

Neuroeconomics for the Study of Social Cognition in Adolescent Depression

William Mellick and Carla Sharp, Department of Psychology, University of Houston
Monique Ernst, National Institute of Mental Health/NIH

Traditional social-cognitive approaches for investigating interpersonal problems in adolescent depression are limited. An important functional domain studied in adolescent depression is reward, but experimental paradigms have largely been nonsocial. In this article, we propose the methods and concepts of neuroeconomics may address this gap. We begin by discussing a well-established social reward model for vulnerability to adolescent depression. We then show how neuroeconomics may extend this model by offering the tools to examine the mechanics of social exchanges, in behavioral and neural terms, that maintain (or pose vulnerability to) depression. In doing so, we propose a neuroeconomic model of adolescent depression in which depression is defined as a perturbation of interpersonal motivational/reward exchange. This model serves to guide future research.

Key words: adolescent depression, neuroeconomics, social cognition. [*Clin Psychol Sci Prac* 22:255–276, 2015]

Major depressive disorder (MDD) is a debilitating mental illness that typically emerges during adolescence (Lewinsohn, Rohde, & Seeley, 1998) and affects approximately 11% of adolescents (Merikangas et al., 2010). An important functional domain that has been studied in the context of adolescent depression is

reward function (Forbes, 2009). However, research has rarely employed social reward paradigms in this regard, despite wide acknowledgment of the interpersonal nature of adolescent depression (Petty, Sachs–Ericsson, & Joiner, 2004). While traditional social-cognitive approaches have been useful to elucidate the interpersonal nature of adolescent depression, in this review article, we propose that the scientific methods offered by the interdisciplinary field of neuroeconomics may be used to describe the alterations of social decision-making in adolescent depression. We show how neuroeconomics may provide an important extension of Davey, Yücel, and Allen's (2008) social reward model of adolescent depression. In all, we propose a neuroeconomic model of adolescent depression in which depression is defined as a perturbation of interpersonal motivational/reward exchange.

Indeed, over the last 20 years, the neural circuitry of reward, in general, has been the focus of much research interest as a promising functional domain that can be targeted for intervention in depression. In fact, impaired reward function meets more endophenotype criteria for depression as compared to other putative endophenotypes (Hasler, Drevets, Manji, & Charney, 2004). Amotivation to obtain reward, less frequent pursuit of rewarding experiences, and reduced enjoyment from reward are central features of depression that have significant clinical consequences, including disinterest and disengagement from a range of activities (i.e., food, sex, hobbies, socialization, and work; Ernst, 2012). Phenomenologically, these symptoms appear to be related to functions of the mesolimbic dopaminergic projections from the ventral tegmental area (VTA) into

Address correspondence to Carla Sharp, Department of Psychology, University of Houston, 126 Heyne Building, Houston, TX 77204. E-mail: csharp2@uh.edu.

the ventral medial prefrontal cortex, amygdala, and ventral striatum (Hasler et al., 2004). Depressed patients demonstrate reduced striatal activation in response to reward, as opposed to an increased activation seen in healthy comparisons. This hyporesponsiveness is associated with anomalous decision-making in the context of rewarding stimuli. Thus, depressed individuals appear to exhibit a form of “motivational blindness” (Diekhof, Falkai, & Gruber, 2008) for mood-incongruent (positive) stimuli, which at the very least supports the maintenance of depression. This motivational blindness may play a causal role in reward processing disturbances in the development of depression, as reduced neural responsivity appears to be present in at-risk (but never-depressed) biological offspring of mothers with a history of depression (Gotlib et al., 2010; Sharp et al., 2014).

Thus, reward function also appears to be a potential endophenotype for adolescent depression. Developmentally speaking, there are dramatic changes in reward processing that occur during adolescence. Adolescence marks the period during which reward sensitivity is at its peak, and this heightened sensitivity to reward is associated with increased novelty-seeking and risk-taking behaviors, which serve important developmental functions (Galván, 2013). The striatum has been shown to be central to this hypersensitivity to reward (Schultz, 1998), and functional connectivity between dopamine-innervated regions (e.g., fronto-striatal and striatal) is strengthened during adolescence (Spear, 2000). It has also been suggested that plasticity in these reward-circuit regions may mediate reward-related behaviors and learning (Galván, 2010). Together, these developmental changes in reward circuitry may provide an important context for the development of mood-related psychopathology (Forbes & Dahl, 2012).

Despite significant advances in the study of reward function in depression in adults (Hasler et al., 2004) and adolescents (Forbes & Dahl, 2012), research has mostly focused on reward and reward-related decision-making in nonsocial contexts; however, *social reward* may be especially salient for adolescents (Ernst, 2012). Indeed, given the interpersonal nature of depression, researchers have been calling for models of social reward to better understand adolescent depression (Forbes, 2009).

In response, Davey et al. (2008) proposed a model in which they delineate how biological and social changes characteristic of normative adolescence interact. This heuristic model focuses on the psychological changes that occur in the context of social reward, which, in turn, increases risk for depression in adolescence. In brief, the authors suggest that the development of the prefrontal cortex, in conjunction with the dopaminergic reward system, allows for the abstract representation of social reward, which is highly salient; a failure to obtain social reward suppresses activity within the reward system, and depression results. In the current article, we extend this model of vulnerability to adolescent depression by showing how the tools offered by the interdisciplinary field of neuroeconomics can be employed to (a) delineate and examine the exact mechanics of real-life interpersonal exchanges that may further maintain depression in adolescents and (b) provide a conceptual model of depression that incorporates neuroeconomic reward, developmental, and social perspectives on adolescent depression. We propose a neuroeconomic model of adolescent depression in which we suggest that a driving force in adolescent depression consists of anomalous decision-making in social exchanges with peers, which leads to social rejection, decreased responsiveness to social reward, and interpersonal stress, thereby serving to maintain depression. As such, we aim to extend Davey and colleagues’ (2008) model from a model of vulnerability to adolescent depression to include the maintenance and worsening of adolescent depression. While this extended model complements that of Davey et al. (2008), in that it focuses on the maintenance of depression, we acknowledge that the processes we describe may also play a role in vulnerability to depression.

We begin by more extensively discussing Davey and colleagues’ (2008) model, as it provides the context in which our model of depression is formulated. We then discuss new tools to examine the mechanics of real-time social exchanges that may result in, or maintain, depression. The field of neuroeconomics is thus introduced, followed by a discussion of reward processing and the neuroeconomic study of nonsocial reward in depression. As there has yet to be a neuroeconomic study of social reward in adolescent depression, we review behavioral economic findings with depressed adults and build support for our model of adolescent

depression as a perturbation of interpersonal motivational/reward exchange. Next, we formulate hypotheses regarding what is to be expected when neuroeconomics are applied to social reward in adolescent depression. Specifically, we examine how depression may interact with psychological principles that govern typical social exchanges, and modify the neural correlates of social decision-making processes. Finally, implications for treatment and future directions are discussed.

DAVEY, YÜCEL, AND ALLEN'S MODEL OF SOCIAL REWARD IN THE VULNERABILITY TO ADOLESCENT DEPRESSION

Davey et al. (2008) identified key biological and social features of adolescent development that interact to influence important psychological changes. These changes may increase risk for depression. Specifically, the adolescent brain undergoes dramatic developmental changes with implications for cognitive (e.g., abstract mental representation), emotional (e.g., increased emotionality), and behavioral (e.g., reward-seeking) functioning. At the onset of puberty, there is proliferation of prefrontal synapses, which is followed by synaptic pruning; concomitantly, myelination proceeds in the prefrontal cortex (Giedd et al., 1999). Pruning is understood as the elimination of infrequently used synapses, such that only highly functional connections are maintained and strengthened, leading to enhanced efficiency of neural networks. These changes in gray and white matter occur during a developmental shift in which the dopaminergic reward system and prefrontal cortex become more functionally connected (Brenhouse & Andersen, 2011; Spear, 2000), and prefrontal cortical firing patterns become more stable and finely tuned, with activity becoming less diffuse and more concentrated across development (Durstun et al., 2006). These changes suggest that the prefrontal cortex plays a substantial role in shaping and representing rewards, which become more complex and distal (requiring sustained engagement), and often embedded within a social context in adolescence.

In addition to these biological changes, marked social transformations occur during adolescence. The interpersonal focus shifts from parents to peers, with an increased emphasis on sociability. The adolescent must now also learn to navigate highly complex social situa-

tions. Peer relationships become increasingly layered during adolescence, such that affiliation with a smaller social group (e.g., immediate friends) extends to widespread social acceptance, as groups with similar social identities tend to interrelate (Brown, 2004). As such, achieving success in the social domain is typically important for a healthy developmental trajectory (Connolly, Geller, Marton, & Kutcher, 1992). To this end, motivation to obtain interpersonal (social) rewards is instrumental to the adolescent's development, and it is the anticipation of future reward that stimulates social reward-seeking behavior (Panksepp, 2005). Importantly, the social experience of adolescence is characterized by instability (Brown, 2004), as friendships and romantic relationships are difficult to maintain and are typically short-lived (Connolly, Furman, & Konarski, 2000). Further complicating the picture, having successful romantic and social group relationships is mutually influential, such that one at times may define the other (Connolly et al., 2000). Therefore, success (and/or failure) with peers may influence romantic relations and vice versa.

These dramatic biological and social changes are posited to lead to psychological changes that result in an increased desire for social rewards. These rewards are usually obtained over an extended period of time (e.g., finally getting a date with a long-time romantic crush). The biological developmental change that most contributes to abstract thinking for social reward is the enhanced functional connectivity between the prefrontal cortex and the dopaminergic system. The continued development of the prefrontal cortex allows for the newfound ability to create hypothetical scenarios or mental representations (Eccles, Wigfield, & Byrnes, 2003). The adolescent also acquires the capacity to play out these scenarios and their potential outcomes (Baird & Fugelsang, 2004). In terms of social changes that influence psychological development, the increased importance of peer relations and social reputation is integral to the development of one's sense of self. The capacity for representing social relationships, as well as one's self-identity, across time (past, present, and future) enables the adolescent to plan for the future. Thus, social rewards are abstractly represented and anticipated over an extended period of time.

In summary, Davey et al. (2008) suggest two overarching factors that contribute to vulnerability to depression in adolescence. First, social rewards are extremely salient during adolescence, but obtaining them can be challenging. Second, the ability to represent social rewards in a temporally extended fashion guides motivation for the pursuit of social reward. Taken together, the failure to obtain social reward may result in interpersonal disappointment and reduced positive affect, in turn decreasing interpersonal motivation. The omission of anticipated reward then inhibits the reward system, resulting in the onset of depression.

THE EXTENSION OF DAVEY AND COLLEAGUES' MODEL TO INCLUDE THE MECHANICS OF REAL-TIME SOCIAL EXCHANGE

Davey and colleagues' (2008) model of depression is highly innovative and makes a significant contribution to the literature by providing a theoretical framework for the relations between the unique salience of social reward and the development of adolescent depression. However, their model stops short at delineating the exact mechanics of how social exchanges between people occur in real time and how these exchanges may result in or maintain depression.

