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MIRRE STALLEN

Social Context Effects on Decision-Making

A Neurobiological Approach

SOCIAL CONTEXT EFFECTS ON DECISION-MAKING:
A NEUROBIOLOGICAL APPROACH

SOCIAL CONTEXT EFFECTS ON DECISION-MAKING: A NEUROBIOLOGICAL APPROACH

Effecten van de sociale context op beslissingen: Een neurobiologische benadering

Thesis

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voor Tijmen

1.

INTRODUCTION

Why do cylists shave their legs?

It's hotter'n hell, 90 degrees (32 C) and we are going out for the evening. My wife is wearing long pants.

"Aren't you going to be hot?" I ask. "Why don't you wear a dress or shorts?"

"I can't, I haven't shaved my legs."
End of questioning, no further explanation needed.

My lovely wife doesn't want to be the only one in a roomful of ladies with silky smooth legs, while she is sporting stubble. Even though I would have to get down on my knees with a magnifying glass to find a tiny emerging follicle.

This is exactly the same reason why cyclists shave their legs. No one wants to go out on a group ride and be the only wooly mammoth in the pack.

Dave Moulton, cyclist*

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*This is the beginning of Dave Moulton's bike blog on why cyclists shave their legs. In contrast to what non-cyclists might think, male cyclists don't shave their legs because of increased aerodynamics, for massage or to prevent hairs from coming in the big chain ring. Instead, those smooth legs are the result of group conformity. See the appendix for Dave Moulton's full blog post.

Social context

Many of our decisions are influenced by the behavior of others. Cyclists shave their legs to conform to the group, women buy shoes that are advertised by celebrities, and Dutch football fans dress in orange to show what national team they support. Indeed, the notion that people are influenced in their decisions by the beliefs and behaviors of others has become widely accepted across the social sciences and has been demonstrated across countless decision-making domains, including product choice (Bearden & Etzel, 1982; Berger & Heath, 2007), memory-based consumer judgments (Puntoni & Tavassoli, 2007), prejudice (Apfelbaum, Sommers, & Norton, 2008), donations to charities (Reingen, 1982), and stock investments (Hong, Kubik, & Stein, 2004). In addition recent interesting field research has shown that our behavior is susceptible to messages about how others typically behave, well shown in environmental contexts such as littering (Keizer, Lindenberg, & Steg, 2008), towel reuse in hotels (Goldstein, Cialdini & Griskevicius, 2008) and energy consumption (Schultz, Nolan, Cialdini, Goldstein, & Griskevicius, 2007).

The aim of this thesis is to explore how the social context influences the neural processes underlying our decision-making. Traditionally, studies of decision-making preliminary focused on situations in which people choose between outcomes that only affect themselves, such as playing a lottery where choices are described in terms of outcomes and probabilities and players have to pick the lottery that they prefer. Though this is a consequential decision, usually the decision-maker only has to take into account his or her own feelings and preferences when making their choice. However, many of our decisions in daily life are made in a social context in which we consider the desires and values of others before deciding, and where the outcome of a decision has consequences not only for one’s self, but for others as well.

In order to study how our decisions are influenced by the social context, this thesis is divided into two parts. The first part is concerned with the effects of social influence on decision-making, or in other words, how our decisions are influenced by the behavior and beliefs of other people. Specifically, this part of the thesis examines the influence of both celebrities and peer groups on the neural processes underlying decision-making. The second part of this thesis investigates the influence of social norms, that is, how our decisions are not only influenced by the behavior of others, but also by our perceptions about what behavior is typically approved of and disapproved of by others. In particular, the second part of this thesis investigates the neural processes involved in cooperation and the neural mechanisms underlying social norm enforcement.

By adopting a neuroscientific approach, this thesis reflects the increased interest in studying the neurobiology of human cognition in order to better understand important cognitive principles, an important advance now seen in social sciences such as Psychology, Economics and Marketing. During the past decade, this interest has resulted in the emergence of novel interdisciplinary research areas known as Social Neuroscience (Lieberman, 2007; Singer, 2009), Neuromarketing (Ariely & Berns, 2010; Smidts, 2002), and Neuroeconomics (Glimcher, 2009). Although these areas are closely related, and the topics they are concerned with partly overlap, the neurobiological study of decision-making is most central to the field of Neuroeconomics. By investigating the neural substrates of choice behavior, scholars in Neuroeconomics aim to get more insight into the psychological processes that underlie decision-making than is possible by using behavioral measures alone (Levallois, Clithero, Wouters, Smidts, & Huettel, 2012). To this end, they have sought to investigate decision-making by combining a variety of methods, including: (i) behavioral studies that examine how manipulation of the decision environment can affect choice itself as well as ancillary measures such as reaction time, skin conductance or eye movements, (ii) studies with brain lesion patients that examine the consequences of abnormal brain function on decision-making, (iii) experiments applying repetitive transcranial manipulation (rTMS) to temporarily disrupt activity within the brain, (iv) electroencephalography (EEG) or magnetoencephalography (MEG) studies which measure the electrical signals of neuronal firing at the scalp, (v) genetic studies looking at the correlation between individual differences in the expression of certain genes and behavior, (vi) research using positron emission topography (PET) to investigate the functioning of brain structures by the use of radioactive isotopes, (vii) pharmacological research to examine the effects of drug administration and neurotransmitters, and (viii) functional magnetic resonance imaging (fMRI) experiments that allow for the relatively direct measurement of real-time neural activity.

