin by understanding the goals or functions of human behaviour [1, 2]. One of the most essential functions of the human brain is to produce counterfactual representations of events, facts and social states. The human brain's ability to produce counterfactuals is probably a source of discovery and creativity. This paper focuses on the brain's role in creativity, describing how the human brain forms creative representations, i.e. counterfactuals. The description is based on the neurophysiological models of Grush [3], Bechara [4] and Montague [5].

Grush [3] demonstrates that creative representations are based on the brain's capability to emulate future events. This emulation process does not consist of expectation based on a linear interpretation of the individual's past experiences; on the contrary, it looks for new opportunities and alternatives.

Bechara [4] argues that the brain forms representations of both the body and the environment. The interaction between these two types of representation in the brain is a source for the "as-if loop" neural pathway, which generates new alternatives for future events. The as-if loop is formed in the amygdala, hippocampus and ventromedial prefrontal cortex.

Montague [5] shows that on a neurophysiological level, after decision-making, the brain produces fictive error signals related to counterfactuals. Based on these fictive signals, we evaluate the validity of our decisions spontaneously. After this process, we feel happiness or regret based on our personal experience of the fictive alternative. This fictive signalling process is a source of creativity and discovery in the human brain. Fictive signals have a neural correlation in the ventral caudate.

The common feature of the previously described models is the idea that creativity is based on a subjective, personal experience of the subject's own future possibilities. Counterfactual thinking is probably a source of human creativity. Glimcher [3] argues that a bridge can be built between the brain and behaviour by adding the concepts of bayesian statistics and irreducible uncertainty to classic game theory. However, the problem with this game theoretical model is that it cannot explain how the creative human brain can produce totally new "games" (cultural artefacts, new scientific theories, innovations), in which the probabilities of gain and cost are completely uncertain, and where the players of the new game are unknown. New empirical and theoretical evidence of the human brain's simulation mechanism is needed to produce a more realistic bridge between the brain and behaviour.

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# The Evolution of Cooperation: Helping Behavior in Capuchin Monkeys (*Cebus apella*)

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Altruism and cooperative behavior, along with spite, play a significant role in human interactions and decision-making, but are often considered an evolutionary puzzle [1]. While some researchers have claimed that helping others without regard to oneself is a uniquely human behavior [2, 3], others have argued that there may be some non-human species capable of showing altruistic regard for others [4]. Here, we extend this body of work to a New World monkey species which has been studied extensively in the study of fairness and inequity aversion [e.g. 5]. While capuchins have also been studied in behavioral economic paradigms and have been shown to have similar behavioral biases to humans [6], relatively little work has examined their cooperative behavior, and specifically, whether or not they will behave altruistically toward human experimenters, and the situations under which they will do so. Here, in two experiments, we examine the circumstances under which capuchins will hand an out-of-reach object to a human experimenter who is either reaching or not reaching for it, and either offering or not offering a reward in exchange for the object. In Experiment 1, when the helping behavior was relatively costly, few capuchins demonstrated any helping behavior, and those who did only did so in the presence of a reward. In Experiment 2, when the helping behavior was less costly, capuchins demonstrated high levels of helping across conditions, but their performance appeared to be driven most significantly by the presence or absence of a reward. Further, capuchins only showed regard for the preferences and goals of others in absence of potential personal gain themselves, suggesting that while they are capable of altruistic behavior, they nonetheless seem to prioritize their own utility over that of the individual they are helping.

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**Title: A Neuroeconomic Analysis of Herding in Finance**

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The influence of others on human choice behaviour is a widely observable phenomenon that results in aggregate behaviour such as the adoption of consumer preferences, political beliefs and investment strategies. Models that explain aggregate behaviour as an outcome of Bayesian updating, or as an action in a social context may impact intrinsic utility, have been developed by economists within the framework of neoclassical assumptions such as utility maximization and selfishness. However, the impact of social information on the neural mechanisms underlying individual decision making has largely been unexplored. We designed a behavioral task which required subjects to view different risky assets followed by social information in the form of previous participants' decisions. They then had to make an investment decision regarding the asset ('adopt'/'reject'). The proportion of invest decisions for each asset class were recorded while varying social information. A repeated measures ANOVA confirmed that preferences differed significantly according to the basic decision parameters of expected value and variance ( $p < 0.05$ ). Subjects preferred assets with higher expected values and lower variance of returns. The proportion of 'adopt' decisions for each asset class was also significantly influenced by social information ( $p < 0.05$ ), with the probability of an adopt decisions increasing when previous participants adopted. We hypothesized that the social context presented to a subject can modulate decision-parameter related activity in the brain. Known reward-processing areas such as the striatum, anterior cingulate and orbitofrontal cortex were investigated as *a priori* regions of interest. Using insights from behavioral economics, social psychology and neuroscience the results have implications for the current understanding of how social information influences individual decision-making.

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# Public versus Private Generosity: Neural Evidence for Different Motives

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According to the 12<sup>th</sup> century Rabbi Maimonides, the "duty of charity" is better fulfilled by anonymous than by public donations. However, people tend to be more generous in public than in private giving situations. Theoretically, private giving should be motivated mostly by the utility directly derived from increases in the public good (i.e., the charity). In contrast, public giving is potentially more complex, as pure altruism may be complemented, or even completely dominated by prestige or signaling motives.

Harbaugh, Mayr, and Burghart<sup>1</sup> implemented a strictly anonymous giving situation in form of a dictator game in which subjects could either accept or reject costly transfers to the charity. The design included "pure, mandatory transfers" of money to the subject or to the charity. Participants' rate of voluntary giving could be predicted independently by the reward-related neural responses to these two types of transfers: The rate of giving was negatively correlated with the response to money for oneself and positively with the response to money for the charity. This result suggests that charitable decisions are based on a rational cost-benefit analysis that integrates both self interest and regard for others (pure altruism).

In the current study we include both private and public giving situations. Giving in public requires consideration of the observers and what they may think about one's actions. Thus, we expect that neural areas associated with "theory of mind", such as para-cingulate cortex, are active in the observed condition and that this activity predicts individual's increased public giving. However, the more important question is whether the same basic cost-benefit model as used in Harbaugh et al. can account for the difference between private and observed giving. In this case, any increase in rate of giving in the observed condition should be accompanied by a corresponding increase in reward-area activity.

Non-student participants ( $N=21$ ) were initially endowed with \$100 and then were scanned while exposed to transfers between \$10 to \$40, either to their own account or to various charities. As in Harbaugh et al., we used both voluntary, costly transfers, as well as pure, mandatory transfers that involved either only the subject or only the charities. All pure, mandatory transfers were anonymous. However, half of the voluntary transfers (including subject responses) were observed by a male and a female confederate via video. The anonymous-observed manipulation was implemented on a trial-by-trial basis and subjects were informed on screen about the status of each trial.

Behavioral results revealed a large overall increase in the rate of accepted donations in the observed (59%) compared to the private (43%) condition,  $t(20)=4.4$ ,  $p<.001$ , as well as substantial individual difference in private/observe difference (from -6% to 56%). Analysis of imaging data is underway.

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# Agent-based Network Model for the Public Goods Game

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The Public goods (PG) game is one of the most commonly used economic games to investigate human cooperation. Empirical behaviors of cooperation and free-riding have been intensively studied, yet the mechanism underlying temporal decision patterns in the PG game is still unclear [1]. The aim of the present study was to investigate if the level of trust and prediction of others' cooperation affect the decision-making patterns in the PG game using human experimental data and an agent-based network model. Thirteen groups which consisted of five healthy male participants played a standard PG game [2] and their cooperation and free-riding behavior was monitored. The PG game consisted of three sessions: session I for the standard design, session II that guarantees to get the money back, and session III that controls the amount of reward the players get to be all same eventually. We found that session I exhibited the lowest cooperation behavior (mean:  $33.1 \pm 22.6\%$ ) among three sessions, and that session II (mean:  $48.8 \pm 19.0\%$ ) and session III (mean:  $75.4 \pm 18.2\%$ ) displayed increased rate of cooperation behavior. Within sessions, the players' cooperation decreased in session I, but increased in session III and oscillated in session II as trials go on for 10 times. To investigate if this cooperation patterns were associated with trust and prediction of others' cooperation, we constructed an agent-based network model that simulated the decision patterns in the PG game. Different from previous models, the model in this study included trust and prediction of others' cooperation, determined by subjective perception of the context, which were updated by the result of the preceding trial. The agent was to cooperate if a decision state activation was larger than the threshold determined by these two factors. Our model was tested within the same game design and the simulated results were compared with human behavioral data. We found that our model successfully reproduced the average cooperation behavior of humans and also the temporal changes in cooperation within and between sessions in the human experiment. This finding suggests that trust and prediction of others' cooperation contribute to the decision-making patterns in the PG game.