Neuroeconomics, a new and interdisciplinary field (discussed in more detail below), allows for the study of social reward in single interpersonal exchanges (e.g., one-shot exchanges) as well as those that occur over time (e.g., multiround exchanges). Thus, behavioral economic games, which constitute the basic tools of neuroeconomics, allow for the study of social exchanges in various timescales and can be valuable for delineating, evaluating, and describing the mechanics of interpersonal exchanges. Prior approaches to understanding the mechanics of interpersonal exchanges in depression have relied heavily on traditional social-cognitive approaches. We discuss this literature first to highlight the limitations of these approaches and then suggest how the field of neuroeconomics can address these limitations.

TRADITIONAL APPROACHES TO EXAMINING SOCIAL COGNITION IN DEPRESSION

Theorists consider depression to be a highly interpersonal illness. When depressed individuals interact with healthy people, they are perceived as socially undesirable, elicit negative emotions in others, and are often

rejected (i.e., Coyne, 1976; Joiner, Metalsky, Katz, & Beach, 1999; Strack & Coyne, 1983). Researchers have naturally looked at social cognition to explain the perturbations in interpersonal relations commonly found in depression. Social cognition refers to the mental processes involved in perceiving, attending to, remembering, thinking about, and making sense of the people in our social world (Moskowitz, 2005). Depression is associated with impaired social cognition, and the extent of these deficits is more pronounced as the severity of depression worsens (Manstead, Doshmambetova, Shearn, & Clifton, 2013). As social cognition in depression has been widely studied, for the sake of brevity, we limit our discussion to impaired theory of mind (ToM: the ability to understand the beliefs and intentions of others), emotion recognition, and the negative biases in cognitive processing found in depression.

With respect to the understanding of others' beliefs and intentions, deficits in depressed individuals have been reported using a range of experimental tasks. Inoue, Tonooka, Yamada, and Kanba (2004) used a cartoon picture story task, depicting a woman who catches a bee in a paper bag and then presents it to the other character (a monkey), who is unaware of what she caught. Remitted MDD participants performed equally well as healthy controls on a first-order false belief question ("What does the monkey think is in the bag?"); however, they performed significantly poorer on a second-order false belief question ("What does the monkey think the woman intends to do?"). Expanding on this finding, using an array of cartoon stories with currently depressed patients, Zobel et al. (2010) found impairment across a spectrum of social-cognitive processes (i.e., understanding others' belief and intentions). Additionally, depressed patients were poorer at providing narratives for the stories, using fewer words and identifying fewer mental states in the stories' characters. Thus, ToM deficits appear to be present in depression, during the course of a depressive episode and while in remission.

Novel ToM tasks, with greater ecological validity, have also been applied to depression. For instance, the Movie for the Assessment of Social Cognition (MASC; Dziobek et al., 2006) is a short film that depicts four people getting together for a dinner one evening, and

the research participant is required to infer various mental states, both within and between characters, in an effort to integrate a real-world social scene. The social dynamics between these characters are complex and highly relevant to adolescence, as themes throughout the film include romantic interest/flirtation (and rejection), sarcastic remarks, and social exchanges (altruism and reciprocity) between friends. The MASC has yet to be used with depressed adolescents, but Wolkenstein, Schönenberg, Schirm, and Hautzinger (2011) found that adults with MDD were less accurate, making more errors associated with reduced or less ToM ability.

In terms of the capacity to recognize or understand others' emotions, depression is generally associated with enhanced salience and elaboration of negative emotion in interpersonal contexts. Depressed individuals have exhibited a bias toward negative emotion, misconstruing depictions of neutral affect as negative more often than healthy controls (Gollan, Pane, McCloskey, & Coccaro, 2008; Leppänen, Milders, Bell, Terriere, & Hietanen, 2004). However, more ecologically valid research methodologies have led to discrepant findings. For example, the Reading the Mind in the Eyes Task (RMET; Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001), in which one must infer the mental states of others based solely on the expression of their eyes, has revealed both an impaired ability to infer mental states in others (Lee, Harkness, Sabbagh, & Jacobson, 2005; Wang, Wang, Chen, Zhu, & Wang, 2008) and healthy functioning in depressed adults (Kettle, O'Brien-Simpson, & Allen, 2008; Wolkenstein et al., 2011). In an effort to remedy these discrepant RMET findings, Manstead et al. (2013) conducted an investigation with both dysphoric and MDD participants and found that the degree of impairment on the RMET was a function of severity of depression, with more severe depression being associated with poorer accuracy. Of note, affective symptoms, rather than nonaffective symptoms, were specifically related to poorer performance on the task.

Beyond ToM and emotion recognition, the affective dysfunction in depression is associated with a range of cognitive deficits (Tavares, Drevets, & Sahakian, 2003), with implications for social-cognitive functioning and

social decision-making. Specifically, depression is associated with a negatively biased cognitive processing style in which negative stimuli are elaborated upon, more difficult to disengage from, and associated with perturbations in cognitive control (Gotlib & Joormann, 2010). Several studies have linked depression to this negative attentional bias (Gotlib, Krasnoperova, Yue, & Joormann, 2004; Kyte, Goodyer, & Sahakian, 2005; Tavares et al., 2003), which is proposed to be instrumental in the development and maintenance of depressive symptoms (Knutson, Bhanji, Cooney, Atlas, & Gotlib, 2008). The extent to which this negative cognitive processing style may influence social exchanges is worthy of investigation.

The above research has been clearly influential in elucidating the social-cognitive basis of depression. However, this research is also characterized by inconsistent findings, small effect sizes, and low predictive validity that may be due to several theoretical and methodological limitations, a number of which have been identified (Sharp, 2012). First, these approaches fail to capture the dynamic interpersonal nature of social cognition, and, because these tasks are largely hypothetical, they are unlikely to fully gain participants' emotional and behavioral investment. Second, these approaches typically consider social cognition as occurring within the individual, rather than as an interaction between two or more individuals. Third, they are not administered in real time, fail to sample real social interactions, and generally lack ecological validity. Lastly, these measures do not allow for the development of mathematically tractable models of social interaction. In other words, there is no way to quantify play-by-play interpersonal exchanges; instead, research participants retrospectively report on global subjective impressions of actual social interactions or predict global patterns of behavior for hypothetical social scenarios. Thus, we remain ignorant of the dynamic and stochastic nature of interpersonal exchanges. In neuroeconomics, social decisions are linked to an economic currency, thereby creating a metric that can then be associated with brain activity through functional neuroimaging. Below, we provide a more detailed description of the neuroeconomic approach.

NEUROECONOMICS: A BRIEF INTRODUCTION

The decisions we make guide the way we navigate our environment, with implications for ourselves and others. Decision-making is a complex process that consists of evaluating options, forming preferences, selecting and executing actions based on preferences, and outcome evaluation (Ernst & Paulus, 2005). Even seemingly inconsequential decisions can be highly complex (Sharp, Monterosso, & Montague, 2012). Moreover, the decisions we make are not always rational, and research has shown that in the context of social exchanges, certain additional psychological processes guide decision-making. For instance, loss aversion refers to people's general tendency to prefer avoiding loss at the expense of potential gains (Kahneman & Tversky, 1984). In other words, when presented with two options of equal weight, people generally assign greater relative value to the loss condition; that is, the amount in satisfaction lost when \$10 is forfeited is greater than the satisfaction gained when \$10 is won. Therefore, people prefer not to lose \$10. Another example of seemingly irrational thinking, the endowment effect, refers to the fact that when people possess an item, they assign greater value to it than to an identical item they do not own (Kahneman, Knetsch, & Thaler, 1990). Thus, they require payment that is greater than its worth if they are to part with it.

The "revolution" brought by behavioral economists like Kahneman and Tversky in the late 1970s and 1980s built on the neoclassical revolution of the 1930s. It was then that economists began to examine the mathematical structure underlying consumer choice and behavior; however, many models focused on how consumers *should* choose (e.g., the best choice in terms of economic utility), rather than what they *actually* chose and the psychological processes that guided these decisions (Glimcher, Camerer, Fehr, & Poldrack, 2009). Throughout the 1940s, theorists continued to develop axiomatic models of choice that failed to consider the influence of psychological principles; as feelings were not easily measurable, they were excluded (Camerer, Loewenstein, & Prelec, 2005). However, these axioms were proven falsifiable, and the pivotal work of Kahneman and Tversky led to the birth of behavioral economics, which argued that psychological principles could be used to improve economic theory

(Glimcher et al., 2009). The study of decision-making had expanded beyond observable behavior, and the concurrent emergence of neuroscience and neuroimaging technology has provided a new means of investigating how the brain makes decisions.

Thus, "neuroeconomics" was coined to refer to a burgeoning field that integrates psychology, economics, and neuroscience in an effort to provide a single unified theory to explain human choice and behavior. The rationale behind the integration of these disciplines stems from the ability of each field to contribute a unique explanation for behavior at different levels of analysis: Economics provides a set of theoretical assumptions to frame and predict behavior within mathematically tractable models; psychology offers explanations for why choice often deviates from such models (i.e., loss aversion, the endowment effect, heuristics, and framing effects); and neuroscience provides researchers with the neurobiological basis of choice behavior (Glimcher & Rustichini, 2004). The end result combines theory from each discipline with behavioral economics and neuroimaging. In creating a unified theory, the neuroeconomic approach seeks to uncover the variables that the brain computes in decision-making, how these computations are implemented and constrained by neurobiological substrates, and how these decisions affect behavioral outcomes (Sharp et al., 2012). As the field is in its nascent stages and continues to take shape, it is important to note that several types of economic decision-making paradigms may be considered "neuroeconomic" (i.e., delay discounting, reward responsiveness tasks), as they involve the allocation of rewards, the valuation of monetary stimuli, hedonic response to reward, and so forth. While these nonsocial paradigms are of great interest, we are mostly interested in the games that occur in the context of social exchange with another person, given that this might be the largest contribution of neuroeconomics to the field of psychopathology and our social conceptualization of adolescent depression.

The neuroeconomic approach has been applied to several psychiatric populations (see a recent special issue in *Biological Psychiatry*, vol. 72(2) for a review). We review some of this research below—starting with neuroeconomic research using behavioral economic tasks in nonsocial contexts, and then discuss games of social exchange.

REWARD PROCESSING AND THE NEUROECONOMIC STUDY OF NONSOCIAL REWARD-RELATED DECISION-MAKING IN DEPRESSION

Neuroeconomics offers a unique approach to the creation of a revised nosology of psychological disorder based on observable behavior and neurobiological substrates, at least as far as reward function is concerned (Sharp, 2012). Anomalous reward processing has been found in a range of psychopathology, including substance use disorders (Knutson, Adams, Fong, & Hommer, 2001), pathological gambling (Monterosso, Piray, & Luo, 2012), schizophrenia (Chau, Roth, & Green, 2004), anxiety (Guyer et al., 2012; Hartley & Phelps, 2012), and depression (Olino et al., 2011). Reward processing anomalies have also been found in individuals at high risk for the development of disorder, before initial onset (Sharp et al., 2014). Collectively, across various forms of psychopathology, findings suggest that reward dysfunction may serve as an endophenotype for psychological disorder, and further investigation of reward processing has the potential to guide etiological models and improve treatment methods.