In this thesis, behavioral methods are combined with both fMRI and pharmacological methods to better understand the principles underlying how we choose and decide in a social context. A brief introduction to the technique of fMRI and to pharmacology research can be found in Box 1 and Box 2 respectively.

Outline of the thesis

The thesis consists of 2 review chapters (Chapters 2 and 6) and 4 empirical chapters (Chapters 3, 4, 5 and 7). **Chapter 2** provides a general introduction to the field of Neuroeconomics. This chapter both outlines an overview as to how Neuroeconomic studies are typically conducted, as well as discusses some primary recent findings in this field as they relate to theories aiming to understand social decision-making.

Part 1 – Social influence

Chapters 3, 4 and 5 investigate how celebrity advertisements and peer group information influence the neural processes of decision-making. **Chapter 3** addresses the question why celebrity endorsers are more effective than non-celebrity endorsers. This chapter examines the effect of fame on both product memory and purchase intention, using fMRI to explore the underlying neural mechanisms. Chapter 4 and 5 both investigate the process of in-group conformity. It is well-known that people often conform to others with whom they identify, however, so far it has been unclear what mechanisms underlie this type of conformity. **Chapter 4** investigates the neural processes underlying in-group conformity by use of fMRI. **Chapter 5** uses pharmacological manipulations to explore whether conformity towards one's in-group is mediated by oxytocin, a neuropeptide often implicated in social behavior.

Part 2 – Social norms

Chapter 6 and chapter 7 focus on the role of social norms in decision-making. **Chapter 6** provides an overview of the neuroscience literature on cooperation, and reviews how social norms and emotions induced by the social context can influence cooperation and its neural correlates. **Chapter 7** explores whether oxytocin plays a role in social norm enforcement and in particular examines whether increased levels of oxytocin in turn increases individual sensitivity to the violation of distributional fairness norms.

Discussion

Chapter 8 concludes the thesis with a summary of the empirical chapters and a discussion of how these findings contribute to both the theoretical literature as well as to the more applied field of consumer decision-making. In addition, the practical impact of the chapters in terms of their potential contribution to policy decision-making is discussed, and suggestions for future research are given.

Box 1 - What is fMRI?

Functional Magnetic Resonance Imaging (fMRI) is a non-invasive method to assess brain activity and is a variant of the more well-known Magnetic Resonance Imaging (MRI) technique, a medical imaging technique that is used to visualize internal body structures. Like MRI, fMRI is based on the principle of nuclear magnetic resonance, which refers to the physical phenomenon in which magnetic molecules in a magnetic field absorb and re-emit radiowaves.

When participating in an fMRI experiment, participants are laying in an MRI scanner, which is basically a large powerful magnet with a strong magnetic field (e.g. 1.5 or 3 Tesla). This magnetic field disrupts the orientation of magnetic molecules in the human body and brain, such as water and hemoglobin, and causes a detectable change in the magnetization of these molecules that is recorded by the MRI scanner. Importantly, this change in magnetization is not the same for all magnetic molecules, as, for instance, hemoglobin bound with oxygen has different magnetic characteristics than deoxygenized hemoglobin. The difference in magnetic characteristics of oxygenized and deoxygenized hemoglobin causes a signal that is also known as the Blood Oxygenation Level Dependent (BOLD) signal. The BOLD signal is the signal that is used to study human brain function in fMRI experiments.

Although the BOLD signal is very likely to reflect the amount of neural activity (active regions require more oxygen than less active regions), it is important to note that fMRI research does not provide a direct measure of brain activity, and that the fMRI results do not imply a causal link between brain activation and behavior. In addition, because the BOLD signal occurs several seconds later than the underlying neural activity, the fMRI signal is slow. This implies that with fMRI it is difficult to measure fast occurring events and that fMRI studies often need to build in relatively long inter-trial timings to prevent overlap from different BOLD signals. In contrast to the low temporal resolution, fMRI has a relatively high spatial resolution and can measure brain structures with a precision of 2-3 millimeters, allowing for the imaging of relatively small structures within the brain. (Huettel et al., 2008).

Box 2 - What are pharmacological studies?

Pharmacological studies examine the function of biochemical substances in human brain and body. They are concerned with both the effect of exogenously administered substances, such as drugs, as well as with endogenous substances, such as hormones and neurotransmitters. Hormones and neurotransmitters are chemical substances that work as signaling molecules in the blood stream and nervous system respectively.

To investigate the role of biochemical molecules in human behavior, the effect of a biochemical substance is often compared with the effect of a placebo, which is a substance that is similar to the biochemical substance of interest, but which contains no effective components. To this end, pharmacological studies either use a within- or between-subjects design. In a within-subjects design, the same group of participants serves more than one treatment, implying that, at different time points, each participant is exposed to both the active substance as well as to the placebo. In a between-subjects design the subject population is typically divided into two groups and half of the participants receive the active substance while the other half receives the placebo. Pharmacological study designs are often randomized, meaning that participants are randomly divided into one of the two groups (between-subjects design), or that the order of substance administration is randomly determined across participants (within-subjects designs). Furthermore, pharmacological studies ought to be double-blind. This means that both the experimenters as well as the participants are unaware of which treatment the participant receives.