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# Neural Substrates of Free-riding and Cooperation

## During the Standard Public Goods Game

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The Public goods (PG) game is an economic game to investigate free-riding and cooperative behaviors of humans. Previous studies have focused on the motivation of cooperative and free-riding behaviors using different PG game designs [1], yet little is known about the neural mechanism underlying the decisions in the game. The aim of the current study was to investigate the neural substrates of cooperation and free-riding decisions. We recorded the electroencephalogram (EEG) from 26 subjects during the performance of the standard PG game [2]. Thirteen groups which consisted of five healthy male participants played the step-level PG game, and the EEG were obtained from two participants in each group simultaneously (i.e., EEG hyper-scanning). Sham recordings were set to the other players to control the conditions. The players' cooperation and free-riding decisions were monitored. EEG source distributions associated with the decisions were estimated using the rotating dipole algorithm with a 500msec window for 10 secs around the decisions and the outcome display. We found that average cooperation rate of the players was  $33.1 \pm 22.6\%$ . Source distribution analysis revealed that the superior temporal gyrus, caudate, posterior cingulate, thalamus, and medial globus pallidus were activated during the decision making for cooperators, while posterior cingulate, precuneus, inferior temporal gyrus, and inferior parietal lobule were significantly activated for free-riders' decision. While posterior cingulate, parahippocampus, putamen, red nucleus, and inferior frontal gyrus were highly activated for cooperators during the outcome display, middle frontal gyrus, putamen, thalamus and posterior cingulate were associated with responses for the outcome. In contrast, the free-riders exhibited active middle temporal gyrus and parahippocampal gyurs initially and the putamen during the outcome display. To our best knowledge, this is the first investigation of temporal brain dynamics during cooperation and free-riding in the PG game. This finding provides with insight into the neural circuit subserving decisions for free-riding and cooperation.

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**The contribution of implicit race bias to estimations of trustworthiness**  
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A crucial component of social-economic interactions is the development of an estimate of whether the other party is to be trusted. In the absence of other information, the final decision to trust can be significantly influenced by social-group membership (Slonim, 2006, Fershtman & Gneezy, 2001). Both trustworthiness estimations (Engel et al, 2007; Winston et al, 2002) and the expression of implicit race bias (Phelps et al, 2000) have been linked to activity in a common neural substrate, the amygdala, a region of the medial temporal lobe involved in emotion and fear learning. We investigated the extent to which trustworthiness ratings of unfamiliar male faces are influenced by implicit race bias.

Observers viewed 291 faces (100 black, 100 white, 91 other) for 1 second each and rated the trustworthiness of the individual in each picture on a scale from 1 to 9 (1 = not-at-all trustworthy, 9 = extremely trustworthy). Immediately afterwards, participants completed a pleasant/unpleasant, black/white Implicit Association Test (IAT) designed to assess the strength of each individual's positive or negative implicit racial bias. Finally, participants completed a series of surveys designed to assess explicit or overt race bias.

We found a strong relationship between an individual's black/white trustworthiness ratings and the magnitude of their black/white implicit bias. For each participant, a black/white trust bias score was calculated by subtracting the mean overall trustworthiness rating for black faces from that for white faces and then normalizing by the standard deviation of all trustworthiness ratings (white, black, and other). Trust bias scores were significantly correlated with implicit bias scores ( $r = 0.58$ ,  $p < 0.01$ ) but not with any explicit measure of race bias. A hierarchical linear regression analysis revealed that a model containing only the explicit measures of bias accounted for 20% of the variance in trust bias scores. Adding the implicit bias scores to the model increased the variance accounted for to 64%, indicating that implicit bias contributes significantly to estimates of trustworthiness. Future work will extend these findings to real economic interactions in a variant of the trust game.

# Reactions to unequal payment are differently modified by medial prefrontal brain regions in women and men

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In a study conducted with male subjects, reward-related brain activity in the ventral striatum was found to increase as the amount of the subject's own reward increased relative to that of another subject [1]. We repeated this experiment with female subjects and additionally obtained comprehensive personality data as well as ratings for the pleasantness of different relative reward levels from all subjects. This allowed us to

- i) test for gender differences in relative reward processing in the brain
- ii) test for associations between brain activity and personality traits across subjects
- iii) test whether self-reported ratings are predictable by brain activity

Results showed that within the ventral striatum, brain reactions to relative rewards are similar in men and women. This confirms our previous results and shows that social comparison plays a major role in reward-related brain activity in women as well. Only in the female subjects, however, we additionally observed an increased activation in the anterior cingulate and the medial prefrontal cortex in situations where a subject's own reward was higher than that of the other subject.

Subjects' pleasantness ratings of different relative reward levels were strongly predicted by a region in the left ventral striatum ( $r = 0.5$ ,  $p < 0.001$ ). Residual variance in pleasantness ratings was significantly explained by activation levels in the medial prefrontal regions that discriminated between female and male subjects ( $r = -0.3$ ,  $p = 0.023$ ).

Taken together these findings suggest that self-reported conscious judgements about social differences are strongly guided by processes in subcortical reward-processing areas. The perceived (or the consciously stated) pleasantness is modified, however, by medial prefrontal regions where higher activations lead to lower pleasantness ratings. This modification is stronger in female than in male subjects indicating stronger social control process in women.

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## **The psychophysiological effects of emotion on decisions with high/low importance**

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Bless, Bohner, and Schwarz (1990) suggested that people have different decision processes in different emotion states. When people are in negative emotion state, they think more analytically, while in positive emotion state they think more heuristically. However, Isen (1993) suggested that not only the emotion state, but also the quality or the importance of the task may influence the decision process. In the present study, the researchers examined how the emotions influenced the decision process when the participants faced decision with different importance. The psychophysiological effects were observed in four different conditions (high importance/positive; high importance/negative; low importance/positive; low importance/negative).

Participants in different importance conditions were instructed differently. In high importance condition, they were instructed that the experiment was commended by a notebook company, their choice and the way to consider the notebook information would be a very important reference to the notebook company. On the other hand, in the low importance condition, the participants were instructed that it was a common psychological experiment. After the instruction, four notebooks would be shown on the computer screen at one time, and participants had to choose one among the four notebooks. During the experiment, the participants listened to different kind of musical excerpts in order to evoke different emotions (happy vs. sad). The musical excerpts to induce happy emotion are: (1) Beethoven : Piano Concerto No.5 in E flat Major Op.73, 'Emperor' : III Rondo – Allegro, (2) Beethoven : Symphony No.7 in A Major, Op.92 : III. Presto; the musical excerpts to induce sad emotion are: (1) Adagio In G Minor, (2) Pathétique (6. Symphonie h-Moll op. 74) Finale: Adagio Lamentoso.

Eighty participants from National Chengchi University, Taipei, Taiwan were recruited. The information of twenty four notebooks was used. On each trial, four of twenty four notebooks were randomly chosen and their detailed information was shown on the computer screen at one time while they were in different condition, and their positions were presented in random order. After the participants decided which notebook they would like to choose, they had to press one bottom to move the information showing phase into the choice phase. During the experiment, the physiological signals (e.g. SCR) were recorded via BIOPAC MP100WS hardware with AcqKnowledge III (v.3.9) software. The sampling rate for all physiological signals was 200 Hz. The brain activity were recorded by NeuroScan from five scalp location: left and right mid-frontal (F3, F4), parietal (P3, P4), and central vertex (Cz).

Results showed that when participants in low importance condition, the skin conductance responses and the alpha band in parietal cortical (P3, P4) before made a decision were more influenced by the emotion state than in high importance condition. That is, the SCR changed a lot between different emotion states in low importance condition, but not in high importance condition. The results suggests that the emotion state may have different effects when participants faced decisions on different importance, which indicates that cognition and emotion have an interaction in the decision making process.

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# Escape from Disgust: Emotion motivates mental and physical avoidance of social targets

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The emotional response elicited by different social targets results in varying behavioral responses in a social exchange. People that are perceived as low in trait warmth and competence have been shown to elicit the basic negative emotion disgust. In American samples, these people tend to be the homeless and drug addicts (Fiske, Cuddy, & Glick, 2002). Our work demonstrates that perceivers spontaneously think less about the minds of these groups, as indicated by a reduction in medial prefrontal cortex activity (MPFC; Harris & Fiske, 2006), and less mental state verb use when describing a day in their lives (Harris, 2007). In addition, the degree of disgust elicited by any person predicts participants estimated likelihood of avoidance (Harris, 2007). These findings are consistent with the function of disgust as an emotion that motivates avoidance and suggests this emotional reaction towards others may not only underlie physical avoidance, but also mental avoidance resulting in dehumanization.