Reward is a rather loaded term given its various meanings, components, and functions. Reward refers to an immediate gain resulting from a choice (Montague, King-Casas, & Cohen, 2006), an environmental incentive that one will approach and later work for to obtain, or something that results in a positive emotional experience (Chau et al., 2004). Thus, *reward* is a multifaceted term that includes aspects of learning and motivation, as well as hedonic processes (Berridge & Robinson, 2003). The neural circuitry of reward is highly distributed, comprising a variety of regions included in the limbic cortico-striatal thalamic circuit with extensive functional connectivity to the mesolimbic dopamine pathway, stemming from dopaminergic neurons in the VTA (Chau et al., 2004). Neuroeconomic studies tracking brain activity to rewarding stimuli (e.g., money, goods, love, and trust) have identified a common set of key structures involved in the processing of social and nonsocial rewards: the orbitofrontal cortex (OFC), ventral striatum (VS), and ventromedial prefrontal cortex (vmPFC; Montague et al., 2006)—all subserved by the dopaminergic system, with the OFC guiding reward valuation and expectation, the VS supporting reward detection and goal represen-

tation, and the vmPFC active in goal representation (Schultz & Dickinson, 2000). Additionally, the dorsal striatum plays a role in coordinating action selection and initiation (Balleine, Delgado, & Hikosaka, 2007), and once goal-directed behavior is initiated, the dorso-medial prefrontal cortex (dmPFC) is activated during conflict detection (de Wit, Kosaki, Balleine, & Dickinson, 2006). However, limiting the definition of the reward system to these regions is an oversimplification. Additional structures have been implicated, such as the amygdala (harm avoidance, associative learning, appetitive and aversive coding) and dorsal anterior cingulate (dACC; conflict and error monitoring), among others (Ernst & Paulus, 2005).

The value of a given reward is coded by the reward system in the form of a prediction error, or the difference between the anticipated value and actual value of the obtained reward. Of note, it is the anticipated value of reward that has been found to motivate behavior toward appetitive stimuli (Davey et al., 2008). This value difference, between anticipated and obtained reward, is coded via dopaminergic neurons, and the magnitude of this discrepancy provides a basis for reward-directed learning: A high-value reward produces a positive prediction error that eventually falls to zero (no new learning occurs), and the omission of an expected reward results in a negative prediction error, thus leading to the extinction of that learned behavior (Schultz & Dickinson, 2000). Research examining the valuation of nonsocial and social reward, *within* subjects in healthy samples, has revealed that the brain utilizes the same neural circuitry for reward valuation of both nonsocial (e.g., money) and social rewards (e.g., smile, frown; Lin, Adolphs, & Rangel, 2012). For example, the brain codes a prediction error, and recruits the same neural circuitry, in the processing of positive (or negative) regard from another person just as it does for nonsocial rewards (Poore et al., 2012). Just as in nonsocial contexts, in which prediction errors guide reinforcement learning (Niv, 2009), social reward-related prediction errors (e.g., acceptance from peers) are also key signals for reinforcement learning in a social context that may alter subsequent social behavior (Jones et al., 2011). Converging evidence suggests that the value assigned to a reward is a *subjective value*, shaped by prior experience, with neuronal firing rates shifting

to encode a value reflective of an individual's particular choice (Glimcher & Fehr, 2013). Using a monetary delayed discounting task, Kable and Glimcher (2007) revealed subjective value to be represented in several brain regions, including the VS, mPFC, and posterior cingulate cortex. Additionally, brain activity in these regions increased in response to larger rewards and decreased with greater delay to reward.

The application of neuroeconomic reward-related paradigms to nonsocial contexts has provided insight into the decision-making of depressed individuals. These paradigms have typically used money as a reward in the context of card guessing (i.e., Delgado, Nystrom, Fissell, Noll, & Fiez, 2000) or probabilistic choice (i.e., the Wheel of Fortune; Ernst et al., 2004). In combination with fMRI, researchers have analyzed the different stages of decision-making and neural response to reward in adults. For instance, in a card-guessing task, depressed participants demonstrated decreased response times following a "win" and had blunted responses in the VS, which correlated with self-reported anhedonia (Steele, Kumar, & Ebmeier, 2007). Using the Wheel of Fortune task, MDD participants have been found to exhibit reduced striatal activity during reward selection, anticipation, and feedback as well as hyperactivity in the OFC during reward selection (Smoski et al., 2009). In remitted patients, the reward circuit is hyperactive during reward anticipation and hypoactive during reward outcomes, suggesting that aberrant frontostriatal response to rewards may represent a trait marker for MDD (Dichter, Kozink, McClellon, & Smoski, 2012). Depressed individuals also have been found to exhibit a failure to modify responses to maximize the attainment of reward (Henriques & Davidson, 2000), an impaired ability to integrate reinforcement history, a favoring of high-probability reward cues in the absence of immediate reward (Pizzagalli et al., 2009), and liberal betting with low odds and conservative betting with high odds (Kyte et al., 2005; Murphy et al., 2001). Furthermore, in the anticipation of decision outcomes, depressed individuals exhibited increased dACC activity for monetary gains (healthy controls manifest this response for losses); neural activity in response to reward is attenuated in the nucleus accumbens (reduced hedonic response) and caudate (reduced reinforcement for actions); and fronto-striatal dysfunction is thought to

underlie poor learning from feedback (Eshel & Roiser, 2010).

Consistent with the adult literature, the study of nonsocial reward in depressed youth has revealed a similar pattern of reduced striatal and increased medial prefrontal response to reward in nonsocial paradigms (Forbes & Dahl, 2012; Forbes et al., 2006, 2009). Following winning outcomes in a card-guessing game, depressed adolescents have demonstrated reduced reward anticipation in the striatum, indicative of poor expectations for future successes (Olinio et al., 2011). Exploring reward dysfunction as a vulnerability to MDD using a similar task, Sharp et al. (2014) found depressed and high-risk girls to respond with reduced right VS activation in the outcome phase of decision-making, and this neural activity was significantly correlated with maternal depression. As with adults, aberrant reward processing is accompanied by atypical choice behavior. For example, in a game of chance, depressed adolescents have been found to respond with impaired evaluation and planning and failed to distinguish between low- and high-magnitude rewards under high-probability conditions (Forbes, Shaw, & Dahl, 2007). This disrupted reward processing appears to be predictive of real-world affective experience (Forbes et al., 2009) and may play a central role in guiding the depressed adolescents as they navigate their social world.

Clearly, the neuroeconomic study of nonsocial reward in depression has been fruitful. However, this research has predominantly been limited to a nonsocial context, with very few studies using social interaction paradigms or focusing on social reward, especially in youth. Social rewards are at the core of everyday interpersonal functioning in both adults and adolescents, and such investigations may further our understanding of the mechanisms of reward dysfunction in depression (Forbes & Dahl, 2012). We now will turn to the few behavioral economic studies that examined the reward-related decision-making of depressed participants in social contexts.

SOCIAL DECISION-MAKING IN DEPRESSION: BEHAVIORAL ECONOMIC FINDINGS IN DEPRESSED ADULTS

People live in highly complex social environments, and the decisions we make often take place in interpersonal

contexts, making them inherently tied to the decisions of others (Rilling & Sanfey, 2011). Behavioral economic games are designed to examine reward-related social decision-making. These games (summarized in Table 1) can be defined by the following: They involve two or more decision-makers (players), who choose among two or more choices; the game outcome depends on the choices of its players, who choose among a range of possible outcomes; and each outcome is assigned a numerical payoff, which is a numerical representation of players' preferences (Camerer, 2003). In turn, a social decision can be defined as a preference "based on a positive or negative concern for the welfare of others, and on what other players believe about them" (Fehr & Camerer, 2007). Behavioral economic games (games of social exchange), combined with functional neuroimaging, are the primary tools used by neuroeconomics for testing and developing theories of decision-making in social contexts. These games have allowed investigators to study a variety of social-cognitive constructs (i.e., trust, reciprocity, and fairness) through the choices people make. Moreover, these games can be modified to

examine new constructs through the manipulation of game format, range of available choices, and so forth. To date, there is a dearth of neuroeconomic research examining social decision-making in depression; however, behavioral economic studies (without the use of fMRI) have been conducted.

Using the prisoner's dilemma, Hokanson, Sacco, Blumberg, and Landrum (1980) manipulated the relative power (e.g., degree of social dominance) of social roles in subclinically depressed and nondepressed adults. When depressed participants were in a high-power role, player interactions were noncooperative and exploitive. Negative emotions were expressed by depressed players, which elicited noncooperativeness, extra punitiveness, and helplessness in nondepressed coplayers. When depressed players were in a low-power role, there were no group differences in gameplay; however, helplessness and self-devaluation were communicated by depressed players, which elicited ingratiating from other players. Haley and Strickland (1986) found women with elevated depressive symptoms to be more aggressive following betrayal, and they were more self-critical regardless of the game's

Table 1. Descriptions of behavioral economic games and expected findings in adolescent depression

Game	Description	Hypothesized Effect of Adolescent Depression	Supportive Findings
Trust game (Berg, Dickhaut, & McCabe, 1995) <i>Constructs:</i> Trust, reciprocity	A game between two players in which the "investor" decides how much of their \$10 to send to the "trustee," an anonymous counterpart in another room. Each dollar sent is tripled along the way, and the trustee then decides how much of the tripled money to keep and return to the investor. Numerous researchers have since modified this game in terms of currency, number of rounds, conditions, etc.	As investor: greater amount allocated to trustee	Unoka et al. (2009)
Ultimatum game (Guth, Schmittberger, & Swarze, 2005) <i>Constructs:</i> Fairness, altruism	A game between two players, a "proposer" and a "responder." Using a predetermined sum of money, the proposer may allocate any portion of that sum to the responder. The responder then decides whether to accept or reject the proposer's offer. With an accepted offer, both players receive the agreed-upon amounts. With a rejected offer, both players receive nothing.	As proposer: higher offers made on average As responder: greater rate of acceptance of low offers	Destoop et al. (2012) Scheele et al. (2013) Harlé et al. (2010)
Dictator game (Kahneman, Knetsch, & Thaler, 1986) <i>Constructs:</i> Cooperation, altruism	A game between two players, the "dictator" and the "recipient." Using a predetermined sum of money, the dictator decides how much of that sum the recipient shall receive. The recipient, in turn, has no power over the situation and must accept whatever is given.	Higher allocations to recipient	Destoop et al. (2012) Scheele et al. (2013)
Prisoner's dilemma <i>Constructs:</i> Cooperation, competition, exploitation	Put simply, the prisoner's dilemma involves two participants engaged in a predicament with one another. They must choose between predetermined options that promote their own benefit, their coplayer's benefit, or their mutual benefits, respectively. Each decision strategy has different results for the players.	Equally or overly cooperative behavior	Haley and Strickland (1986)

outcome. These results are similar to Hokanson and colleagues' (1980) study in that cooperation appeared to be undermined by features of depression. Also, depressed players exhibited a negative self-view, which may have elicited reactions in other players. The nature of this reaction may vary over time, beginning with ingratiation and ending in rejection.