The pharmacological studies in this thesis explore the role of oxytocin in decision-making. Oxytocin is a peptide that is synthesized in the hypothalamus and that functions as both a hormone and a neurotransmitter. Oxytocin (derived from the Greek word ὠκυτοκίνη, meaning ‘quick birth’) is named for its role in the progression of labor. However today, oxytocin may be best known for its function in the regulation of social behavior (Meyer-Lindenberg, Domes, Kirsch, & Heinrichs, 2011).

2.

NEURO-ECONOMICS

Abstract

Many of our decisions are made in the context of highly complex social interactions. By combining neuroscientific measures with formal models of game theory, researchers have gained insight into the mechanisms underlying social decision-making. Early findings from this interdisciplinary effort have already begun to show how reasoning about the intentions of others is important for interactive behavior, how the reward system of the brain is directly involved in cooperation and social exchange, and how the experience of emotions plays a vital role in successful decision-making. The Neuroeconomic approach to social decision-making offers exciting potential to move beyond speculation about the processes that determine our decisions in interactive contexts, and to extend our knowledge about the functioning of the human brain.

Based on Stallen & Sanfey (2011). Neuroeconomics and Game Theory. *Wiley Encyclopedia of Operations Research and Management Science.*

Introduction

Everyday decisions are made in a social context in which the outcome of a decision has consequences not only for one's self, but for others as well, and where we need to consider the desires and values of others before deciding. Game theory is a collection of models aiming to understand such instances of interactive decision-making (Von Neumann & Morgenstern, 1947). These models make clear mathematical predictions about behavior in social situations by describing what strategies decision makers converge on as they try to maximize their payoff. To study complex social processes, such as trust, cooperation and reputation, game theory offers a rich variety of well-designed multiplayer games. Recently, a new interdisciplinary field has emerged, popularly known as Neuroeconomics, which aims to better understand how people make decisions by integrating research from several different fields. As part of this approach, researchers have begun to investigate the neural correlates of social decision-making using some of these games.

In this chapter, we first provide a brief introduction as to how Neuroeconomic studies are typically conducted. Following this, we describe the main findings of current Neuroeconomic studies as they relate to game theory, and we conclude with an outline of potential future research directions in this field.

Current research

Recent research in Neuroeconomics has begun to investigate the processes underlying social decision-making using game theoretic paradigms. In contrast to standard behavioral studies in game theory, the Neuroeconomic approach allows for the discrimination and modeling of processes that are hard to separate at the behavioral level. The combination of game theoretic models with the on-line measurement of brain activity during instances of decision-making offers the promise of increasing our understanding of the processes and factors that are involved in social decision-making.

An additional benefit of the Neuroeconomic approach is that it has the potential to inform game theory models. This can be helpful, since actual decision behavior in game theory tasks often deviates from the models' predictions. Game theory models assume that players in a social context interact rationally, with full information, and that they make purely self-interested decisions.

However, several decades of laboratory experiments by psychologists and economists have found that players rarely behave according to these strict game theoretic strategies (Camerer, 2003). Instead, players often appear to care about the welfare of others, and additionally value factors like reciprocity and fairness. Identification of the neural mechanisms underlying social interaction in game theory paradigms may result in a more precise characterization of behavior and, subsequently, game theory models may be adapted to better fit decision-making behavior.

Although Neuroeconomics is still a relatively young discipline, there have already been many studies conducted which have used game theoretic approaches to gain insight into the neural basis of social decision-making. The current findings can be usefully summarized in three themes: (i) reasoning about the intentions of others, (ii) social reward, and (iii) the role of emotions in decision-making, each of which will be expanded upon in the remainder of this section.

Reasoning about the intentions of others

One focus of game theory is to model reciprocal exchange, which has been studied extensively in the laboratory with games like the trust game (Berg, Dickhaut, & McCabe, 2005; King-Casas et al., 2005; Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005) and the prisoner's dilemma game (Krueger et al., 2007; Rilling et al., 2002; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004a; Sally, 1995). A trust game is played with two players. One is termed the investor, who is endowed with a particular monetary amount, and the other is termed the trustee. The investor is instructed to choose how much of his endowment she would like to pass on to the trustee and how much she will keep for herself. Once this decision is made, the experimenter multiplies the transferred amount money by some factor (usually 3 or 4) and passes it to the trustee. At this point the trustee has the option to return money to the investor or to keep all money to herself. If the trustee decides to return money, thereby honoring the trust of the investor, both players finish the game with more money than they originally had. However, if the trustee decides to keep the money and thus does not repay the trust, the investor ends up with a loss and the trustee is the only one who benefits.

As indicated above, game theory assumes that a decision maker acts in a rational and self-interested manner, and therefore the classical economic prediction would be that a trustee in the trust game would never repay the trust of the investor. The investor in turn, will realize this and should therefore never invest in the trustee in the first place. However, although game theory predicts no transactions to occur, behavioral experiments have consistently shown that players in the trust game do in fact engage in social interaction: The majority of investors send money to the trustees and most of the time this trust is reciprocated with payments back to the investor (Camerer, 2003).