We examined the neural mechanisms underlying social avoidance by allowing participants the opportunity to avoid these social targets or not. Participants were scanned using fMRI while looking at pictures of disgusting targets and social in-groups targets (e.g., college students). Participants were instructed to press a button whenever a colored picture frame appeared around the picture. In the escape condition, the button-press terminated the display of the image, while in the non-escape condition the image remained for two seconds after the button press. We assessed participants' reaction time in each condition and whether or not they could report the avoidance rule after the task. We found that participants generally were faster to press the button during the escape trials, and this effect was greater for the participants who reported learning the avoidance rule. This suggests that participants avoid disgusting targets more quickly when given the opportunity for escape. We also found that activation in the insula decreased and activation in the MPFC increased in the escape condition to disgust pictures. These findings provide initial evidence that when a person's avoidance behavior to dehumanized targets is congruent with the function of disgust, the opportunity for avoidance may diminish responses in brain regions previously linked to disgust (e.g., insula). Future studies will link this avoidance motivation to behavioral responses in economic games to dehumanized social targets.

# Neuroeconomics in Stressed Rats.

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Patterns of decision-making between multiple reward options may be influenced by the qualitative value of each reward, the relative amount of each reward, the likelihood of the reward occurrence, and the degree of difficulty to obtain the reward. Using an automated figure-8 maze [1, 2], we have investigated the effects of stress on decision-making choice behavior in male Sprague-Dawley rats. Animals were trained until they were able to complete 40 laps (trials) in less than 30 minutes. From the center arm of the maze, the rat entered either the right or the left arm to obtain a reward. Afterwards, the animal returned to the center arm, where there was another reward and a new trial began. During initial training, each reward volume was equal (0.04 ml), and the probability of reward on any trial was .8 for each arm of the maze. Under these training parameters, the animals exhibited relatively stable numbers of left and right arm visits. Rats reliably increased their responses to one side of the maze in two conditions: when the reward volume was increased relative to the other reward, and when the probability of one reward was reduced from the initial value. However, given a combined test of volume increase and probability decrease of one reward, rats resumed their initial baseline response pattern, approximately half to each side. After experiencing acute uncontrollable stress (60 min restraint + 60 intermittent tailshocks), rats were significantly impaired in biasing their behavior toward the maze arm providing relatively larger reward. These results indicate that stress impairs decision-making processes in rats.

## Acknowledgments

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## **INFLUENCE OF UNCONSCIOUS EMOTIONS ON FINANCIAL DECISION-MAKING SITUATION**

The rationale behind the study is the economic theories that assume that people choose between alternative courses of action based on a rational evaluation of the consequences. However, the neuroscientific research has demonstrated that emotions are important, if not prerequisite, for all decision making, and therefore also for financial decision making. The very purpose of emotions is to evaluate the significance of the stimulus for an individual to direct his or her behavior by reinstating circumstances that evoke positive emotions and avoiding circumstances that evoke negative emotions. Furthermore, emotions can occur without awareness and interact with, for example, attitudes and preferences, thereby contributing to decision making. This study investigated how unconscious emotions affect financial decision-making in the situation in which the decision must be made fast in an uncertain situation.

Subjects were exposed to images of happy or fearful facial expressions by affective subliminal presenting paradigm while scanned in fMRI. In a control condition, no subliminal images were shown. Images were shown four times per trial (16 ms) followed immediately by a mask. Although the subjects were not aware of the presented images, they induced either positive (i.e., happy facial expressions) or negative (i.e., fearful facial expressions) emotion, concluded from appropriate brain activations. After emotional induction, subjects were asked to make a financial decision in a situation where they did not know the expected value of their decision and had no solid basis for their decision. The results show that images presented outside of awareness elicited brain activation according to their valence. Furthermore, the influence of induced positive and negative emotion on investing probability is discussed.

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Quantifying Expressions of Emotion in Psychological Games:  
Theory, Experiments, and Econometrics

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Recent works in neuroeconomics have emphasized the effects of emotions on social and strategic decision-making. The literature on “psychological games” provides a way to model and quantify these effects, by extending the payoff structure of traditional games to allow players to have preferences over the belief of others. A number of recent theoretical and experimental studies have elegantly shown the utility of this idea in modeling social emotions such as shame and guilt. One weakness of this literature is the relatively impoverished way with which these emotions are measured and quantified. Here we present a new method to quantify facial emotion expression signals players send other players during game play. In particular, we use state of the art facial animation software to allow players to create and send dynamic facial expressions during a game. In addition to being highly emotionally salient, the software records facial action unit movements with high temporal resolution, which allows us to extract emotional functional behavior from data by means of functional data analysis. Quantifying emotions enables us to analyze the impact of such psychological variable on the experiment result, e.g., the efficiency gains of a smile in generating reciprocity.

# The Neural-Like Assumptions and Parameters in the Agent-Based Computational Economic Models

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Recently, the relation between neuroeconomics and agent-based computational economics (ACE) has become an issue concerning the agent-based economics community [1, 2]. Neuroeconomics can interest agent-based economists when they are inquiring for the foundation or the principle of the software-agent design, normally known as agent engineering. It has been shown in many studies that the design of software agents is non-trivial and can determine, in a quite significant way, what will emerge from the respective ACE models. Therefore, it has been questioned for rather a period regarding whether we can sensibly design these software agents, which including both the choice of software agent models (such as reinforcement learning, Gibbs-Boltzmann discrete choice learning, genetic algorithms, genetic programming) and the parameter setting associated with the chosen model (such as risk attitude, intensity of choice, memory [3], attention control, search intensity). In this paper, we shall start a formal inquiry by surveying a large group of agent-based economic models with a focus on examining the models and parameters used to build software agents. We then single out a list of models (assumptions) and parameters which are neural scientific. It is hoped that the present or the future of neuroeconomics can respond accordingly to symbolize collaboration between the two new fields in economics.

## Acknowledgements

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## Salvaging orbito-frontal cortex: improved fMRI image reconstruction for neuroeconomics

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A significant obstacle to the study of decision-making and emotion using standard functional MRI is distortion and the loss of signal in the brain regions near air/tissue/bone interfaces, such as the amygdala and orbito-frontal cortex. However, some of these areas are crucially linked to the study of decision making (O'Doherty 03), emotion (Phelps 04) and neuroeconomics (Plassmann 07). Neuroeconomic research will need to develop new methods to accurately relate activity in these areas to decision variables proposed in theory. We demonstrate how a multi-echo gradient echo (MEGRE) EPI sequence in combination with a novel image reconstruction algorithm can significantly improve measurements of the BOLD signal in these areas.

Standard fMRI image reconstruction makes the simplifying assumption that the phase encoded MR signal is acquired instantaneously, or equivalently, it makes the assumption that the acquisition takes time but that the background magnetic field is uniform. When either of these assumptions hold it is possible to use fast Fourier transform algorithms to quickly reconstruct a spatial image of the MR signal sources and then measure BOLD effects at these locations. In the real world, differences in magnetic susceptibility between air, tissue and bone lead to significant non-uniformity in the magnetic field across the head and the extended time required to acquire the phase encoded data renders these assumptions imperfect, inducing distortions in images reconstructed using the standard Fourier transform methods. Further, the inhomogeneities in the magnetic field cause some of the actual signal to completely decay by the time standard data acquisition begins. Our method compensates for some of the effect of these violated assumptions at the cost of increased computational demand.

Standard fMRI acquisitions designed to maximize the BOLD contrast acquire data in a time window centered at approximately 30ms ( $\sim 1/R_2^*$ ). At conventional imaging resolution (3mm x 3mm) approximately 15ms is available before this window for additional data acquisition. We use this "dead-time" to embed additional readouts for dynamic estimation of the magnetic field (Roochansingh 03, Sutton 05) and for partial recovery of signal from regions with fast decay (Poser 06). Furthermore we collect data under reversed gradients for accurate correction of magnetic field induced distortions (Chang 92). This novel acquisition scheme allows for simultaneous estimation of the magnetic field and the reconstruction of reduced distortion images with partial recovery of susceptibility induced signal loss. Using the "dead time" means that these improvements do not increase acquisition time relative to standard EPI sequences.

We collected data at 3T (Siemens Allegra) in simple fMRI tasks designed to elicit activation in effected areas, including a monetary value localizer. We demonstrate more robust task-related activations within single individuals that are more precisely aligned with the underlying anatomy as compared to conventional EPI acquisition. We believe that this combination of MEGRE EPI and non-linear image reconstruction could greatly improve investigations of the orbito-frontal cortex and other regions with large susceptibility induced magnetic field variation.

This work was funded in part by a grant from the McKnight Foundation.