Although there have been few ultimatum game studies of adult depression, extant findings suggest that depression is associated with atypical considerations of fairness in social exchanges. As proposers, depressed players have been found to make higher offers than healthy comparisons (Destoop, Schrijvers, De Grave, Sabbe, & De Bruijn, 2012; Scheele, Mihov, Schwederski, Maier, & Hurlmann, 2013). These results suggest that depressed players act hyperfairly to others. In terms of responder behavior, findings are unequivocal. Harlé, Allen, and Sanfey (2010) found depressed players to accept an excessive rate of unfair offers, despite reporting stronger negative emotional reactions when accepting them. Other results suggest that depressed responders behave comparably to controls (Destoop et al., 2012) or, alternatively, that they reject an abundance of unfair offers (Scheele et al., 2013). Importantly, these studies differed in terms of patient characteristics and the range of offer sizes available. For example, Scheele et al. (2013) gave players a wider range of offer sizes from which to choose. This approach may be particularly useful in delineating more subtle influences of depression. Overall, the discrepancies between these findings, in terms of responder behavior, suggest that future ultimatum game studies are warranted.

Using an extension of the basic trust game, Unoka, Seres, Áspán, Bódi, and Kéri (2009) investigated interpersonal (trust) versus general risk-taking in depressed inpatients and healthy controls. The trust game was played under two conditions. In the first condition, the trustee was another player (trust game), and in the second condition, the trustee was a lottery that randomly determined how much was sent back (general risk game). The investment strategies of depressed players did not significantly differ from controls in either game condition. However, the depressed group did invest more in the trust game, 6.5 versus 6.1 monetary units transferred. These findings suggest that depressed individuals do in fact trust in the cooperativeness of others.

Collectively, these behavioral economic findings, though somewhat mixed, suggest that depression may have distinct influences on social decision-making. For instance, adult depression is associated with atypical social cooperation (Haley & Strickland, 1986) and excessive fairness (Destoop et al., 2012; Scheele et al., 2013). It has been posited that features of depression likely influence decision-making in social interactions, as the depressed individual may question his or her social behavior and its outcomes (Kyte & Goodyer, 2008). To this end, we now provide our neuroeconomic model of adolescent depression and hypothesize how specific features of depression (i.e., low self-efficacy and low self-worth) may influence social decision-making. Specifically, we suggest that depression undermines behavioral economic principles (i.e., inequality aversion) that govern typical social exchanges.

AN EXTENDED MODEL OF SOCIAL REWARD: ADOLESCENT DEPRESSION AS A PERTURBATION OF INTERPERSONAL MOTIVATIONAL/REWARD EXCHANGE

Thus far, this review has aimed to integrate a range of research to provide the foundation for an extended model of social reward in adolescent depression. This model is visually presented in Figure 1.

Davey et al. (2008) proposed a model in which they delineate how biological and social changes characteristic of normative adolescence interact, such that important psychological changes in the context of social reward occur, which in turn increases risk for depression in adolescence. In summary, they suggest that the development of the prefrontal cortex, in conjunction with the dopaminergic reward system, allows for the abstract representation of social reward, which is highly salient during adolescence; a failure to obtain social reward suppresses the reward system, and depression results. We extend this model of vulnerability to depression to include the mechanics of social reward-related decision-making in the maintenance of depression. As previously stated, while we focus on the maintenance of depression, the processes included in Figure 1 also may apply to vulnerability to depression.

We propose that the neuroeconomic study of social reward in adolescent depression will reveal anomalous decision-making that serves to maintain depression. The most integral piece of our model is the idea that

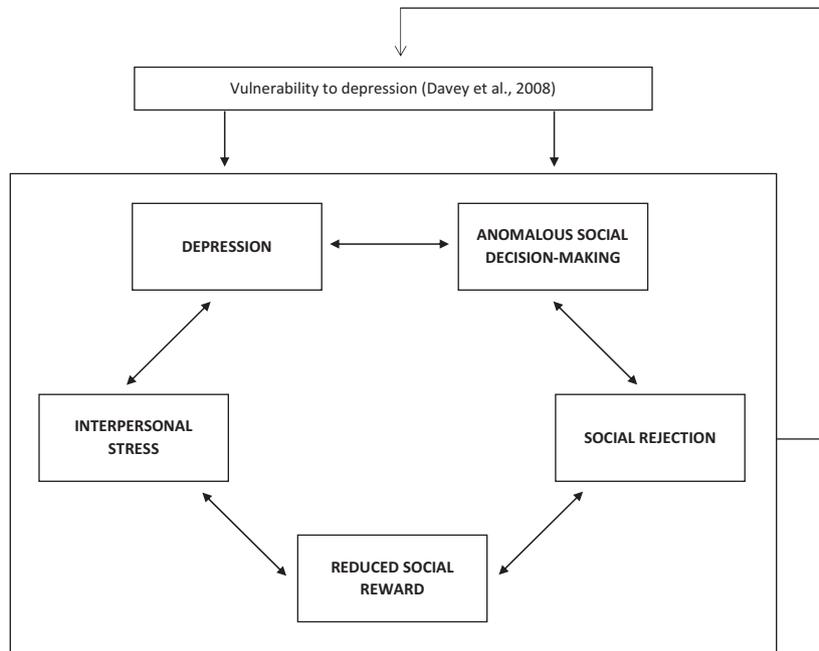


Figure 1. A neuroeconomic model of adolescent depression. The proposed neuroeconomic model of adolescent depression characterizes adolescent depression as a perturbation of interpersonal motivational/reward exchange. We suggest that atypical social decision-making, evaluated through neuroeconomic methods, may delineate important interpersonal mechanisms of depression. Specifically, we suggest that depression distinctly influences psychological principles that govern typical (healthy) social exchanges. These perturbations of interpersonal reward/exchange lead to social rejection, which then reduces social reward. Here, we suggest that anhedonia is an acquired deficiency or a consequence of rejection; however, we do not exclude the possibility that anhedonia may also play a causal role in the lead-up to social rejection. While the model depicted above appears to exclusively describe interpersonal processes that may maintain depression, the recursive arrow linking the maintenance model of depression with Davey and colleagues' (2008) vulnerability model of depression depicts that the same processes may be involved in predisposing vulnerability to depression.

atypical social decision-making, evaluated through neuroeconomic methods, may delineate important interpersonal mechanisms of depression. Specifically, we suggest that depression distinctly influences psychological principles that govern typical (healthy) social exchanges. These perturbations of interpersonal reward/exchange lead to social rejection, which then reduces social reward. Here, we suggest that anhedonia is an acquired deficiency or a consequence of rejection; however, we do not exclude the possibility that anhedonia may also play a causal role in the lead-up to social rejection.

To illustrate our model, consider an ultimatum game with Laura, a depressed adolescent, and Beth, her healthy peer. Beth will be playing as the proposer (making offers) and Laura will be the responder (accepting or rejecting offers). As a reference, consider the fact that proposers typically offer about 40-50% of

the total pot, and lesser offers tend to be rejected by responders (Cooper & Dutcher, 2011). With a pot of \$10, Beth would be expected to offer \$4 or \$5, on average, during the course of the game, that is, if her coplayer conformed to conventional behavior and rejected low offers. Instead, Laura accepts a higher rate of unfair offers than a healthy girl would, which changes the course of the game. In the end, Beth leaves the game with a disproportionate amount of earnings, as compared to Laura. Beth may interpret Laura's behavior as a cue that Laura may not deserve to be respected and/or is not worthy of friendship. Beth may also wonder why Laura was accepting of so little. In other words, Laura's decision to accept such low offers may have sent the signal that she is socially undesirable, overly submissive, and rather different from Beth. The result of this interaction is that Beth rejects Laura. This causes significant interpersonal stress

and disappointment, exacerbating Laura's depressive symptoms, which then influence her decision-making in future social exchanges. This anomalous social decision-making perpetuates her depression.

In testing this model, future neuroeconomic/behavioral economic studies should include postgame assessments to determine each player's (depressed and nondepressed) appraisals of the other player's performance, as well as their emotional and behavioral responses. This would shed light on whether atypical social decisions do in fact promote rejection. Findings suggest the choices made by depressed individuals elicit negative emotional and behavioral reactions in healthy coplayers (Hokanson et al., 1980), and we predict similar findings across a range of games. We now lay out our hypotheses for how adolescent depression may influence social decision-making via disruption of the psychological principles that govern typical social exchanges. Then, we extend our discussion to the potential neural correlates associated with social reward-related decision-making in adolescent depression.

POTENTIAL HYPOTHESES DERIVED FROM THE EXTENDED NEUROECONOMIC MODEL OF ADOLESCENT DEPRESSION

We formulate our hypotheses by drawing on behavioral economic findings in adult depression, as well as neuroeconomic/behavioral economic findings with healthy participants. For an overview of the hypothesized effect of depression, and supporting evidence, please refer to Table 1.

Given the well-known developmental psychopathology principle that typical and atypical development intersect to confer risk for psychiatric disorders (Cicchetti & Cohen, 2006), we expect that certain features of typical adolescent development will be magnified in adolescent depression. In examining how depression may result in atypical social exchanges, we focus specifically on three psychological principles that have emerged from the behavioral economic literature: inequality aversion, the certainty effect, and the endowment effect. Each principle will be defined, and we will discuss any relevant normative developmental considerations. From there, we will integrate behavioral economic findings with depressed adults and then downwardly extend our discussion to adolescent

depression with a focus on how features of depression (i.e., low self-worth) may explain the expected atypical social decision-making strategies. Finally, we further expand this discussion to include hypotheses regarding the neural correlates of social decision-making in adolescent depression.

Inequality aversion refers to the fact that if an individual believes that another person is treating them unfairly (i.e., making too low of an offer), they will punish that person at their own expense (Fehr & Schmidt, 1999). In other words, they will pass up the opportunity for gain (receiving "less" is more than nothing) simply to spite the unfair person. The ultimatum game, which lends itself to the study of inequality aversion, has revealed significant developmental differences in decision-making strategies. As compared to healthy adults, adolescents are "overly" fair as they make larger offers and reject fewer unfair offers (Hoffmann & Tee, 2006). In essence, healthy adolescents, as compared to adults, exhibit a form of reduced inequality aversion; they offer more and take less during social exchanges with peers. This may be due to the enhanced salience of social reward during adolescence (Ernst, 2012).

In extending the principle of inequality aversion to depression, adult behavioral economic findings are somewhat inconclusive. As responders in the ultimatum game, depressed players have been found to display reduced inequality aversion, accepting more unfair offers (Harlé et al., 2010); an equal degree of inequality aversion, with similar rejection rates (Destoop et al., 2012); and a heightened sense of inequality aversion, rejecting more offers (Scheele et al., 2013). As proposers, depressed players have been found to be excessively fair (Destoop et al., 2012; Scheele et al., 2013), which suggests reduced inequality aversion. Taken together, we expect depressed adolescents to exhibit reduced inequality aversion (or excessive fairness), as compared to healthy adolescents, making larger offers and rejecting fewer offers in the ultimatum game. These choices may result from the depressed adolescent's feelings of worthlessness and low self-esteem, which make them less deserving of a "fair" share. Thus, they bestow more to the other player. Alternatively, these depressive choices may intend to serve a protective function in an effort to maintain social

connections in the threat of exclusion (see Allen & Badcock, 2003), but instead serve to promote social rejection.