In a standard laboratory prisoner's dilemma game, game theoretic predictions are also usually violated. The prisoner's dilemma game is quite similar to the trust game, except that in the prisoner's dilemma game both players simultaneously choose whether to cooperate with the other or not, without knowing their partner's choice. The payoff for both players depends on the interaction of their choices, such that a player's individual earnings are highest when he or she defects and the other cooperates, with the cooperating player receiving only a small amount. Mutual cooperation, in contrast, is rewarding for both players, although individual earnings are lower than during unilateral defection. Game theory would predict that in the prisoner's dilemma game both players should decide to defect, but again, this appears to be not in accordance with the experimental data, as behavioral experiments typically find mutual cooperation occurring about half of the time. Given that standard game theoretic models are often inaccurate at describing individual decision-making, how can Neuroeconomic studies shed light on why human behavior appears at odds with classical economic predictions?

One potentially interesting contribution may come from how the brain perceives and computes the intentions of others, suggesting that we value not only the monetary outcome of a social interaction, but are also concerned with the message our partner conveys by his or her behavior. Several neuroimaging studies have shown a consistent network of areas to be involved during reciprocal exchange in both the trust game and prisoner's dilemma game (Krueger et al., 2007; McCabe, Houser, Ryan, Smith, & Trouard, 2001; Rilling et al., 2004a). For example, one of the earliest Neuroeconomic studies on the trust game found that activity in the paracingulate cortex was higher when subjects played the game with another human being as opposed as to a computer opponent (McCabe et al., 2001). Increased activation in this same region was also found in a following MRI study using the trust game (Krueger et al., 2007). In this study, trust building was examined by having several pairs of strangers play a nonanonymous multiround trust game, while alternating their roles as trustor and trustee. Both players were each in a separate MRI scanner, with both brains scanned simultaneously during the game. Using within- and between-brain analyses, the results showed that the paracingulate cortex was particularly active during the first phase of the multiround game for players that reciprocated their partner's decision to trust. In later stages of the game, the activity in this region decreased for this group of reciprocators. This result suggested that the paracingulate cortex is important during the early trust building phases of a relationship and that it plays less of role during the maintenance stage of trust.

Other areas that have consistently been associated with reciprocal exchange are the posterior superior temporal sulcus and the temporal-parietal junction. Together with the anterior paracingulate cortex, these regions have been strongly implicated in the cognitive capacity of perspective taking, an ability often termed as Theory of Mind (Frith & Frith, 2006; Saxe, 2006). The concept of Theory of Mind is defined as the understanding that others have their own intentions and individual perspective of the world, and that these may differ from your own. The finding that regions related to Theory of Mind are involved in reciprocal exchange games suggests that players in the trust game and prisoner's dilemma game attempt to infer the strategy of their opponent and subsequently act on the belief they have about their partner's intentions. Therefore, if we perceive that a partner treats us badly when they have the opportunity to do otherwise, we may punish that person. However, if we believe that our partner had no choice in their behavior, we may decide to be more lenient (Fehr & Gächter, 2002). Furthermore, these regions also seem to play a role in people's ability to determine whether the actions of others are meaningful. Many neuroimaging studies have found that game interactions with human partners produce stronger activity in Theory of Mind regions than identical interactions with purported computer partners (Gallagher, Jack, Roepstorff, & Frith, 2002; McCabe et al., 2001; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004b).

Interestingly, areas important for Theory of Mind may also be involved in the decision to behave selfishly or altruistically. A study on altruism found that activity in the posterior superior temporal cortex correlated with individual's tendency to engage in helpful behavior (Tankersley, Stowe, & Huettel, 2007). Of course, in addition to the cortical network related to Theory of Mind other areas may be relevant for reasoning about the intentions of others. For example, the anterior cingluate cortex seems to represent information about which player in a trust game is responsible for a specific outcome (themselves or their partner), as its activity correlates with the agent-responsibility ("me" or "not me") of an action (Tomlin et al., 2006). Future research is expected to increase our understanding on the neural mechanism of Theory of Mind even further by investigating what additional areas may be involved in the network as well. Furthermore, our knowledge of the specific functions of these regions is still limited. This situation will improve as more studies in this domain will be conducted.

Social reward

In addition to the involvement of brain structures related to Theory of Mind, research on the trust game and prisoner's dilemma game have indicated another area that is critical to social decision making: the striatum (Delgado, Frank, & Phelps, 2005; King-Casas et al., 2005; Rilling et al., 2002, 2004a). The striatum is located in the center of the brain and is a major input station of midbrain dopamine neurons that play a primary role in the processing of rewards. Single-cell recordings in nonhuman primates have demonstrated that dopamine neurons in the striatum track reward prediction errors, with unexpected rewards increasing the firing rate of dopamine cells whereas the omission of expected rewards leads to a decrease in firing rate (Schultz, 2006; Schultz, Dayan, & Montague, 1997). This reinforcement-learning mechanism is thought to be important for the learning of reward values of stimuli in the environment, thereby allowing for the improvement of choices over time.

In parallel to these primate studies, the striatum in humans is known to be involved in reward processing. Using neuroimaging and PET, researchers have discovered that this area responds to primary rewards such as liquids, foods and sexual stimuli (Arnow et al., 2002; Berns, Mcclure, Pagnoni, & Montague, 2001; O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003; Redouté et al., 2000), but also to money (Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001; Knutson, Westdorp, Kaiser, & Hommer, 2000) or more abstract rewards like reputation or status (Izuma, Saito, & Sadato, 2008; Zink et al., 2008). Importantly, reward-related activity has also been associated with social decision-making behavior. Several neuroimaging studies have demonstrated that this area responds to the decision of one's partner to either reciprocate or not reciprocate cooperation (Delgado et al., 2005; King-Casas et al., 2005; Rilling et al., 2002, 2004a). For example, in the prisoner's dilemma game, the striatum is activated when cooperation is reciprocated and deactivated if not reciprocated (Rilling et al., 2002, 2004a).