# Interpretable Classifiers for fMRI Improve Prediction of Purchases

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Despite growing interest in applying machine learning to neuroimaging analyses, few studies have gone beyond classifying sensory input to directly predicting behavioral output. With spatial resolution on the order of millimeters and temporal resolution on the order of seconds, functional magnetic resonance imaging (fMRI) is a promising technology for such applications. However, fMRI data's low signal-to-noise ratio, high dimensionality, and extensive spatiotemporal correlations present formidable analytic challenges. We applied different machine learning algorithms to previously acquired data [1] to examine the possibility of using fMRI activation in three regions -- the nucleus accumbens (NAcc), medial prefrontal cortex (MPFC), and insula -- to predict purchasing behavior in humans. Our goal was to generate an interpretable spatiotemporal model as well as improve classification accuracy. Our new approach -- sparse penalized discriminant analysis (sparse PDA) -- enabled automatic selection of correlated variables, yielding highly interpretable models at the voxel-wise level that generalized well to new data. Relative to other commonly employed classifiers, sparse PDA not only increased interpretability but also improved classification accuracy. This approach promises to improve inferences about which brain areas contribute when to purchasing decisions, and more broadly, it provides a general framework for using neuroimaging data to predict choice. Further, recent findings in statistics [2] allow SPDA to be efficiently extended to whole-brain analysis over multiple time points (hundreds of thousands of predictor variables). Applying a method like SPDA that automatically selects relevant voxels in space and time to whole-brain data should eliminate the need for ROIs and  $p$ -value coefficient thresholding in most analyses, generating parsimonious data-driven maps of all voxels contributing to choice at each time point.

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# Neural Computations Underlying Hypothetical vs. Real Decision Making

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Researchers often have to infer real willingness to pay (WTP) for a product or policy, for example, from preferences stated in hypothetical situations. Despite its wide use, evidence casts doubt on this method of using hypothetical choices to estimate actual preferences—people tend to overstate their preference in a hypothetical situation, that is, hypothetical willingness to pay overestimates real willingness to pay [1]. Efforts to remove this “hypothetical bias” have met limited success [2-3] and the causes of hypothetical biases have not been well understood to date. In this study, we attempt to understand at a neural level why behavior differs in hypothetical and real situations. Using functional MRI, we scanned human subjects while they made both hypothetical and real purchase decisions about various consumer goods. We first found that both of the decision-making processes engage the anterior cingulate, the orbitofrontal cortex (OFC), and the striatum. However, the intensity and the size of the activations during real decision-making are significantly greater than in the hypothetical decision-making. Furthermore, the activations in those areas are parametrically modulated by WTP in both hypothetical and real decision-making. The correlations with WTP in a real situation are significantly higher than in a hypothetical condition. This suggests that the brain employs different decision rules in these two distinct modalities. We propose the use of the diffusion model [4] to describe how the brain operates differently to reach a decision in the hypothetical versus real situations. The diffusion model has several implications in regards to decision time; these are tested using the behavioral data. Finally, we show that the model can replicate the actual data by way of simulations.

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# Virtuous Decisions: Exemplarity In and Out of the Laboratory

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Virtuous exemplars are paradigmatic examples of morality in action. These people are puzzling because they seem to lack expected preferences with regard to self, reciprocity, and inequity aversion, all of which inform current models of economic, moral, and social decision-making.<sup>1</sup> To better understand decision-making in virtuous exemplarity, it is necessary to establish a link between exemplars in the real world and exemplary action in behavioral paradigms used to great effect in the laboratory. Such an approach will also improve the external validity of behavioral economics experiments, providing a quantitative association with actions of people in the real world. We developed an approach to associate real-world exemplars (RWEs) and behavioral paradigm exemplars (BPEs) in a three-step process. The first step identifies the BPEs in the laboratory according to their performance on two economic games: the Public Goods Game and the newly developed Rescuer Game. The Rescuer Game is a variant of the Reverse Dictator game, in which Player 1 is free to take money from Player 2 and Player 3 may “rescue” Player 2 (i.e., replenish part or all of Player 2’s pot). We also identify a number of typical and highly self-regarding participants as comparison groups. The second step measures the semantic association between RWEs and BPEs in terms of how they describe their own decisions and actions, using Latent Semantic Analysis.<sup>2</sup> The third step measures the association between this linkage value and our BPE measures: 1) decisions about money in economic games; 2) neuroimaging during those decisions; and 3) self-report measures of empathy, prosocial tendency, and abstract valuation (e.g., authority, pleasure, patience). Our RWE group is comprised of individuals who have been caregivers within the L’Arche community for 5 years or more. The details of this approach and our preliminary results associating behavioral and neural markers with RWEs will be presented.

## Acknowledgements

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## **The Length of Feedback Interval and Inter-Trial Interval Effects Decision-Making in Choice Tasks**

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We examined the role of feedback interval and inter-trial interval on the degree of exploration or exploitation in a choice task. In Experiment 1 participants chose from one of four decks of cards on each trial and earned points which were used to garner a monetary bonus. Participants were placed in either a Short or Long feedback interval condition. After making a choice, participants in the Short condition were told how many points they earned after waiting 500ms, while participants in the Long condition waited 5,000ms. After receiving feedback participants in each condition waited 500ms for the next trial to begin. We analyzed the data using a well-known reinforcement learning model that parameterizes the degree to which each participant exploits the option with the highest expected value, or explores other options with lower expected values. Results indicate that participants in the Long feedback-interval condition were more likely to exploit the option with the highest expected value, and were less willing to explore other options. In contrast, participants in the Short feedback-interval condition were more willing to explore options with lower expected values. In Experiment 2 we again placed participants in either a Short or Long feedback interval-condition, but increased the inter-trial interval from 500ms in Experiment 1 to 5,000ms. While participants in the Short feedback interval condition displayed slightly more exploratory behavior than participants in the Long condition, the difference was not significant. Thus, the longer inter-trial interval attenuated the effect of feedback interval on the degree of exploration or exploitation found in Experiment 1. This study suggests that the timing of the feedback presentation and the trial presentation can affect decision making strategies. Implications for fMRI experiments, where long inter-trial intervals are often necessary, are discussed.

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# **Meal patterns of mice under systematically varying procurement and consummatory costs for food in a closed economy**

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Much research in the field and in laboratory studies has focused on behavioral economics of food intake in several species. Operants such as lever press, nose poke, or key peck have been used to generate demand functions that express the relationship between the cost of food and the amount of food consumed. There have been very few such studies of motivated food seeking and demand in mice, and none has examined systematically consummatory cost or meal patterns. Using albino (CD1) male mice, the present study compares food intake and meal patterns across a series of ratio consummatory schedules. Two operants, lever press and nose poke, were compared in a between groups design. A closed economy was used in which the mice were in the test chambers for 23 h/day and earned all of their food via the operant under four fixed (FR5, FR10, FR25, FR50), variable (VR10, VR20, VR50) and progressive (PR1.25, PR1.5, PR1.75) ratios. When averaged across all schedules, mice in the nose poke group consumed more food. Mice were run for 4 days at each ratio; there were no systematic differences between the first and last day indicating that behavioral adjustments to schedule changes occurred very rapidly. Meal number significantly differed when two criteria for the definition of 'a meal' (15 and 30 min) were used.

## **Acknowledgements**

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## **How fame affects the encoding of products:**

An fMRI-study into the effect of celebrity endorsers on neural processing

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Every day people get exposed to a large number of commercial stimuli. Each of these advertisements tries to capture one's attention to raise awareness for their product or brand. A popular way to differentiate an advertisement from others is to make use of a celebrity endorser. It has been hypothesized that the success of celebrity endorsers can be explained by associative processing<sup>1</sup>. Because consumers have invariably more knowledge about a celebrity than about an unknown endorser, a celebrity endorser will be more effective in the creation of associations than an unknown endorser. The number and strength of the associations that are created during the endorsement process will subsequently determine the probability that the product will be recognized at a later stage, e.g. in store.

The present experiment aims to clarify if the effectiveness of celebrity advertising can indeed be explained by associative encoding. In addition, we investigate what the nature of these associations is, i.e. if they are mainly semantic or affective. As people are more familiar with a celebrity than with an unknown person, viewing a celebrity may trigger the activation of semantic knowledge. In this case we expect neural activity to take place in the left lateral prefrontal and parietal cortex and the left temporal pole<sup>2</sup>. Another possibility is that a celebrity context elicits the experience of affective associations. If this is true, we hypothesize to find an enhancement of neural activity within brain areas implicated in the processing of social affective information, such as the striatum, amygdala and orbitofrontal cortex<sup>3</sup>.

In the current fMRI paradigm participants were randomly shown series of an equally attractive famous or non-famous female face that was paired with a product (shoe). The task for the participant was to judge whether the shoe did belong to the female whose face was presented next to the product. To show that the faces of the celebrities and non-famous females were matched on attractiveness as intended, participants rated all faces at the end of the experiment. Additionally, the faces of the celebrities were rated on likeability and familiarity. Results of a recognition test that took place after scanning showed that products presented together with a famous face were better remembered than products paired with a non-famous face. This confirms the effectiveness of celebrity endorsers.