Next, we turn to the *certainty effect*, which refers to people's tendency to overweight likely outcomes (e.g., guaranteed) in comparison with those that are uncertain or risky (e.g., 30% chance of success; Tversky & Kahneman, 1986). In other words, people typically opt for the safe bet rather than a riskier option with greater payoff. Current findings led us to two alternative hypotheses regarding depression and the certainty effect, which is dependent on game type (trust versus ultimatum). Trust game studies with healthy adolescents have found that trust increases and peaks during adolescence, as compared to childhood and adulthood (van den Bos, Westenberg, van Dijk, & Crone, 2010; Sutter & Kocher, 2007). The fact that adolescents make the highest investments in trustees indicates a relatively greater degree of risk-taking in the context of social reward (see Steinberg, 2005). We expect that adolescent depression will be associated with even greater trust, or a reduced certainty effect. This hypothesis draws first from the fact that depressed adults have made higher offers (albeit nonsignificant) than controls in the trust game (Unoka et al., 2009). Second, it might be that excessive trust in depression unfolds as an exaggeration of a normal feature of adolescent development (increased trust).

When we apply the certainty effect to the ultimatum game, we may instead find that low efficacy results in a magnified certainty effect in depression. In terms of responder behavior, it could be argued that rejecting low offers in early rounds, in hopes that it will lead to higher offers by the proposer in subsequent rounds, is a risky strategy because the responder is forgoing an immediate and guaranteed offer, albeit a low one, for the opportunity at a higher offer later. The desire to take this strategy may depend on one's sense of self-efficacy or the belief that one's behavior as a responder has the power to influence the proposer's choices. The relations between low self-efficacy and depression are well established, such that low self-efficacy is associated with greater depression (Bandura, Pastorelli, Barbaranelli, & Caprara, 1999; Muris, 2002). Regarding the sense of an inability to affect the other player's behavior, depression has long been conceptualized as a

disorder in which individuals feel that they are inept at creating changes within their environment (Benassi, Sweeney, & Dufour, 1988). In line with "depressive realism" (see Alloy & Abramson, 1988), it may not be that depressed individuals feel incapable of altering the other player's behavior; instead, they exhibit a more "realistic" view of the influence their choices have on subsequent rounds of the game. As such, depressed players may be less able to overestimate the likelihood of a contingency between their decisions in prior rounds and future coplayer responses (Moore & Fresco, 2012). As proposers in the ultimatum game, depressed players make higher offers (Destoop et al., 2012; Scheele et al., 2013), which may be due to the fact that they are sensitive to interpersonal rejection (see Downey & Feldman, 1996) or that they are generally risk averse (see Yuen & Lee, 2003) and unwilling to take the chance that the other player will reject a lower offer.

The last principle of note, the *endowment effect*, refers to the fact that people assign a greater (than expected) value to an item within their possession, such that they require payment that exceeds market value if they are to part with it (Kahneman et al., 1990). Converging evidence suggests that depression is associated with some form of reverse endowment effect (see Lerner, Small, & Loewenstein, 2004). For instance, in the ultimatum game, depressed adults make higher offers than healthy comparisons (Destoop et al., 2012). Thus, when a valued item was in their possession (e.g., money), they were actually *more* willing to part with it. Findings from the trust game study by Unoka et al. (2009) are also in line with this notion. We expect adolescent depression to also be associated with a reversed endowment effect.

Sensitivity to reward, in the context of social exchanges, is also worth considering. We expect the hyposensitivity to nonsocial reward in adolescent depression (Forbes & Dahl, 2012) to extend to interpersonal contexts. As such, a reduced salience of social reward may result in the depressed adolescent assigning a lesser value to exchange currencies, making anomalous offers to other players. Behavioral economic games typically use money as rewards. Given the robust finding that depression is associated with reduced hedonic response to monetary outcomes (Ernst et al., 2004;

Pizzagalli et al., 2009; Smoski et al., 2009), the use of alternative reward-related stimuli, ones that may be more motivating to depressed adolescents, may reduce potential confounds.

The next question to consider is how the above hypotheses regarding behavioral responses in social exchange games may map onto brain function. Since a neuroeconomic study of social reward in depression has yet to be conducted, we predominantly draw on the neural correlates in healthy participants and then speculate as to what we expect in adolescent depression. We focus our discussion on three common games: the ultimatum game, the prisoner's dilemma, and the trust game.

In the ultimatum game, receipt of fair offers is associated with ventral striatal activity, whereas receipt of unfair offers is associated with anterior insula activation and the experience of negative emotions (Rilling, King-Casas, & Sanfey, 2008). During social exchanges, the anterior insula has been implicated in detecting social norm violations (King-Casas et al., 2008; Kishida, King-Casas, & Montague, 2010) and is highly activated in response to perceived unfairness. Depressed adults have been found to accept more unfair offers despite having a greater negative emotional response during such social exchanges (Harlé et al., 2010). Given this emotional response, we would expect greater insula activity in depressed versus healthy adolescents. In healthy participants, reduced vmPFC is associated with a greater rejection rate of offers (Koenigs & Tranel, 2007). Since depression has been linked to a greater acceptance of unfair offers, we expect that heightened vmPFC activity may inhibit the insula in depression. It may not be that depressed adolescents are less sensitive to social norm violations, *per se*; they may just be less likely or willing to act on them. This explanation would fall in line with the consistent finding that depression is associated with abnormally high vmPFC activity (Koenigs & Grafman, 2009).

During cooperative social interaction (in the prisoner's dilemma), the ventral and dorsal striatum, vmPFC, and rostral anterior cingulate cortex (ACC) are activated (Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004). Importantly, the brain recruits the same neural circuitry for the processing of both nonsocial

and social rewards (Lin et al., 2012). As reduced striatal activity in response to nonsocial reward is a key feature of adolescent depression (Forbes et al., 2009), it is likely that cooperation (a social reward) also elicits a hypoactive striatal response. Rewarding (nonsocial) stimuli, in the form of positive autobiographical memories, have been associated with decreased vmPFC activity in depression (Keedwell, Andrew, Williams, Brammer, & Phillips, 2005); the extent to which these findings translate to interpersonal contexts is unclear. Similarly, we can only speculate from nonsocial reward research as to what may be found in terms of the ACC. Depressed individuals have exhibited abnormal ACC activity during the receipt of nonsocial reward, recruiting dorsal rather than rostral regions (Eshel & Roiser, 2010), and similar results may be found in the context of social reward.

Utilizing a multiround two-player trust game (investor and trustee), King-Casas et al. (2005) found the reciprocity of one player to predict the future trust of their coplayer. The "intention to trust" was linked to the caudate nucleus. The reputation of the other player was thought to be coded by caudate activity, which shifted during phases of the social exchange. For nonsocial reward in depression, there is hypoactivity of the caudate in relating action-outcome relationships (Pizzagalli et al., 2009). In a social context, similar reduced caudate activity may influence the intention to trust. Lesion studies have revealed impaired vmPFC functioning to be associated with reduced trust and reciprocity (van den Bos & Güroğlu, 2009). Therefore, vmPFC hyperactivity in depression (Koenigs & Grafman, 2009) may also relate to excessive trust and reciprocity. Trust game studies have demonstrated that, across adolescence, there is developmental shift from self-interest in early adolescence to the consideration of others and increased perspective taking in late adolescence (Crone, 2013). These changes are associated with differential neural recruitment beginning with more anterior activation (anteromedial prefrontal cortex) that shifts to posterior regions (temporo-parietal junction). As traditional social-cognitive measures (i.e., second-order false belief tasks; Inoue et al., 2004) have shown that adult depression is associated with impaired perspective taking, we may expect to find that adolescent depression interferes with this typical (cognitive/neural) developmental shift,

thereby influencing subtle changes in social-cognitive processing that occur in late adolescence (see Dumontheil, Apperly, & Blakemore, 2010).

IMPLICATIONS FOR TREATMENT

Interpersonally based areas for intervention in adolescent depression include promoting social engagement and building positive social skills (Mason, Schmidt, Abraham, Walker, & Tercyak, 2009); however, these targets are relatively broad. Neuroeconomics can identify *specific* aspects of disrupted interpersonal functioning. These findings may assist in the development and/or refinement of adolescent depression-specific psychotherapies. Those aimed at improving social functioning and problem-solving skills, such as interpersonal psychotherapy for depressed adolescents (IPT-A; Mufson, Weissman, Moreau, & Garfinkel, 1999), may best be informed. By identifying specific social exchange deficits, neuroeconomic games may also serve as novel assessment tools.

Game results, from large collections of social exchange data, can be used to develop a mathematically tractable neurobiological and behavioral classification of adolescent depression. From there, games may serve as tools for providing assessments of patients at the start of, and throughout, treatment. The direction and magnitude of choices made by the patient informs the clinician of treatment target(s), and game results can indicate treatment progress over time. For detecting adolescents at risk for depression or those with sub-threshold symptoms, neuroeconomic games may serve as screeners that can help guide prevention and early intervention efforts.

Perhaps the most synergistic and innovative application of neuroeconomics is through the adoption of games as tools for behavioral experiments in cognitive therapy. Behavioral experiments, or planned experiments undertaken by patients, are excellent at facilitating cognitive change (Bennett-Levy et al., 2004). Behavioral economic games may serve as behavioral experiments allowing the clinician and patient, or outside confederates, to examine moment-to-moment social-cognitive thoughts, emotions, and behaviors as they occur during social exchanges. Given the clinician's cognitive formulation of the patient, the context of these games may be manipulated in several ways for specificity in treatment (i.e., with whom the game is

played, history of prior exchanges). Game results can then be used to test the hypotheses regarding the patient's belief(s) about himself/herself or others. Thus, these games can be used to examine and treat social cognition as it occurs during social interactions.

Neuroeconomics may also be applied to behavioral activation approaches to treating adolescent depression. Neuroeconomic games can be made into video games designed to actively engage adolescents. Performance-based incentives, such as game points or medals, can be provided to motivate the patient and add positive reinforcement. After each gaming session, the patient may log his or her pleasure and sense of accomplishment rating, which can be stored to track improvement over time. Thus, the patient can reflect on progress using interactive data. To promote success in social exchanges, games can be manipulated in various ways. For instance, rejecting unfair offers can be made easier, or it could be made more difficult to make large offers. Through this training, the adolescent can learn decision-making strategies for successful social exchanges. As a result, the salience of social reward may increase.

Finally, neuroeconomics may reveal aberrations of neural processing in interpersonal functioning in depression, thus assisting developers of pharmacological treatments. Neuroeconomics provides a novel means for measuring the effect and/or efficacy of medications on brain function in a real-world social context. Identifying potential deviations from normal brain development that are correlated with or caused by adolescent depression may provide strategic points of intervention.

CONCLUSION AND FUTURE DIRECTIONS

This review discussed how neuroeconomics may serve as a valuable tool for investigating social cognition in adolescent depression. Thus far, neuroeconomic research has led to a more comprehensive understanding of the reward system and nonsocial reward in adult and adolescent depression. However, a highly interpersonal disorder like depression would benefit from being studied within a social context. While traditional approaches to the study of social cognition in depression have been informative, they have several limitations (see Sharp, 2012). Perhaps most importantly, these methods fail to capture actual social interactions as they occur *between* people. Neuroeconomics provides

the tools for investigating these real-world social exchanges in an effort to further understand interpersonal dysfunction in depression.