Additionally, the striatum appears to update the trustworthiness of a partner, as activity in this area has been associated with increased cooperation or reciprocity in subsequent rounds of a prisoner's dilemma (Rilling et al., 2002) or trust game (King-Casas et al., 2005). A further study using the trust game paradigm showed that reward prediction errors in the striatum are significantly dependent on prior experiences, such as the moral reputation of players (Delgado et al., 2005). Providing investors with a fictional profile of the moral reputation of their partners (either morally good, bad or neutral) before the start of a trust game resulted in reduced striatal activity when people interacted with morally good or bad partners, but not with neutral partners. Presumably this modulation of striatal activity was absent when players interacted with neutral partners because the behavior of the neutral partners was more unpredictable, as no prior information was given on their reputation. This finding demonstrates that prior beliefs may influence the processing of social feedback information, thereby guiding future cooperation.

Reward-related activity in social decision-making has not only been associated with positive, mutual cooperation. A study using PET showed that signals in the striatum were also enhanced when players punished free riders (non-reciprocators that benefit from others in a trust game), suggesting that players may derive satisfaction from punishing defectors (De Quervain et al., 2004). Additionally, studies have reported activity in reward networks when participants engaged in charitable donations at a personal cost to themselves (Hare, Camerer, Knoepfle, & Rangel, 2010; Moll et al., 2006). For example, a recent study (Harbaugh, Mayr, & Burghart, 2007) provided participants with an endowed amount of money and then observed them using fMRI while they engaged in a variety of donation situations. The researchers found that reward areas were activated when participants observed a donation to a charity and, importantly, that this activation was enhanced when the donation was made voluntarily.

These Neuroeconomic results are important for game theoretic approaches, as they show that regions underlying social decision-making overlap with classical reward circuitry, thereby suggesting that cooperative and reciprocal behavior may be experienced directly as rewarding by players, independent of any monetary reward. This provides valuable evidence that social motivations are indeed important when engaging in social decision-making, and that we need to consider rewards other than money when constructing models of behavior in these contexts. Furthermore, the results on charitable donations are intriguing as they have relevant implications for decision-making at a societal level. The fact that mandatory transfers to a charity elicit reward-related activity suggests that even taxation may produce satisfaction in certain situations.

The role of emotions

In addition to research on strategizing and social reward, another fruitful direction within Neuroeconomics is the growing insight that emotions play a crucial role in social decision-making. This idea is in contrast to classical models of economic decision-making, which assume that decisions are the results of a rational and deliberate evaluation of the available choice options. However, although these models have provided a strong foundation for the development of central decision-making theories, more recent research showed that this rationality assumption is often violated (Kahneman, Slovic, Tversky, 1982; Tversky & Kahneman, 1974)

Early work in this domain showed that patients with prefrontal brain damage and associated emotional deficits performed worse on a gambling task than healthy participants (Bechara, Damasio, Tranel, & Damasio, 1997). The area that was damaged in these patients was the ventromedial prefrontal cortex, a region that later was found to be essential for the activation and successful integration of emotion-related memories in the anticipation of future consequences of actions (Bechara, Damasio, Tranel, & Damasio, 2005). Building from this pioneering research, researchers have continued to discover that emotions play a vital role in determining decisions.

A standard game that is frequently used to illustrate that the emotions have an effect on decision-making is the ultimatum game. In this well-studied task, two players are required to split a sum of money that is provided by the experimenter. One of the players is deemed the proposer, the other the responder. The proposer is instructed to specify the division of the money between the two players, and is allowed to make any split he or she wants. The responder can then accept or reject the offer; accepting means the money is split as proposed and rejecting means that neither player receives anything. Since game theory predicts people are motivated purely by self-interest, the standard game theoretic solution for the responder is to accept any amount that is offered. The proposer should anticipate this and therefore offer the responder the smallest amount possible. However, a considerable amount of behavioral research showed that this prediction is at odds with observed behavior in the laboratory and the field: Proposers generally propose an equal split and responders reject offers that are 20% of the total amount or less (Guth, Schmittberger, & Schwarze, 1982). This very robust finding indicates that people's behavior in the ultimatum game appears not to be motivated solely by financial self-interest.

Neuroeconomic studies have attempted to specify the processes underlying the reactions of responders to unfair offers in the ultimatum game. An early study by Sanfey and colleagues (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003) found that activity in the anterior insula correlated with the degree of unfairness of an offer. Additionally, this region was more active for offers made by a human partner as opposed to a computer partner. In terms of the responder decision, activation in this area predicted the player's decision to either accept or reject the offer, with a higher level of activity for rejections than for acceptances. The activation of the insula in the ultimatum game is particularly interesting in light of its suggested association with negative emotional states. Previous studies showed that activation in this area is consistently seen in studies to pain and disgust, and to autonomic arousal (Calder, Lawrence, & Young, 2001; Damasio et al., 2000). Based on these findings, anterior insula activity in the ultimatum game can be interpreted as a reflection of the responder's negative emotional state to an unfair offer.