To investigate whether the persuasive influence of celebrities on product processing can be explained by the formation of either semantic or affective associations we initially contrasted trials in which a famous face is paired with a product with trials in which the famous face is presented without a product. Subsequently this contrast was compared to the same contrast of the non-famous face condition. Imaging data is under analysis at the time of writing.

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# The Effect of Retail Brand Frames on the Evaluation of Product Packaging – First Insights from Consumer Neuroscience

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In economic and psychological theory the “framing effect” is an important concept for the identification of judgement biases within subjects’ choices. Recent studies provide evidence that the “framing effect” occurs due to the integration of conscious and unconscious implicit and explicit background knowledge in the decision-making process. The promising field of consumer neuroscience may offer new perspectives to observe both conscious and unconscious effects of framed decision-processes. Research in the field of retail marketing is important for manufactures in order to select the best marketing channel strategy, the choice of appropriate distribution channels and the optimal decisions regarding the price policy and the retailer. However very little is known about optimal strategies of product positioning and about the influence different retail chains may exert on customer’s product perception and evaluation.

Our study tried to connect this important marketing channel research and the confounding effect of framing information. We investigated the behavioral decision-making and the correlating cortical activity pattern of 11 subjects from the young adult segment (18–26 years), by comparing individual attractiveness evaluations of 30 packages within an unframed task and a framed task. The unframed task consisted of the attractiveness evaluation of product packages alone, whereas in the framed task we presented product packages together with selected retail brands. Besides the fMRI data analysis we compared the behavioral data (the attractiveness rating) of the unframed task with the behavioral data of the framed task on the basis of two indices. First we calculated the individual judgement bias  $B$  - a relative share - for each retail brand and for the framed and unframed tasks in total. Those judgement biases indicate the direction of the subjects attractiveness evaluation with  $-1 < B < 1$ . Secondly we calculated a susceptibility index  $SI$ , the standard deviation of the individual judgment biases  $B$ . The  $SI$  can range between 0 (no judgement bias and no susceptibility to the framing information) and 1 (total judgement bias and susceptibility to the framing information).

Results of the fMRI data analysis showed positive relations between significant cortical activity changes and increased values of the susceptibility index. On the **group level analysis** we found significant activation pattern within regions of the inferior frontal lobe in five participants whose  $SI$  has been higher than 0,029, the Median of all 11 individual susceptibility indices. The observed brain areas of the inferior frontal cortex are associated with the retrieval of episodic memory, semantic memory, the processing of (abstract) word stimuli, and executive control. It can be hypothesized that more susceptible subjects show a more intensive involvement in the decision-making process and through a higher degree of cognitive processing they may integrate episodic memories as well as conception-related knowledge into the decision-making process. Because of this the retrieved memories associated with the framing information may bias their choice. On the **single subject analysis**, a first consistent result was the significantly increased cortical activity within regions of the medial prefrontal cortex for subjects with a high susceptibility index. Activations in the medial prefrontal cortex were particularly found in the ventromedial prefrontal cortex (BA 10). This region is associated with the processing of emotions, memories, sensorial information and decision-making. Another result on the single subject level has been the activation of the anterior cingulate that we detected for the participant with the highest susceptibility index. This structure seems to be involved in the emergence of emotions and the evaluation of stimuli according to their attractiveness. Another possibility is that the anterior cingulate simplifies decision-making through the integration of information about positive and negative reinforcements (Deppe et al., 2007).

Our findings offer interesting insights for the importance of the “psychological” “framing effect” in marketing channels, especially in product and price policy. Because of the presented inter and intrapersonal differences in individual judgement biases it should be important for manufacturers to implement consumers’ susceptibility, product positioning and the biasing effects of retail brands in their product and price strategy portfolio. Beyond this we found neural correlates of the judgement biases within regions of the medial prefrontal cortex and anterior cingulate. This confirmed recent findings in other studies regarding the “framing effect” and marketing relevant decisions.

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# Hemispheric Processing of Metaphors in Advertisements

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Previous research has shown that the right hemisphere (RH) is uniquely involved in the comprehension of metaphors [1, 3]; however, currently little is known about how the two hemispheres of the brain process advertisements. The Fine-Coarse Semantic Coding Theory proposes a possible explanation for this RH advantage in metaphor comprehension [2]. Specifically, this theory states that the left hemisphere (LH) activates closely related word meanings (i.e., fine coding), whereas the RH activates weakly related word meanings (i.e., coarse coding). In the current study, we used the divided visual field paradigm to investigate the contribution of the left and right hemispheres in the comprehension of metaphors used in ad slogans. A total of 99 undergraduates (30 males, 69 females) participated in the study for course credit. All participants were right-handed, native English speakers. Participants were exposed to a combination of metaphoric slogans (e.g., “Run on air”), literal translations of metaphoric slogans (e.g., “These shoes are really light”), neutral slogans (e.g., “All the sugar and twice the caffeine”), and filler slogans (e.g., “Live life in your own lane”). The results show an overall advantage in the RH for the comprehension of *both* literal and metaphoric slogans. Interestingly, there was a significant difference between the two types of slogans in the RH, with greater facilitation for the literal slogans. Also of interest, we found no LH advantage for the literal slogans. It is possible that the advantage in the RH for both literal and metaphoric slogans is due to the very nature of slogans, themselves. Ad slogans in their own right are different from sentences typically encountered in everyday speech and reading. Therefore, perhaps even the literal translations of the metaphoric slogans require broader, more distantly related meanings [2]. These research findings help contribute to the current understanding of the role of the RH in language comprehension. Furthermore, these findings contribute to the current marketing literature on the use of metaphors in ads. These results suggest that both metaphoric and literal slogans require a different level of processing among consumers. Overall, the results of this study suggest that the RH plays a greater role than the LH in the comprehension of advertisement slogans.

## Acknowledgements

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# Saturday, September 27, 2008

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8:30 – 10:00 am

*Continental Breakfast*

*Grand Ballroom Lobby*

## **Valuation I: Non-Risky and Multiple Attributes**

*Kokopelli Parlor II*

10:00 – 10:30 am	Bernd Figner	Asymmetries in intertemporal discounting: neural systems and the directional evaluation of immediate vs future rewards	Bernd Figner, Eric J. Johnson, Grace Lai, Amy Krosch, Jason Steffener, Elke U. Weber
10:35 – 11:05 am	Brian Knutson	Neural antecedents of the endowment effect	Brian Knutson, G. Elliott Wimmer, Scott Rick, Nick G. Hollon, Drazen Prelec, George Loewenstein
11:10 – 11:40 am	Steven Kennerley	Neurons in the frontal lobe encode the value of multiple decision variables	Steve Kennerley, Aspan Dahmubed, Antonio Lara, Jonathan Wallis
11:45 – 12:15 pm	Tali Sharot	Choice shapes, and reflects, expected hedonic outcome	Tali Sharot, Benedetto De Martino, Raymond J Dolan

12:20 – 1:30 pm

*Lunch*

*The Canyons Pavilion*

## **Valuation II: Risky Attributes**

*Kokopelli Parlor II*

1:35 – 2:05 pm	Kenway Louie	Value-based gain control: relative reward normalization in parietal cortex	Kenway Louie, Lauren Grattan, Paul Glimcher
2:10 – 2:40 pm	Vasco Galhardo	Neuroeconomy of pain: rodent gambling task impairment induced by chronic pain models	Vasco Galhardo, Miguel Pais-Vieira, Manuela Pinto, Deolinda Lima
2:45 – 3:15 pm	Kaisa Hytonen	How prior gains and losses influence our decisions under risk: an fMRI study	K. Hytonen, G. Baltussen, M.J. van den Assem, V. Klucharev, A. Smidts, G.T. Post
3:20 – 3:50 pm	Peter Bossaerts	Neurobiological foundations for "dual system" theory in decision making under uncertainty: fMRI and EEG evidence	Peter Bossaerts, Ulrik Beierholm, Cedric Anen, Helene Tzieropoulos, Steven Quartz, Rolando Grave de Peralta, Sara L. Gonzalez

*Evening free, dinner on your own*

# Asymmetries in Intertemporal Discounting: Neural systems and the directional evaluation of immediate vs future rewards

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When asked whether they would be willing to wait a month to receive \$33 instead of receiving \$30 today, most people choose \$30 today. In contrast, when asked whether they would prefer to speed up the receipt of \$33 in a month by receiving \$30 today instead, most people exhibit patience and take the \$33 in a month. This asymmetry in discounting — relative impatience for delaying consumption and relative patience for accelerating consumption [1] — suggests differences in the processing of choices depending on the direction of the evaluation. Query Theory, a causal cognitive-process model of preference construction, was recently proposed to explain this and other choice inconsistencies [2,3]. Weber et al. [2] showed that the directional asymmetry in discounting is caused by the different order in which memory is queried for reasons favoring immediate versus future consumption, with earlier queries resulting in a richer set of responses, and reasons favoring immediate consumptions being generated earlier for delay vs acceleration decisions.