The neuroeconomic approach provides multiple levels of analysis with the potential for more integrated theories of social cognition in adolescent depression. However, to reach that point, the field requires more methodological consistency, and experimental paradigms should be adolescent appropriate. Researchers should aim for a consensus as to how adolescent groups are delineated (e.g., early, mid-, and late adolescents). While chronological age has traditionally been used, converging evidence suggests that pubertal stage is a better indicator of development (Goddings, Burnett Heyes, Bird, Viner, & Blakemore, 2012). Richards, Plate, and Ernst (2013) proposed several potential confounds in the reward literature that stem from the nature of experimental paradigms. These confounds should be considered when integrating findings across studies. There are substantial differences in the degree of behavioral engagement for passive-viewing versus performance-dependent tasks. For performance-dependent tasks, assessing motivation is imperative as disengagement may lead to invalid results. A novel decision-making task, the Effort-Expenditure for Rewards Task (EEfRT; Treadway, Buckholz, Schwartzman, Lambert, & Zald, 2009), is able to account for motivation by differentiating between effort to obtain reward and desire for reward. Thus, this task is able to parse out some of the primary factors (motivation versus hedonic response) involved in reward-related decision-making.

There are also developmental considerations that must be addressed. Simply because tasks are adult appropriate does not ensure that they are suitable for adolescents. For instance, adults and adolescents generally differ in terms of reaction time and accuracy in behavioral-dependent tasks. Lastly, the rewarding stimuli should be appealing to adolescents in an effort to ensure motivation and engagement. In all, future studies should be designed to take these (and other) adolescent-focused considerations into account.

The further enhancement of the interpersonal quality of social exchanges also needs attention. Although neuroeconomics allows for the examination of social reward due to the interpersonal nature of the games,

these games typically rely on monetary currencies as incentives. It may be argued that it is difficult to separate the social value component of the exchange from the monetary value itself, despite research suggesting that monetary reward and social reward are similarly encoded in the brain (Montague et al., 2006). In this regard, manipulating the context of the game, specifically who the game is played with (i.e., parent, friend, or stranger), may shed light on the social value component. In cases when other players are not available, using large normative data sets of human-to-human interactions, computers may generate decision-making strategies that mimic these types of interpersonal relationships (King-Casas & Chiu, 2012).

Despite the need to address these methodological limitations, the neuroeconomic study of depression in adults and adolescents has been uniquely informative. In our neuroeconomic model of social reward, we posit that atypical decision-making during social exchanges is a key mechanism in the maintenance of adolescent depression. The extent to which perturbations of social exchange influence the cyclic nature of depression presents exciting opportunities for future research.

REFERENCES

- Allen, N. B., & Badcock, P. B. (2003). The social risk hypothesis of depressed mood: Evolutionary, psychosocial, and neurobiological perspectives. *Psychological Bulletin, 129*(6), 887–913. doi:10.1037/0033-2909.129.6.887
- Alloy, L. B., & Abramson, L. Y. (1988). *Depressive realism: Four theoretical perspectives*. New York, NY: Guilford Press.
- Baird, A. A., & Fugelsang, J. A. (2004). The emergence of consequential thought: Evidence from neuroscience. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences, 359*(1451), 1797–1804
- Balleine, B. W., Delgado, M. R., & Hikosaka, O. (2007). The role of the dorsal striatum in reward and decision-making. *Journal of Neuroscience, 27*(31), 8161–8165. doi:10.1523/JNEUROSCI.1554-07.2007
- Bandura, A., Pastorelli, C., Barbaranelli, C., & Caprara, G. (1999). Self-efficacy pathways to childhood depression. *Journal of Personality and Social Psychology, 76*(2), 258–269. doi:10.1037/0022-3514.76.2.258
- Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The “Reading the Mind in the Eyes” Test Revised Version: A study with normal adults, and adults with Asperger syndrome or high-functioning

- autism. *Journal of Child Psychology and Psychiatry*, 42(2), 241–251. doi:10.1111/1469-7610.00715
- Benassi, V. A., Sweeney, P. D., & Dufour, C. L. (1988). Is there a relation between locus of control orientation and depression? *Journal of Abnormal Psychology*, 97(3), 357. doi:10.1037/0021-843X.97.3.357
- Bennett-Levy, J., Westbrook, D., Fennell, M., Cooper, M., Rouf, K., & Hackmann, A. (2004). Behavioural experiments: Historical and conceptual underpinnings. In J. Bennett-Levy, G. Butler, M. Fennell, A. Hackman, M. Mueller, D. Westbrook, ... D. Westbrook (Eds.), *Oxford guide to behavioural experiments in cognitive therapy* (pp. 1–20). New York, NY: Oxford University Press.
- Berg, J., Dickhaut, J., & McCabe, K. (1995). Trust, reciprocity, and social history. *Games and Economic Behavior*, 10(1), 122–142. doi:10.1006/game.1995.1027
- Berridge, K. C., & Robinson, T. E. (2003). Parsing reward. *Trends in Neurosciences*, 26(9), 507–513. doi:10.1016/S0166-2236(03)00233-9
- van den Bos, W., & Güroğlu, B. (2009). The role of the ventral medial prefrontal cortex in social decision making. *Journal of Neuroscience*, 29(24), 7631–7632. doi:10.1523/JNEUROSCI.1821-09.2009
- van den Bos, W., Westenberg, M., van Dijk, E., & Crone, E. A. (2010). Development of trust and reciprocity in adolescence. *Cognitive Development*, 25, 90–102. doi:10.1016/j.cogdev.2009.07.004
- Brenhouse, H. C., & Andersen, S. L. (2011). Developmental trajectories during adolescence in males and females: A cross-species understanding of underlying brain changes. *Neuroscience & Biobehavioral Reviews*, 35(8), 1687–1703. doi:10.1016/j.neubiorev.2011.04.013
- Brown, B. B. (2004). Adolescents' relationships with peers. *Handbook of Adolescent Psychology*, 2, 363–394
- Camerer, C. (2003). *Behavioral game theory: Experiments in strategic interaction*. Princeton, NJ: Princeton University Press.
- Camerer, C., Loewenstein, G., & Prelec, D. (2005). Neuroeconomics: How neuroscience can inform economics. *Journal of Economic Literature*, 43, 9–64. doi:10.1257/0022051053737843
- Chau, D., Roth, R., & Green, A. (2004). The neural circuitry of reward and its relevance to psychiatric disorders. *Current Psychiatry Reports*, 6(5), 391–399. doi:10.1007/s11920-004-0026-8
- Cicchetti, D., & Cohen, D. J. (2006). *Developmental psychopathology, Vol 1: Theory and method* (2nd ed.). Hoboken, NJ: John Wiley & Sons
- Connolly, J., Furman, W., & Konarski, R. (2000). The role of peers in the emergence of heterosexual romantic relationships in adolescence. *Child Development*, 71(5), 1395–1408. doi:10.1111/1467-8624.00235
- Connolly, J., Geller, S., Marton, P., & Kutcher, S. (1992). Peer responses to social interaction with depressed adolescents. *Journal of Clinical Child Psychology*, 21(4), 365–370. doi:10.1207/s15374424jccp2104_6
- Cooper, D. J., & Dutcher, E. G. (2011). The dynamics of responder behavior in ultimatum games: A meta-study. *Experimental Economics*, 14(4), 519–546. doi:10.1007/s10683-011-9280-x
- Coyne, J. C. (1976). Depression and the response of others. *Journal of Abnormal Psychology*, 85(2), 186–193. doi:10.1037/0021-843X.85.2.186
- Crone, E. A. (2013). Considerations of fairness in the adolescent brain. *Child Development Perspectives*, 7, 97–103. doi:10.1111/cdep.12022
- Davey, C. G., Yücel, M., & Allen, N. B. (2008). The emergence of depression in adolescence: Development of the prefrontal cortex and the representation of reward. *Neuroscience & Biobehavioral Reviews*, 32(1), 1–19. doi:10.1016/j.neubiorev.2007.04.016
- Delgado, M. R., Nystrom, L. E., Fissell, C. C., Noll, D. C., & Fiez, J. A. (2000). Tracking the hemodynamic responses to reward and punishment in the striatum. *Journal of Neurophysiology*, 84(6), 3072–3077
- Destoop, M., Schrijvers, D., De Grave, C., Sabbe, B., & De Bruijn, E. A. (2012). Better to give than to take? Interactive social decision-making in severe major depressive disorder. *Journal of Affective Disorders*, 137(1–3), 98–105. doi:10.1016/j.jad.2011.12.010
- Dichter, G. S., Kozink, R. V., McClernon, F., & Smoski, M. J. (2012). Remitted major depression is characterized by reward network hyperactivation during reward anticipation and hypoactivation during reward outcomes. *Journal of Affective Disorders*, 136(3), 1126–1134. doi:10.1016/j.jad.2011.09.048
- Diekhof, E., Falkai, P., & Gruber, O. (2008). Functional neuroimaging of reward processing and decision-making: A review of aberrant motivational and affective processing in addiction and mood disorders. *Brain Research Reviews*, 59(1), 164–184. doi:10.1016/j.brainresrev.2008.07.004
- Downey, G., & Feldman, S. I. (1996). Implications of rejection sensitivity for intimate relationships. *Journal of Personality and Social Psychology*, 70(6), 1327–1343. doi:10.1037/0022-3514.70.6.1327
- Dumontheil, I., Apperly, I. A., & Blakemore, S. J. (2010). Online usage of theory of mind continues to develop in late adolescence. *Developmental Science*, 13(2), 331–338. doi:10.1111/j.1467-7687.2009.00888.x