Another brain region that was engaged during unfair offers in the ultimatum game was the right dorsolateral prefrontal cortex, a region that, in contrast to the anterior insula, usually has been associated with cognitive processes, such as the implementation of goal-directed behavior. Activation in this area was greater than activation in the insula when responders accepted unfair offers, and less when they rejected these offers. To investigate the function of the dorsolateral prefrontal cortex in the decision to accept or reject an unfair offer, activity in this brain region has been disrupted using TMS (Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006; van't Wout, Kahn, Sanfey, & Aleman, 2005). After receiving TMS at the right dorsolateral prefrontal cortex, the acceptance rate of unfair offers increased, suggesting that the dorsolateral prefrontal cortex plays a causal role in the implementation of fairness-related behavior.

The finding of separable neural correlates for decisions based on emotion (rejections of an unfair offer) and deliberation (acceptance of an unfair offer) suggests that there is not a unitary system at the neural level which is on control of decision-making. Indeed, several neuroimaging studies showed that emotional processes seem to reliably engage a different set of brain structures than cognitive processes (Dalgleish, 2004; Sanfey & Chang, 2008). This distinction provides some support for dual-process theories, which hypothesize that decision-making is the result of an interaction between an automatic, affective system and a more controlled, deliberative system. However, explaining decision-making in terms of the interaction between different subsystems violates traditional economic theory as standard economic models typically describe human behavior as being governed by a unitary process. Future economic models of decision-making could usefully take into account the Neuroeconomic evidence for the differential processing of emotional and deliberative information.

The future

Many of our most important decisions are made in a social context. In the preceding sections we presented an overview of how Neuroeconomics has contributed thus far to the understanding of social decision-making behavior.

These findings have demonstrated that the brain has the ability to rapidly recognize and act on the intentions of others, that key regions involved in reward-based learning also underlie choices in social settings, and that emotions play a crucial role in social decision-making situations. Despite these advances, the current state of knowledge regarding the mechanisms underlying social decision-making is still rather limited. However, due to the explosion of research in this field, and to continual refinement and advances in neuroscientific methodology, this area of research offers much promise in the years to come.

One potentially fruitful avenue of research is the investigation of how parameters of decision processes are represented in the brain using a formal modeling approach (Beer et al., 2008; van Winden, Stallen, & Ridderinkhof, 2008). By connecting the parameters of formal (game theoretic) models with neural activity, a more precise characterization of the mechanisms underlying decision-making can be described. In turn, by examining whether correlates of game theory parameters are present or absent in the brain, this approach may provide additional constraints on models that aim to predict social decision-making behavior.

Future studies are also likely to benefit from advancements in neuroscientific methods. For instance, fMRI measurement techniques continuously are being improved. The traditional, and still most-common, approach to investigate brain function is the localization of function to specific isolated brain areas. However, a more recent way of examining neural function is to look at the communication between neural networks. Currently, these brain connectivity methods are becoming increasingly popular and Neuroeconomic data generated by this alternative approach can yield useful insights into the neural networks that are relevant for decision-making.

A final interesting direction for future research is to investigate the role of hormonal and genetic factors in decision-making. For instance, oxytocin, a peptide that functions both as a neurotransmitter and as a hormone, appears to modulate a broad profile of human social behaviors. In a trust game, intranasal administration of this peptide increased the amount of money transferred by the investor (Kosfeld et al., 2005). A related neuroimaging study showed that this change in trusting behavior was associated with a modulation of activity in the neural systems mediating both fear and reward processing (Baumgartner, Heinrichs, Vonlanthen, Fischbacher, & Fehr, 2008). Additionally, higher levels of oxytocin have been associated with more generous offers towards strangers in an ultimatum game (Barraza & Zak, 2009; Zak, Stanton, & Ahmadi, 2007). Another hormone potentially of importance for social decision-making is testosterone. A recent study showed that men high in testosterone were more likely to reject relatively low offers in an ultimatum game (Burnham, 2007). Subsequent research also examined whether testosterone levels affect the decision of the proposer. However, as is often the case in early studies contrasting findings have been reported, as one study found that artificially raised testosterone levels decreased the generosity of proposers (Zak et al., 2009), whereas another study found opposite results (Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2009).

Researchers have also begun to examine whether genetic variation within people can explain individual differences in social decision-making behavior. Results from a twin study to the heritability of ultimatum game behavior showed that more than 40 percent of the variation of responder’s rejection rate was explained by genetic effects. Furthermore, studies of oxytocin and vasopressin – a peptide with a structure very similar to that of oxytocin – have shown that the genetic polymorphisms for oxytocin and vasopressin receptors are associated with the allocation of funds in economic games that measure altruistic behavior (Israel et al., 2008; Israel et al., 2009; Knafo et al., 2008).

Clearly, the future looks promising for a Neuroeconomic approach of social decision-making. Exploration of new research domains and the development of more advanced techniques offer fruitful opportunities for the study that combines the mathematical models of game theory with techniques of modern neuroscience. This approach will benefit both the predictive accuracy of economic models by constraining their parameters based on neural substrates as well as further our knowledge of how the brain functions.

3.

CELEBRITIES AND SHOES

Abstract

Celebrity endorsement is omnipresent. However, despite its prevalence, it is unclear why celebrities are more persuasive than (equally attractive) non-famous endorsers. The present study investigates which processes underlie the effect of fame on product memory and purchase intention by the use of functional magnetic resonance imaging methods. We find an increase in activity in the medial orbitofrontal cortex (mOFC) underlying the processing of celebrity-product pairings. This finding suggests that the effectiveness of celebrities stems from a transfer of positive affect from celebrity to product. Additional neuroimaging results indicate that this positive affect is elicited by the spontaneous retrieval of explicit memories associated with the celebrity endorser. Also, we demonstrate that neither the activation of implicit memories of earlier exposures nor an increase in attentional processing is essential for a celebrity advertisement to be effective.