Extending McClure et al.'s paradigm [4], we conducted an fMRI study ( $N = 21$ ) investigating participants' neural activation underlying acceleration vs delay decisions, contrasting in both cases choices between an immediate and a future reward with choices between two future rewards.

As predicted, we found hyperbolic discounting only in the delay, but not the acceleration condition, with more impatient choices if a reward was immediately available as opposed to when both rewards were available in the future. Consistent with these behavioral results, we found increased activity in anterior insula, anterior and posterior cingulate, orbitofrontal and medial prefrontal cortex for trials involving immediate rewards in the delay compared to the acceleration condition. Additional analyses of differential neural activation during different types of choices under the two goal conditions are underway. Results will be further augmented by analyses of eye tracking data for Query Theory predictions, as well as diffusion tensor imaging data.

The results of our study show that the neural processing of identical choice options differs with the goal of the decision (delaying versus accelerating consumption). Multiple-systems accounts of intertemporal choice in their current form (like the beta-delta model, [4]) cannot account for the full complexity of intertemporal choice at both the behavioral and neural level and will need to be expanded.

## Acknowledgements

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SNE Abstract 2008

Neural antecedents of the endowment effect

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The “endowment effect” refers to the tendency to place greater value on items that one owns – an anomaly that violates the reference-independence assumption of rational choice theories. We investigated neural antecedents of the endowment effect in an event-related functional magnetic resonance imaging (fMRI) study. During scanning (with a GE 1.5 T scanner, voxel size = 4 mm cubic, TR = 2000 msec, spiral in/out pulse sequence), 24 subjects considered 6 products paired with 18 different prices under buying, choosing, or selling conditions. Subjects showed greater nucleus accumbens (NAcc) activation for preferred products across buy and sell conditions combined, but greater mesial prefrontal cortex (MPFC) activation in response to low prices when buying versus selling. During selling, right insular activation for preferred products predicted individual differences in susceptibility to the endowment effect. These findings are consistent with a reference-dependent account in which ownership increases value by enhancing the salience of the possible loss of preferred products.

Keywords: endowment, reward, gain, loss, accumbens, prefrontal, insula, human, fMRI

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# Neurons in the frontal lobe encode the value of multiple decision variables

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Damage to the frontal lobe, in particular to anterior cingulate cortex (ACC), lateral prefrontal cortex (LPFC) and orbital frontal cortex (OFC), impairs decision-making in a variety of contexts. A possible explanation for these impairments is that neurons here represent decision value across multiple decision variables. To explore how these three frontal areas contribute to decision-making, we trained two rhesus macaques (*Macaca mulatta*) to make choices between pictures associated with different values varied along three physically different valuation scales. Each picture was associated with a specific probability of obtaining a fixed amount of juice (probability trials), a specific amount of juice (payoff trials) or a specific number of lever presses required to obtain a fixed amount of juice (cost trials). We simultaneously recorded the activity of 610 neurons (257 from LPFC, 213 from ACC and 140 from OFC) while subjects made their choices. Neuronal activity was examined in the 1500ms period when the pictures were displayed but before a response was permitted. The two subjects differed in the response used to make their choice (Subject A/B = arm/eye movement) which allowed us to examine the relationship between choice value and the effector used to obtain the outcome.

The most prevalent selectivity was in ACC, where 84% of the neurons encoded value for at least one decision variable, followed by OFC (56%) and LPFC (49%). Neurons that encoded multiple decision variables were more common in ACC (57%) and OFC (30%) than in LPFC (19%). There was no clear preference for neurons to encode a particular decision variable or combination of variables. Neurons encoding the motor response were more common in ACC (50%) and LPFC (43%) than in OFC (30%). Neurons encoding decision value were equally present in both subjects (66%), yet motor selective neurons were more common in the subject responding by arm (67%) than by eye movement (27%). Time-course analyses revealed that decision value was encoded ~200ms before the upcoming motor response.

Our results indicate that many frontal neurons encode an abstract value signal in the sense that choice value is encoded irrespective of the physical manner in which choice value is manipulated. This value signal is effector independent and is temporally separate from motor preparation processes, which suggests that choice value is computed before the appropriate physical action is selected. Finally, the encoding of value across multiple decision variables appears to be much stronger in ACC than OFC or LPFC, emphasizing the importance of ACC in the neural circuitry underlying optimal decision-making.

## Acknowledgements

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## **A neural correlate of estimated hedonic reaction predicts choice**

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Humans can estimate the hedonic outcome of future events by simulating those events in their minds. Here we identify brain activity that tracks expectations of hedonic reaction during simulation, and predicts later choice. We combined participants' estimations of the pleasure they will derive from future events with fMRI data recorded while they imagined those events, both before, and after making choices. Remarkably, activity in the caudate nucleus predicted the choice participants made when forced to choose between two alternatives they had previously rated equally. Moreover, post choice the selected alternatives were valued more strongly than pre-choice, while discarded ones were valued less. This post-choice preference change was mirrored in caudate nucleus response. The findings indicate that activity in a brain region implicated in subjective valuation predicts choice even in instances when behavioral evaluation does not.

### **Acknowledgements**

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# Value-based gain control: relative reward normalization in parietal cortex

Kenway Louie, Lauren Grattan, and Paul Glimcher

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Value information is a critical component of the decision-making process. In the lateral intraparietal area (LIP), visuomotor neurons are strongly modulated by reward variables such as expected gain, prior probability, and reward income, suggesting that individual LIP neurons represent the subjective value of specific saccades [1,2]. In this decision framework, population activity initially encodes the values of the available targets; comparison of these values results in action selection and output of choice information to downstream oculomotor structures. We explore here the neural mechanism underlying value representation during decision-making and how such mechanisms influence choice behavior in the presence of alternative options.

We first explicitly examined the effect of target value outside the classical response field (RF) on single neuron activity. Even though such targets elicit no activity when presented alone, when presented in a choice situation with a target in the RF they strongly modulate LIP activity. Specifically, the activity of LIP neurons decreases significantly as the value of targets outside the RF increase. The activity of these same neurons increase when target value in the RF increases, as previously reported for LIP. Examined together, these results show that LIP neurons encode a relative measure of saccade value, normalized across available options.

What is the form of this normalization? Many visual cortical processes, including gain control in V1 and responses to multiple stimuli in MT, can be explained by a form of divisive normalization originally proposed by Heeger [3]. To fully characterize value normalization in this context, we recorded single LIP neurons during a multiple option choice task. In each trial, the monkey fixates a central cue and views either one, two, or three peripheral targets, each associated with a different reward size. We find that the activity of LIP neurons driven by a RF target is reduced in a value-dependent manner by the various combinations of alternative targets; this suppression is fully explained in both single neurons and the LIP population by a value-based divisive normalization model. Furthermore, when there is no target in the RF, the presentation of alternative targets suppresses LIP activity further, below fixation baseline levels; these additional results are accounted for by the addition of a single baseline parameter to the Heeger normalization equation. This existence of value-based normalization in parietal cortex suggests that divisive normalization may represent a general mechanism of cortical operation. Furthermore, the finding that decision processes rely on relative representations of value may explain why and how choice behavior responds to multiple options and changing choice sets [4].

## Acknowledgements

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# **Neuroeconomy of Pain: rodent gambling task impairment induced by chronic pain models**

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Uncovering the roles of the orbitofrontal cortex and the amygdala in reward-based decision-making strategies has relied heavily in studies using either spontaneous lesions or induced tampering of these regions. However, substance abusers, compulsive gamers, and chronic pain patients also display risk-prone behavior in cognitive gambling tasks even in the absence of discrete brain lesions. Unfortunately, complex decision-making tasks suitable for small mammals are uncommon and almost no studies have addressed poor performance in frontal-based cognitive tasks. We developed a novel behavioural task – the Rodent Gambling Task [1] – based on repetitive reward-based two-option decisions coupled to rewards of different value and probability, and studied its performance by both control, animals with lesion of either amygdala or orbitofrontal cortex, and chronic pain animals. Briefly, the task consisted on consecutive trials in which a rat entered an operant chamber and had to choose between two levers to recover a food reward. During the 15 days of the training phase both levers gave equal pseudo-random rewards with one food pellet in 8 out of 10 visits. In the probe trial, one of the levers was modified to give 3 food pellets, but only in 3 of 10 visits - high risk. The pattern of 90 consecutive choices was used to calculate the lever-choice index. We found that control animals begin with a preference for the high-risk lever, but after 90 trials shift to the low-risk option. On the contrary, chronic pain animals prefer the high-risk lever, similarly to animals with OFC or amygdalar lesions. Since no brain damage is caused by the model of chronic pain, we performed an HPLC analysis to assess the pain-induced alterations in the dopaminergic and serotonergic tonic levels of the OFC and amygdala. We found an increase in the levels of dopamine and serotonin at the amygdala, and a decrease of both at the OFC. Moreover, we found an individual fixed ratio of OFC/AMYG neurotransmitter levels, that was also altered by chronic pain.