- Durston, S., Davidson, M. C., Tottenham, N., Galvan, A., Spicer, J., Fossella, J. A., & Casey, B. J. (2006). A shift from diffuse to focal cortical activity with development. *Developmental Science*, *9*(1), 1–8. doi:10.1111/j.1467-7687.2005.00454.x
- Dziobek, I., Fleck, S., Kalbe, E., Rogers, K., Hassenstab, J., Brand, M., ... Convit, A. (2006). Introducing MASC: A movie for the assessment of social cognition. *Journal of Autism and Developmental Disorders*, *36*(5), 623–636. doi:10.1007/s10803-006-0107-0
- Eccles, J. S., Wigfield, A., & Byrnes, J. (2003). Cognitive development in adolescence. *Handbook of Psychology*, *4*, 325–350
- Ernst, M. (2012). The usefulness of neuroeconomics for the study of depression across adolescence into adulthood. *Biological Psychiatry*, *72*(2), 84–86. doi:10.1016/j.biopsych.2012.02.027
- Ernst, M., Nelson, E. E., McClure, E. B., Monk, C. S., Munson, S., Eshel, N., ... Pine, D. S. (2004). Choice selection and reward anticipation: An fMRI study. *Neuropsychologia*, *42*(12), 1585–1597. doi:10.1016/j.neuropsychologia.2004.05.011
- Ernst, M., & Paulus, M. P. (2005). Neurobiology of decision making: A selective review from a neurocognitive and clinical perspective. *Biological Psychiatry*, *58*(8), 597–604. doi:10.1016/j.biopsych.2005.06.004
- Eshel, N., & Roiser, J. P. (2010). Reward and punishment processing in depression. *Biological Psychiatry*, *68*(2), 118–124. doi:10.1016/j.biopsych.2010.01.027
- Fehr, E., & Camerer, C. F. (2007). Social neuroeconomics: The neural circuitry of social preferences. *Trends in Cognitive Sciences*, *11*(10), 419–427. doi:10.1016/j.tics.2007.09.002
- Fehr, E., & Schmidt, K. M. (1999). A theory of fairness, competition, and cooperation. *Quarterly Journal of Economics*, *114*(3), 817–868. doi:10.1162/00335539956151
- Forbes, E. E. (2009). Where's the fun in that? Broadening the focus on reward function in depression. *Biological Psychiatry*, *66*(3), 199–200. doi:10.1016/j.biopsych.2009.05.001
- Forbes, E. E., & Dahl, R. E. (2012). Research review: Altered reward function in adolescent depression: What, when and how? *Journal of Child Psychology and Psychiatry*, *53*(1), 3–15. doi:10.1111/j.1469-7610.2011.02477.x
- Forbes, E. E., Hariri, A. R., Martin, S. L., Silk, J. S., Moyses, D. L., Fisher, P. M., ... Dahl, R. E. (2009). Altered striatal activation predicting real-world positive affect in adolescent major depressive disorder. *American Journal of Psychiatry*, *166*, 64–73. doi:10.1176/appi.ajp.2008.07081336
- Forbes, E. E., May, C., Siegle, G. J., Ladouceur, C. D., Ryan, N. D., Carter, C. S., ... Dahl, R. E. (2006). Reward-related decision-making in pediatric major depressive disorder: An fMRI study. *Journal of Child Psychology and Psychiatry*, *47*(10), 1031–1040. doi:10.1111/j.1469-7610.2006.01673.x
- Forbes, E. E., Shaw, D. S., & Dahl, R. E. (2007). Alterations in reward-related decision making in boys with recent and future depression. *Biological Psychiatry*, *61*, 633–639. doi:10.1016/j.biopsych.2006.05.026
- Galván, A. (2010). Adolescent development of the reward system. *Frontiers in Human Neuroscience*, *4*, 1–9. doi:10.3389/neuro.09.006.2010
- Galván, A. (2013). The teenage brain: Sensitivity to rewards. *Current Directions in Psychological Science*, *22*(2), 88–93. doi:10.1177/0963721413480859
- Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A., ... Rapoport, J. L. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience*, *2*(10), 861–863. doi:10.1038/13158
- Glimcher, P. W., Camerer, C. F., Fehr, E., & Poldrack, R. A. (2009). *Neuroeconomics: Decision making and the brain*. San Diego, CA: Elsevier Academic Press.
- Glimcher, P. W., & Fehr, E. (2013). *Neuroeconomics: Decision making and the brain* (2nd ed.). San Diego, CA: Elsevier Academic Press.
- Glimcher, P. W., & Rustichini, A. (2004). Neuroeconomics: The consilience of brain and decision. *Science*, *306*(5695), 447–452. doi:10.1126/science.1102566
- Goddings, A. L., Burnett Heyes, S., Bird, G., Viner, R. M., & Blakemore, S. J. (2012). The relationship between puberty and social emotion processing. *Developmental Science*, *15*(6), 801–811. doi:10.1111/j.1467-7687.2012.01174.x
- Gollan, J. K., Pane, H. T., McCloskey, M. S., & Coccaro, E. F. (2008). Identifying differences in biased affective information processing in major depression. *Psychiatry Research*, *159*(1–2), 18–24. doi:10.1016/j.psychres.2007.06.011
- Gotlib, I. H., Hamilton, J. P., Cooney, R. E., Singh, M. K., Henry, M. L., & Joormann, J. (2010). Neural processing of reward and loss in girls at risk for major depression. *Archives of General Psychiatry*, *67*(4), 380–387. doi:10.1001/archgenpsychiatry.2010.13
- Gotlib, I. H., & Joormann, J. (2010). Cognition and depression: Current status and future directions. *Annual*

- Review of Clinical Psychology*, 6, 285–312. doi:10.1146/annurev.clinpsy.121208.131305
- Gotlib, I. H., Krasnoperova, E., Yue, D. N., & Joormann, J. (2004). Attentional biases for negative interpersonal stimuli in clinical depression. *Journal of Abnormal Psychology*, 113, 121–135. doi:10.1037/0021-843X.113.1.121
- Güth, W., Schmittberger, R., & Schwarze, B. (2005). An experimental analysis of ultimatum bargaining. In M. H. Bazerman & M. H. Bazerman (Eds.), *Negotiation, decision making and conflict management* (Vol. 1–3; pp. 342–363). Northampton, MA: Edward Elgar.
- Guyer, A. E., Choate, V. R., Detloff, A., Benson, B., Nelson, E. E., Perez-Edgar, K., ... Ernst, M. (2012). Striatal functional alteration during incentive anticipation in pediatric anxiety disorders. *American Journal of Psychiatry*, 169(2), 205–212. doi:10.1176/appi.ajp.2011.11010006
- Haley, W. E., & Strickland, B. R. (1986). Interpersonal betrayal and cooperation: Effects on self-evaluation in depression. *Journal of Personality and Social Psychology*, 50(2), 386–391. doi:10.1037/0022-3514.50.2.386
- Harlé, K. M., Allen, J. B., & Sanfey, A. G. (2010). The impact of depression on social economic decision making. *Journal of Abnormal Psychology*, 119, 440–446. doi:10.1037/a0018612
- Hartley, C. A., & Phelps, E. A. (2012). Anxiety and decision-making. *Biological Psychiatry*, 72, 113–118. doi:10.1016/j.biopsych.2011.12.027
- Hasler, G., Drevets, W. C., Manji, H. K., & Charney, D. S. (2004). Discovering endophenotypes for major depression. *Neuropsychopharmacology*, 29(10), 1765–1781. doi:10.1038/sj.npp.1300506
- Henriques, J. B., & Davidson, R. J. (2000). Decreased responsiveness to reward in depression. *Cognition and Emotion*, 14(5), 711–724. doi:10.1080/02699930050117684
- Hoffmann, R., & Tee, J.-Y. (2006). Adolescent–adult interaction and culture in the ultimatum game. *Journal of Economic Psychology*, 27, 98–116. doi:10.1016/j.joep.2005.06.014
- Hokanson, J. E., Sacco, W. P., Blumberg, S. R., & Landrum, G. C. (1980). Interpersonal behavior of depressive individuals in a mixed-motive game. *Journal of Abnormal Psychology*, 89(3), 320–332. doi:10.1037/0021-843X.89.3.320
- Inoue, Y., Tonooka, Y., Yamada, K., & Kanba, S. (2004). Deficiency of theory of mind in patients with remitted mood disorder. *Journal of Affective Disorders*, 82(3), 403–409. doi:10.1016/j.jad.2004.04.004
- Joiner, T. R., Metalsky, G. I., Katz, J., & Beach, S. H. (1999). Depression and excessive reassurance-seeking. *Psychological Inquiry*, 10(4), 269–278. doi:10.1037/a0013866
- Jones, R. M., Somerville, L. H., Li, J., Ruberry, E. J., Libby, V., Glover, G., ... Casey, B. J. (2011). Behavioral and neural properties of social reinforcement learning. *Journal of Neuroscience*, 31(37), 13039–13045. doi:10.1523/JNEUROSCI.2972-11.2011
- Kable, J. W., & Glimcher, P. W. (2007). The neural correlates of subjective value during intertemporal choice. *Nature Neuroscience*, 10(12), 1625–1633. doi:10.1038/nn2007
- Kahneman, D., Knetsch, J. L., & Thaler, R. H. (1986). Fairness and the assumptions of economics. *Journal of Business*, 59(4), S285–S300. doi:10.1086/296367
- Kahneman, D., Knetsch, J. L., & Thaler, R. H. (1990). Experimental tests of the endowment effect and the Coase theorem. *Journal of Political Economy*, 98(6), 1325–1348. <http://www.jstor.org/stable/2937761>
- Kahneman, D., & Tversky, A. (1984). Choices, values, and frames. *American Psychologist*, 39(4), 341–350. doi:10.1037/0003-066X.39.4.341
- Keedwell, P. A., Andrew, C., Williams, S. C., Brammer, M. J., & Phillips, M. L. (2005). The neural correlates of anhedonia in major depressive disorder. *Biological Psychiatry*, 58(11), 843–853. doi:10.1016/j.biopsych.2005.05.019
- Kettle, J. L., O'Brien-Simpson, L., & Allen, N. B. (2008). Impaired theory of mind in first-episode schizophrenia: Comparison with community, university and depressed controls. *Schizophrenia Research*, 99(1–3), 96–102. doi:10.1016/j.schres.2007.11.011
- King-Casas, B., & Chiu, P. H. (2012). Understanding interpersonal function in psychiatric illness through multiplayer economic games. *Biological Psychiatry*, 72(2), 119–125. doi:10.1016/j.biopsych.2012.03.033
- King-Casas, B., Sharp, C., Lomax-Bream, L., Lohrenz, T., Fonagy, P., & Montague, P. (2008). The rupture and repair of cooperation in borderline personality disorder. *Science*, 321(5890), 806–810. doi:10.1126/science.1156902
- King-Casas, B., Tomlin, D., Anen, C., Camerer, C. F., Quartz, S. R., & Montague, P. (2005). Getting to know you: Reputation and trust in a two-person economic exchange. *Science*, 308(5718), 78–83. doi:10.1126/science.1108062
- Kishida, K. T., King-Casas, B., & Montague, P. R. (2010). Neuroeconomic approaches to mental disorders. *Neuron*, 67(4), 543–554. doi:10.1016/j.neuron.2010.07.021