Based on Stallen, Smidts, Rijpkema, Smit, Klucharev & Fernandez (2010). Celebrities and shoes on the female brain: The neural correlates of product processing in the context of fame. *Journal of Economic Psychology,* 31(5), 802-811.

Introduction

The use of celebrities as endorsers in product advertising is popular. Over the last twenty-five years, the number of advertisements relying on a famous presenter has increased considerably (Pringle and Binet, 2005). Nowadays, the typical format of a celebrity print advertisement is straightforward: Brad Pitt for Tag Heuer watches, George Clooney for Nespresso, or Kate Moss for Rimmel cosmetics; just pairing the face of a famous individual with a brand seems to do the trick. No explicit and extensive message appears required to convince the consumer of the qualities of the advertised product only because the product has been associated with a celebrity.

Consumer research has indeed shown that celebrity endorsement may enhance the recall of advertising messages, increase the recognition of brand names and make advertisements more believable (Friedman and Friedman, 1979; Kamins et al., 1989; Petty et al., 1983). However, whether celebrities are also able to improve purchase intentions is less clear. Some studies reported that commercials using celebrities did enhance consumers' likelihood of buying the advertised brand (Heath et al., 1994; Ohanian, 1991; Petty et al., 1983), whereas others were not able to demonstrate such an effect (see Erdogan, 1999). Recent research by Rossiter and Smidts (2012) suggested that the underlying cause of these contrasting findings is that the majority of these studies did not take the perceived expertise of the celebrity for the endorsed product into account. They posited that for persuasion, consumers need to identify the presenter as having technical knowledge about the advertised product or as being an experienced user of it. A follow-up neuroimaging study supported this hypothesis by demonstrating that a single exposure to an expert celebrity with a product indeed resulted in a long-lasting positive effect on memory and purchase intention for the product, whereas exposure to a non-expert celebrity endorser did not (Klucharev et al., 2008). Examination of the brain mechanisms underlying this persuasive effect of expertise indicated that an expert context induced feelings of trust towards the product and increased semantic elaboration of the celebrity-product association, leading to a deeper encoding of the product in memory. Moreover, this research showed that the brain does assess the expertise of a celebrity very rapidly and without explicit endorsement (Klucharev et al., 2008).

The present study

The work by Klucharev and coworkers (2008) on the neurobiological account of expertise illustrates the relevance of neuroscientific methods for consumer research as this study specified more precisely which processes underlie the persuasive effect of expertise than would have been possible with the use of behavioral methods alone. The aim of the present study was to increase the understanding of celebrity endorsement even further by examining which processes underlie the persuasive effect of fame.

Given the large fees popular celebrities are asking for endorsements, advertisers need to understand what the added value is of a celebrity endorser compared to a non-famous one. Earlier research on celebrity endorsement explained the effectiveness of celebrities in terms of a conditioning process: the pairing of a positively valenced stimulus (a celebrity) with an initially neutral stimulus (a product) results in a transfer of affect from the valenced to the neutral stimulus (from celebrity to product) (Till et al., 2008; Walther et al., 2005). However, this evaluative conditioning account does not elaborate on *why* the perception of a celebrity results in the experience of positive affect.

One explanation we suggest is that the perception of a famous face may bring to mind facts (e.g. a celebrity's latest movie) and personal episodes (e.g. a movie night with friends) that are related to the presenter. These memories will be inherently positive since celebrity endorsers are generally selected because of their popularity and associations with nice events. The positive affect that is experienced during the retrieval of these memories may subsequently be transferred to the product associated with the celebrity.

Another (non-exclusive) explanation is that the perception of a celebrity face triggers the retrieval of implicit memories, i.e. memories that are independent of conscious remembering (Schacter, 1987; Schacter and Buckner, 1998). Earlier exposure to a stimulus has been shown to be sufficient to increase the positive affect experienced toward that stimulus at a later moment (Harmon-Jones and Allen, 2001; Zajonc, 2001). Because consumers have obviously been exposed more often to the face of a celebrity than to that of an unknown endorser, implicit memories of earlier exposures to a celebrity may cause consumers to experience more positive feelings during exposure to a famous person than when perceiving a non-famous presenter.

Both explanations above describe a celebrity endorser as being a positively valenced stimulus. However, some influential psychological frameworks have conceptualized emotion along two dimensions: valence (how positive or negative) and arousal (how exciting or calm) (Bradley et al., 1992; Russell, 1980). Possibly, a celebrity endorser does not only elicit the experience of positive affect, but is perceived to be more arousing than an unknown endorser as well. If this is true, we expect celebrity advertisements to receive more attention than advertisements with unknown presenters since arousing stimuli are known to be processed with more attention than non-arousing ones (e.g. LaBar et al., 2000). The increase in attention towards a celebrity advertisement may enhance the depth of processing of the product-celebrity paring and in turn facilitate the retrieval of explicit memories linked to the celebrity. As the retrieval of explicit memories may be important to establish a transfer of positive affect from celebrity to product, attention may play an important role during celebrity endorsement situations. A recent study by Pleyers and colleagues (2009) indicated that attention is indeed of importance for the process of affect transfer. They found that the conditioning of products with positively valenced stimuli was sensitive to the amount of attentional resources available.