In conclusion, we show that chronic pain alone induces a shift in the dopaminergic and serotonergic ratios between the two areas, and that this loss of neurochemical balance parallels the observed shift in gambling task performance. Our results suggest that this pattern of poor decision-making behaviour may result from pain-induced allostasis maintained by an hyperactive reward-seeking system coupled with a defective valuative system.

## **Acknowledgements**

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# How Prior Gains and Losses Influence Our Decisions Under Risk: An fMRI Study

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A large body of behavioral experiments has convincingly shown that the risk attitudes for a given risky choice problem generally depend on the outcomes of previous choice problems. Most notably, Thaler and Johnson [1] show that the average decision-maker tends to take more risk if she has a chance to gain back a previously experienced loss, the “break even effect” (BEE). After experiencing a gain which cannot be lost, she also has a greater risk appetite, the “house money effect” (HME). These effects are pervasive also outside the behavioral laboratory; see, for instance, Post *et al.* [2].

The present study investigates the neuronal drivers underlying these well-known behavioral effects. We have developed a sequential choice paradigm for functional magnetic resonance imaging (fMRI), in which subjects systematically show the two behavioral effects. Our paradigm enables us to compare the brain activities during decision making after previous gains, losses, and neutral outcomes while controlling for other variables in the choice problems.

We first analyze the affective reactions to the realization of gains and losses. Gains activate the ventral striatum and the medial frontal cortex, whereas losses activate the inferior and medial frontal cortex, in line with existing results in the neuroscience literature. Our further analysis aims to show that these affective reactions have predictive power for the subsequent choice behavior on a trial-by-trial basis.

Next, we study ‘history effects’ on risky decision making: we compare the brain activity during choice problems following gains, losses, and neutral outcomes. Separate neuronal networks are active after gains and losses. Choices that were preceded by good outcomes were related to caudate activity, whereas choices preceded by bad outcomes generated activity in anterior cingulate and right inferior frontal gyrus.

Finally, we explore the neuronal activity related to risk attitude itself. First, when comparing games where participants choose the risky lottery over the certain offer, we see a large distributed network that includes the medial and orbitofrontal cortex [3]. Second, we will further explore the neuronal networks that are sensitive to risk-seeking attitude by using parametrical model that utilizes individual BEE and HME effect sizes. In sum, we show that prior experiences modulate decision-maker’s risk attitude and explore the underlying neuronal mechanisms of history effects and risk attitude.

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# Neurobiological foundations for "dual system" theory in decision making under uncertainty: fMRI and EEG evidence

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It has been suggested that human decision making involves (at least) two systems: one reflexive and fast, and a second one reflective but slow (for a survey, see [1]). This "dual system" conjecture is consistent with many aspects of human behavior, such as the tendency to apply heuristics when fast answers are needed ([2]). As far as decision making under uncertainty is concerned, however, there has so far only been suggestive evidence of a neurobiological foundation to this dual system theory. Here we discuss two experiments on the matter.

The first experiment was prompted by the realization that, in past experiments (e.g., [3]), the evidence in favor of dual system theory was based on a comparison of differential brain activations across subjects, leaving open the possibility that a single but subject-specific neural system generated observed behavior. Our experiment, in contrast, was meant to generate dual neural signals in an intra-subject analysis. The experiment concerned learning in a three-option ranking game. It was designed to generate minimal correlation (0.43) between valuations from the reflective system (interpreted here, as in [4], as the Bayesian, model-based learning system) and the reflexive system (simple reinforcement learning based on past actions). fMRI analysis of brain activation revealed, among others, distinct activations in medial prefrontal cortex correlating with the two values; the usual prediction error activations in striatal areas correlated only with the prediction error from reflexive learning. Our findings may seem to contradict recent reports of a single valuation signal in intertemporal choice tasks [5] or tasks contrasting known probabilities (pure risk) and ambiguity [6]. However, our experiment built on a situation where, true to the spirit of dual-system theory, values could be computed based on two different principles.

Our second experiment dealt with strategic uncertainty in a social situation. The goal was, among others, to ascertain the speed of the reflective system. Using the trust game, we found that we could stratify subjects into two groups. One group used well-adapted strategies. EEG recordings revealed activation of a reflective (conflict-resolution) system, evidently to inhibit impulsive emotional reactions after disappointing outcomes. After other outcomes, however, members of this group showed the same event-related potentials (ERP) topography as the second group. Members of this second group followed ill-adapted strategies and did not show differential activation after disappointing outcomes. The time resolution of EEG allowed us to ascertain that the reflective system is relatively fast, and that its activation (at around 320 ms) coincides with the interval where the first signs of conscious perception are usually observed.

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## Sunday, September 28, 2008

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8:00 – 9:00 am

*Continental Breakfast*

*Grand Ballroom Lobby*

### **Learning: From Rodent to Human**

*Kokopelli Parlor II*

9:00 – 9:30 am	Paul Phillips	Predicted rewards continue to elicit dopamine release when the predictor fails to acquire incentive value	Paul E. M. Phillips, Jeremy J. Clark, Christina A. Akers, Scott B. Ng-Evans, Shelley B. Flagel, Sarah M. Clinton, Terry E. Robinson, Huda Akil
9:35 – 10:05 am	Adam Kepecs	How uncertainty boosts learning: Dynamic updating of decision strategies	A. Kepecs, N. Uchida, Z.F. Mainen
10:10 – 10:40 am	Saleem Nicola	Nucleus Accumbens dopamine and the decision to engage in reward-seeking	Saleem M. Nicola, Howard L. Fields
10:45 – 11:25 am		<i>Break &amp; Hotel Check-Out</i>	<i>Grand Ballroom Lobby</i>
11:30 – 12:00 pm	John Pearson	Firing rates of neurons in posterior cingulate cortex predict strategy-switching in a k-armed bandit task	John Pearson, Benjamin Y. Hayden, Sridhar Raghavachari, Michael L. Platt
12:05 – 12:35 pm	Robb Rutledge	A neural representation of reward prediction error identified using an axiomatic model	Robb B. Rutledge, Mark R. Dean, Andrew Caplin, Paul W. Glimcher



## **Predicted rewards continue to elicit dopamine release when the predictor fails to acquire incentive value**

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Previous research utilizing both electrochemical and electrophysiological techniques has demonstrated a shift in phasic dopamine activity from unconditioned to conditioned stimuli after Pavlovian conditioning. The prevailing interpretation of these data is that the dopamine signal represents a reward prediction error and that conditioned cues elicit dopamine responses because they have predictive value. A competing view posits that appetitive stimuli and conditioned cues elicit dopamine responses because they possess incentive value, and that the dopamine signal itself represents the attribution of this incentive. However, a separate assessment of these potential functions has remained a difficult challenge. Using an electrochemical technique, phasic dopamine activity was assessed in the nucleus accumbens core throughout training on a conditioned approach task in rats selectively bred for their locomotor response to novelty. High responders to novelty (HR) exhibit “sign-tracking” behavior (known as sign-trackers; ST) when trained on an approach task, whereas low responders (LR) exhibit “goal-tracking” behavior (known as goal-trackers; GT) under the same conditions. Cue-elicited approach to conditioned stimuli (i.e. sign-tracking behavior) is thought to result from both the gain in predictive strength of the stimuli and its acquisition of incentive salience. In contrast, goal-tracking behavior is characterized by cue-elicited approach to the site of reward delivery, suggesting that the cue has acquired predictive value but not the incentive salience required to produce approach. Based on these observations, it was hypothesized that phasic dopamine signals in response to conditioned and unconditioned cues would differ between ST and GT over the course of learning. The behavioral results from the selectively bred rats showed that HR rats were exclusively ST and LR rats were exclusively GT. HR-bred rats that reliably approached the cue (ST) demonstrated the characteristic decrease in dopamine responses to food delivery once it was predicted by the cue and a complete transfer of the response to the cue during training. In contrast, LR-bred rats that reliably approached the site of food delivery during cue presentation (GT) maintained a phasic dopamine response to food delivery throughout training despite its prediction by the cue. In addition, LR rats failed to exhibit complete transfer of the dopamine signal to the predictor. It is concluded that transfer of phasic dopamine signals from unconditioned to conditioned stimuli requires an attribution of incentive salience to the conditioned stimulus, not just a gain in predictive strength.