- Knutson, B., Adams, C. M., Fong, G. W., & Hommer, D. (2001). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *Journal of Neuroscience*, *21*(16), RC159
- Knutson, B., Bhanji, J. P., Cooney, R. E., Atlas, L. Y., & Gotlib, I. H. (2008). Neural responses to monetary incentives in major depression. *Biological Psychiatry*, *63*(7), 686–692. doi:10.1016/j.biopsych.2007.07.023
- Koenigs, M., & Grafman, J. (2009). The functional neuroanatomy of depression: Distinct roles for ventromedial and dorsolateral prefrontal cortex. *Behavioural Brain Research*, *201*(2), 239–243. doi:10.1016/j.bbr.2009.03.004
- Koenigs, M., & Tranel, D. (2007). Irrational economic decision-making after ventromedial prefrontal damage: Evidence from the ultimatum game. *Journal of Neuroscience*, *27*(4), 951–956. doi:10.1523/JNEUROSCI.4606-06.2007
- Kyte, Z., & Goodyer, I. (2008). Social cognition in depressed children and adolescents. In C. Sharp, P. Fonagy, & I. Goodyer (Eds.), *Social cognition and developmental psychopathology* (pp. 201–237). New York, NY: Oxford University Press.
- Kyte, Z. A., Goodyer, I. M., & Sahakian, B. J. (2005). Selected executive skills in adolescents with recent first episode major depression. *Journal of Child Psychology and Psychiatry*, *46*(9), 995–1005. doi:10.1111/j.1469-7610.2004.00400.x
- Lee, L., Harkness, K. L., Sabbagh, M. A., & Jacobson, J. A. (2005). Mental state decoding abilities in clinical depression. *Journal of Affective Disorders*, *86*(2–3), 247–258. doi:10.1016/j.jad.2005.02.007
- Leppänen, J. M., Milders, M., Bell, J., Terriere, E., & Hietanen, J. K. (2004). Depression biases the recognition of emotionally neutral faces. *Psychiatry Research*, *128*(2), 123–133. doi:10.1016/j.psychres.2004.05.020
- Lerner, J. S., Small, D. A., & Loewenstein, G. (2004). Heart strings and purse strings: Carryover effects of emotions on economic decisions. *Psychological Science*, *15*(5), 337–341. doi:10.1111/j.0956-7976.2004.00679.x
- Lewinsohn, P. M., Rohde, P., & Seeley, J. R. (1998). Major depressive disorder in older adolescents: Prevalence, risk factors, and clinical implications. *Clinical Psychology Review*, *18*(7), 765–794. doi:10.1016/S0272-7358(98)00010-5
- Lin, A., Adolphs, R., & Rangel, A. (2012). Social and monetary reward learning engage overlapping neural substrates. *Social Cognitive and Affective Neuroscience*, *7*(3), 274–281. doi:10.1093/scan/nsr006
- Manstead, A. S., Dosmukhambetova, D., Shearn, J., & Clifton, A. (2013). The influence of dysphoria and depression on mental state decoding. *Journal of Social and Clinical Psychology*, *32*(1), 116–133. doi:10.1521/jscp.2013.32.1.116
- Mason, M. J., Schmidt, C., Abraham, A., Walker, L., & Tercyak, K. (2009). Adolescents' social environment and depression: Social networks, extracurricular activity, and family relationship influences. *Journal of Clinical Psychology in Medical Settings*, *16*(4), 346–354. doi:10.1007/s10880-009-9169-4
- Merikangas, K., He, J., Burstein, M., Swanson, S. A., Avenevoli, S., Cui, L., ... Swendsen, J. (2010). Lifetime prevalence of mental disorders in U.S. adolescents: Results from the National Comorbidity Survey Replication-Adolescent Supplement (NCS-A). *Journal of the American Academy of Child and Adolescent Psychiatry*, *49*(10), 980–989. doi:10.1016/j.jaac.2010.05.017
- Montague, P., King-Casas, B., & Cohen, J. D. (2006). Imaging valuation models in human choice. *Annual Review of Neuroscience*, *29*, 417–448. doi:10.1146/annurev.neuro.29.051605.112903
- Monterosso, J., Piray, P., & Luo, S. (2012). Neuroeconomics and the study of addiction. *Biological Psychiatry*, *72*(2), 107–112. doi:10.1016/j.biopsych.2012.03.012
- Moore, M. T., & Fresco, D. M. (2012). Depressive realism: A meta-analytic review. *Clinical Psychology Review*, *32*(6), 496–509. doi:10.1016/j.cpr.2012.05.004
- Moskowitz, G. B. (2005). *Social cognition: Understanding self and others*. New York, NY: Guilford Press.
- Mufson, L., Weissman, M. M., Moreau, D., & Garfinkel, R. (1999). Efficacy of interpersonal psychotherapy for depressed adolescents. *Archives of General Psychiatry*, *56*(6), 573–579. doi:10.1001/archpsyc.56.6.573
- Muris, P. (2002). Relationships between self-efficacy and symptoms of anxiety disorders and depression in a normal adolescent sample. *Personality and Individual Differences*, *32*(2), 337–348. doi:10.1016/S0191-8869(01)00027-7
- Murphy, F. C., Rubinsztein, J. S., Michael, A., Rogers, R. D., Robbins, T. W., Paykel, E. S., & Sahakian, B. J. (2001). Decision-making cognition in mania and depression. *Psychological Medicine*, *31*(4), 679–693. doi:10.1017/S0033291701003804
- Niv, Y. (2009). Reinforcement learning in the brain. *Journal of Mathematical Psychology*, *53*(3), 139–154. doi:10.1016/j.jmp.2008.12.005
- Olino, T. M., McMakin, D. L., Dahl, R. E., Ryan, N. D., Silk, J. S., Birmaher, B., ... Forbes, E. E. (2011). "I won, but I'm not getting my hopes up": Depression moderates the relationship of outcomes and reward anticipation.

- Psychiatry Research: Neuroimaging*, 194(3), 393–395. doi:10.1016/j.pscychresns.2011.04.009
- Panksepp, J. (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and Cognition*, 14(1), 30–80. doi:10.1016/j.concog.2004.10.004
- Petty, S. C., Sachs-Ericsson, N., & Joiner, T. E., Jr. (2004). Interpersonal functioning deficits: Temporary or stable characteristics of depressed individuals? *Journal of Affective Disorders*, 81(2), 115–122. doi:10.1016/S0165-0327(03)00158-7
- Pizzagalli, D. A., Holmes, A. J., Dillon, D. G., Goetz, E. L., Birk, J. L., Bogdan, R., ... Fava, M. (2009). Reduced caudate and nucleus accumbens response to rewards in unmedicated individuals with major depressive disorder. *American Journal of Psychiatry*, 166(6), 702–710. doi:10.1176/appi.ajp.2008.08081201
- Poore, J. C., Pfeifer, J. H., Berkman, E. T., Inagaki, T. K., Welborn, B. L., & Lieberman, M. D. (2012). Prediction-error in the context of real social relationships modulates reward system activity. *Frontiers in Human Neuroscience*, 6, 1–11. doi:10.3389/fnhum.2012.00218
- Richards, J. M., Plate, R. C., & Ernst, M. (2013). A systematic review of fMRI reward paradigms used in studies of adolescents vs. adults: The impact of task design and implications for understanding neurodevelopment. *Neuroscience and Biobehavioral Reviews*, 37(5), 976–991. doi:10.1016/j.neubiorev.2013.03.004
- Rilling, J. K., King-Casas, B., & Sanfey, A. G. (2008). The neurobiology of social decision-making. *Current Opinion in Neurobiology*, 18(2), 159–165. doi:10.1016/j.conb.2008.06.003
- Rilling, J. K., & Sanfey, A. G. (2011). The neuroscience of social decision-making. *Annual Review of Psychology*, 62, 23–48. doi:10.1146/annurev.psych.121208.131647
- Rilling, J. K., Sanfey, A. G., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2004). The neural correlates of theory of mind within interpersonal interactions. *NeuroImage*, 22(4), 1694–1703. doi:10.1016/j.neuroimage.2004.04.015
- Scheele, D., Mihov, Y., Schwederski, O., Maier, W., & Hurlmann, R. (2013). A negative emotional and economic judgment bias in major depression. *European Archives of Psychiatry and Clinical Neuroscience*, 263(8), 675–683. doi:10.1007/s00406-013-0392-5
- Schultz, W. (1998). Predictive reward signal of dopamine neurons. *Journal of Neurophysiology*, 80(1), 1–27
- Schultz, W., & Dickinson, A. (2000). Neuronal coding of prediction errors. *Annual Review of Neuroscience*, 23, 473–500. doi:10.1146/annurev.neuro.23.1.473
- Sharp, C. (2012). The use of neuroeconomic games to examine social decision making in child and adolescent externalizing disorders. *Current Directions in Psychological Science*, 21(3), 183–188. doi:10.1177/0963721412444726
- Sharp, C., Kim, S., Herman, L., Pane, H., Reuter, T., & Strathearn, L. (2014). Major depression in mothers predicts reduced ventral striatum activation in adolescent female offspring, with and without depression. *Journal of Abnormal Psychology*, 123(2), 298–309. doi:10.1037/a0036191
- Sharp, C., Monterosso, J., & Montague, P. (2012). Neuroeconomics: A bridge for translational research. *Biological Psychiatry*, 72(2), 87–92. doi:10.1016/j.biopsych.2012.02.029
- Smoski, M. J., Felder, J., Bizzell, J., Green, S. R., Ernst, M., Lynch, T. R., & Dichter, G. S. (2009). fMRI of alterations in reward selection, anticipation, and feedback in major depressive disorder. *Journal of Affective Disorders*, 118(1–3), 69–78. doi:10.1016/j.jad.2009.01.034
- Spear, L. P. (2000). The adolescent brain and age-related behavioral manifestations. *Neuroscience & Biobehavioral Reviews*, 24(4), 417–463. doi:10.1016/S0149-7634(00)00014-2
- Steele, J. D., Kumar, P. P., & Ebmeier, K. P. (2007). Blunted response to feedback information in depressive illness. *Brain: A Journal of Neurology*, 130(9), 2367–2374. doi:10.1093/brain/awm150
- Steinberg, L. (2005). Cognitive and affective development in adolescence. *Trends in Cognitive Sciences*, 9(2), 69–74. doi:10.1016/j.tics.2004.12.005
- Strack, S., & Coyne, J. C. (1983). Social confirmation of dysphoria: Shared and private reactions to depression. *Journal of Personality and Social Psychology*, 44(4), 798–806. doi:10.1037/0022-3514.44.4.798
- Sutter, M., & Kocher, M. G. (2007). Trust and trustworthiness across different age groups. *Games and Economic Behavior*, 59, 364–382. doi:10.1016/j.geb.2006.07.006
- Tavares, J. V. T., Drevets, W. C., & Sahakian, B. J. (2003). Cognition in mania and depression. *Psychological Medicine*, 33(6), 959–967. doi:10.1017/S0033291703008432
- Treadway, M. T., Buckholtz, J. W., Schwartzman, A. N., Lambert, W. E., & Zald, D. H. (2009). Worth the ‘EEfRT’? The effort expenditure for rewards task as an objective measure of motivation and anhedonia. *PLoS ONE*, 4(8), e6598. doi:10.1371/journal.pone.0006598.t004
- Tversky, A., & Kahneman, D. (1986). Judgment under uncertainty: Heuristics and biases. In H. R. Arkes & K.

- R. Hammond (Eds.), *Judgment and decision making: An interdisciplinary reader*, (pp. 38–55). New York, NY: Cambridge University Press.
- Unoka, Z., Seres, I., Áspán, N., Bódi, N., & Kéri, S. (2009). Trust game reveals restricted interpersonal transactions in patients with borderline personality disorder. *Journal of Personality Disorders*, 23(4), 399–409. doi:10.1521/pedi.2009.23.4.399
- Wang, Y., Wang, Y., Chen, S., Zhu, C., & Wang, K. (2008). Theory of mind disability in major depression with or without psychotic symptoms: A componential view. *Psychiatry Research*, 161, 153–161. doi:10.1016/j.psychres.2007.07.018
- de Wit, S., Kosaki, Y., Balleine, B. W., & Dickinson, A. (2006). Dorsomedial prefrontal cortex resolves response conflict in rats. *Journal of Neuroscience*, 26(19), 5224–5229. doi:10.1523/JNEUROSCI.5175-05.2006
- Wolkenstein, L., Schönenberg, M., Schirm, E., & Hautzinger, M. (2011). I can see what you feel, but I can't deal with it: Impaired theory of mind in depression. *Journal of Affective Disorders*, 132(1–2), 104–111. doi:10.1016/j.jad.2011.02.010
- Yuen, K., & Lee, T. (2003). Could mood state affect risk-taking decisions? *Journal of Affective Disorders*, 75, 11–18. doi:10.1016/S0165-0327(02)00022-8
- Zobel, I., Werden, D., Linster, H., Dykieriek, P., Drieling, T., Berger, M., & Schramm, E. (2010). Theory of mind deficits in chronically depressed patients. *Depression and Anxiety*, 27(9), 821–828. doi:10.1002/da.20713

Received January 22, 2014; revised November 5, 2014; accepted November 14, 2014.