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# How uncertainty boosts learning: Dynamic updating of decision strategies

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Making optimal decisions requires that decision strategies be updated based on the successes and failures of similar decisions made in the past. Reinforcement learning theory proposes that a quantitative prediction error—the difference between expected and observed outcomes—drives learning. According to this theory, the size of the updates should depend on the current estimates of uncertainty: one should learn more when uncertain and less when certain. However, there is only limited direct evidence for these predictions, in part because quantitative measurements of learning increments are difficult to assess experimentally.

To study this issue we used an olfactory categorization task performed by rats and examined the trial-by-trial updating of behavioral strategy. During categorization tasks the decision-boundary is learned through reinforcement but may undergo continual updating during performance thereafter. Therefore we focused on the on-going behavioral adjustments in the absence of explicit changes in task contingencies, after overt learning asymptoted.

Animals dynamically adjusted their decision strategy even after extensive training. For difficult decisions (those near the category boundary) the outcome is very informative about location of the decision boundary, while the outcome of pure odor trials (far from the decision boundary) reveals little about the boundary. Accordingly, the decision boundary should be adjusted more following difficult trials with high uncertainty than for trials with no uncertainty. Indeed, we found that rats biased their decisions toward the more recently rewarded direction as if their decision boundary was shifted. This bias, however, was only observed for difficult decisions, suggesting that the category boundary and not the side-bias was being updated. Moreover, the magnitude of this bias was proportional to the uncertainty of the previous decision, as predicted.

These data can be quantitatively explained by a delta learning rule,  $d\mathbf{w} = \epsilon \cdot c \cdot (\mathbf{y} - \mathbf{y}^*)$ , in which the learning rate is modulated by decision confidence,  $c$ . We show that a trial-by-trial confidence estimate can be naturally computed in this class of models along with the choice [choice:  $\mathbf{y} = \text{sgn}(\mathbf{w}'\mathbf{x})$ ; confidence:  $c = \text{abs}(\mathbf{w}'\mathbf{x})$ ]. This is a sensible confidence measure, because after calibration using a sigmoid transform it yields a veridical estimate of behavioral accuracy.

To understand the neural basis of this process we recorded neurons in the orbitofrontal cortex of rats performing the mixture categorization task. We found a population of neurons whose firing during the reward anticipation period closely resembled the expected signal of decision confidence. About half of these neurons also carried information about the reward outcome of the previous trial based on a regression analysis.

These results show that on-going category learning depends on a computationally advantageous updating strategy based on a graded prediction error signal and some orbitofrontal cortex neurons carry information relevant for this learning process.

# Nucleus Accumbens Dopamine and the Decision to Engage in Reward-seeking

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When food is available, hungry animals exert effort to obtain it. If reward availability is reduced (e.g., by imposing, during an operant task, an intertrial interval during which reward is unavailable), animals exert correspondingly less effort. In this situation, the probability of reward-seeking during the inter-trial interval is lower than when reward is available. What are the neural circuits that determine the probability of reward-seeking? The dopamine projection from the midbrain to the ventral striatum/nucleus accumbens (NAc) may be critical. A recent literature survey indicated that a fairly reliable predictor of the dependence of a behavioral task on NAc dopamine is the interval between reward availability: performance of tasks with long intervals between reward often depend on NAc dopamine, whereas those with shorter intervals do not [1]. We hypothesized, therefore, that NAc dopamine plays a greater role in regulating the rate of responding on tasks with temporally sparse reward availability.

To test this hypothesis, we trained separate groups of rats on tasks in which the reward was available in exchange for a single lever press. The interval between receipt of reward and the next time at which reward was available was varied across groups (but fixed for each individual rat). Injection of dopamine receptor antagonists into the NAc reduced performance in the groups with longer inter-reward intervals (10, 20 or 30 sec) to a much greater extent than in those with shorter intervals (0 or 3 sec). These results confirm the hypothesis stated above, but they do not explain why different neural circuits control responding depending on the density of reward availability. We hypothesized that when reward is not available, animals become disengaged from reward-seeking behavior. Furthermore, we propose that activation of dopamine receptors in the NAc is required for animals to become re-engaged in reward-seeking. As a consequence, animals in tasks where reward availability is rich rarely become disengaged and therefore animals can perform these tasks without an intact NAc dopamine projection. These hypotheses were confirmed by analyzing videos of rats performing a task in which reward was unavailable for 10 sec after the previous reward. After obtaining reward, the animals often moved away from the lever and reward receptacle (i.e., they disengaged from reward-seeking), and returned just before or after reward was again available. Injection of dopamine receptor antagonists into the NAc increased the amount of time spent in the disengaged state, indicating that NAc dopamine is required to end the disengaged state and resume reward-seeking.

Our results imply that the correlation between reward availability and an animal's willingness to exert effort to obtain it is due, in part, to a specific neural and behavioral state that occurs when the temporal interval between reward availability is sufficiently large that animals become disengaged from reward-seeking behavior. The decision (to press the lever or not) occurring when the animal is already engaged in reward-seeking behavior is made by a neural circuit (not dependent on NAc dopamine) that is not the same as the NAc dopamine-dependent circuit that controls this decision when the animal is disengaged. If the role of NAc dopamine is limited to the decision to become active, this suggests an alternative interpretation of neural signals in the NAc, recorded in electrophysiological and functional imaging studies, that correlate with reward prediction even in fully engaged subjects. The neural circuits underlying these signals may not drive the decisions made during the task, but rather promote greater behavioral activation.

## Acknowledgements

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## **Firing rates of neurons in posterior cingulate cortex predict strategy-switching in a k-armed bandit task**

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Among the most important decisions animals face are those that pit current-best options (exploitation) against the potential of unknown options (exploration). Such considerations are especially important in dynamic foraging environments, where systematic information-gathering is thought to be crucial to the maximization of long-term reward. As a result, strategic considerations are expected to take on added significance, as the correct choice of strategy may vary depending upon environmental conditions. A previous imaging study found evidence for exploration in frontal cortex and intraparietal sulcus and for reward in prefrontal cortex and striatum. However, physiological studies have implicated posterior cingulate cortex (CGp) in both risky decision-making and the processing of reward, leading to the hypothesis that this region may also play a role. We performed single-unit recordings in CGp in rhesus monkeys performing a version of the k-armed bandit task in which the values of four fixed targets varied dynamically trial-to-trial. We observed subjects alternating between bouts of distinct “explore” and “exploit” behavioral strategies, based on task conditions, and found that >50% of neurons distinguished between these modes. We compared subjects' behavior with optimal performance as determined by modeling, and find evidence for a neural “strategy switch” signal in CGp.

# **A neural representation of reward prediction error identified using an axiomatic model**

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The midbrain dopamine neurons are thought to encode a reward prediction error (RPE) signal, the difference between experienced and predicted reward. Functional imaging studies have provided evidence that BOLD activity in dopamine projection areas including the nucleus accumbens is consistent with this theory. However, the RPE theory has never been formally tested; no experiment has asked whether dopamine signals meet necessary and sufficient conditions for any RPE system.

We anatomically identified the nucleus accumbens in human subjects using structural MRI and then tested whether BOLD responses in this area demonstrate all of the properties required of a RPE system. Caplin and Dean have recently derived an axiomatic basis for the RPE hypothesis rooted in economic theory. This axiomatic model specifies three easily testable conditions for the entire class of RPE models. Briefly, the axioms will be satisfied if activity is: 1) increasing with prize magnitude, 2) decreasing with lottery expected value, and 3) equivalent for outcomes from all lotteries with a single possible outcome. These three conditions are both necessary and sufficient for any RPE signal. If they hold, there is a way of defining experienced and predicted reward such that the signal encodes RPE with respect to those definitions.

We tested for compliance with these axioms by using functional MRI to measure BOLD responses in a task where subjects received real monetary prizes. Subjects (n=12) were endowed with \$100 at the beginning of each of two scanning sessions. In each trial, subjects pressed a button to select one of two visually presented lotteries and then immediately played that lottery. For example, a subject might choose a lottery with equal probabilities of winning or losing \$5 and then, after a brief delay, find out that they won \$5. We used the BOLD responses at the outcome time to test whether activity in the nucleus accumbens satisfies the axioms of the RPE model. We find that activity in this dopamine projection area satisfies the three axioms, that it can serve as a RPE signal. We also find that BOLD responses to positive and negative RPEs have different temporal dynamics and, perhaps consistent with behavioral studies of loss aversion, negative RPEs have twice the effect of positive RPEs on BOLD signal.

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