In sum, the goal of the present study was threefold. First, we examined whether the conditioning account of celebrity endorsement was supported by the neural activity underlying the encoding of a product in the context of fame, i.e. whether the brain areas involved indicated a process of affect transfer. Second, we investigated whether the positive affect associated with a celebrity resulted from the retrieval of explicit facts and episodes, from the retrieval of implicit memories, or from the retrieval of explicit and implicit memories together. And third, we explored the role of arousal-driven-attention in celebrity endorsement.

Neural correlates

To investigate the underlying processes of the persuasive effect of celebrity endorsers, we designed an experiment imitating the typical format of a celebrity advertisement: showing a famous face together with a product without any explicit persuasive message. While their brain activity was being recorded with a functional magnetic resonance imaging (fMRI) scanner, we presented young female subjects with photographs of equally attractive famous and non-famous faces together with photos of products.

First of all, as the orbitofrontal cortex has been shown to encode the learning of associations between neutral and reinforcing stimuli (Rolls and Grabenhorst, 2008), we hypothesized to find increased activity in the orbitofrontal cortex when presenting products together with a celebrity face. As, according to the conditioning account of fame the perception of a celebrity gives rise to positive emotions, a celebrity face may function as a reinforcing stimulus whereas the product is a neutral stimulus. In particular, we expected to find an increase in activity in the medial part of the orbitofrontal cortex during the encoding of stimulus-reinforcement associations between a famous face and a product, as the medial orbitofrontal cortex has been correlated with the subjective liking of several rewarding stimuli (Beer et al., 2008; Grabenhorst et al., 2008; Plassmann et al., 2008; Rolls et al., 2009), whereas the lateral part has been more often linked to the evaluation of negative reinforcers (Kringelbach, 2005; Kringelbach and Rolls, 2004; Rolls and Grabenhorst, 2008).

To examine whether the positive affect experienced upon the perception of a celebrity endorser is the result of the retrieval of explicit knowledge related to the famous endorser or the result of earlier exposures to the celebrity face (i.e. implicit memories), we compared the neural activation patterns underlying the presentation of a famous face with the brain activity related to the presentation of a non-famous face. If the retrieval of explicit memories is important for the experience of positive affect, we expected famous faces to induce either more extensive activations in brain regions associated with the retrieval of factual knowledge, also classified as semantic knowledge (e.g. remembering an endorser's latest hit movie), or in brain areas associated with the retrieval of episodic memories, which are context-specific memories that are unique to each individual (e.g. remembering what happened after you saw that specific endorser's movie) (Tulving, 1972; Wiggs et al., 1999). In case the perception of a celebrity triggers both the retrieval of semantic and episodic memories, both memory networks will be activated during the presentation of a famous face. Retrieving semantic information, as compared to episodic experience, has been shown to activate consistently the superior prefrontal cortex and middle temporal gyrus, predominantly in the left hemisphere (Simons and Spiers, 2003; Wiggs et al., 1999). The retrieval of episodic memories has mainly been associated with an increase in activity in the left parietal and medial prefrontal cortex, and the medial temporal lobe (Maguire, 2001; Wagner et al., 2005).

Instead of eliciting affect by the activation of explicit knowledge, celebrity endorsers may be experienced as more rewarding because of their implicit familiarity to consumers. If celebrity endorsers indeed evoke the experience of positive affect due to earlier exposures, we expected exposure to a famous face to elicit activity in the striatum, as previous studies showed that this area is responsive to the reward value associated with a face (Aharon et al., 2001; Kampe et al., 2001).

We also tested the hypothesis that celebrities would enhance attentional processing because they are more arousing than unknown endorsers. Past research has suggested that processing in higher-order visual cortex in the occipital lobe and the inferior temporal cortex is modulated by attentional processing (Kanwisher and Wojciulik, 2000). Thus, if celebrities enhance the depth of processing of an advertisement, we expected to find an increase in activity in these brain regions during the presentation of a celebrity endorser.

The experiment

Participants

Twenty-six right-handed Dutch females (mean age 20.6 years) participated in the experiment. Subjects received a financial compensation of 24.5 euros (± 32 dollars) for participation. As familiarity with celebrities was essential for the present study, subjects were selected using a questionnaire screening their interest in celebrities and fashion. All subjects reported to be healthy, on no medication and free from any history of neurological or psychiatric illness, head trauma or drug abuse. Written informed consent was obtained from each subject according to the local medical ethics committee. Data of the first three subjects had to be discarded due to problems with the response recording during scanning, resulting in 23 subjects for final analyses.

Stimuli

Twenty digital color portraits of international and Dutch female celebrities (movie-, music and TV-stars) and 20 digital color portraits of non-famous females were selected from publicly available internet sources. Only female presenters were selected to prevent any effects of gender on subjects' perception of the photograph. Furthermore, attractiveness between the celebrities and non-famous females was matched based on attractiveness ratings by 6 young females not used as subjects in the further experiment. Four hundred and eighty digital photos of female shoes were collected from publicly available internet sources as products. Choosing shoes as products was optimal for two reasons. First, they are present in a large variety in an everyday shopping context. This is important to prevent any effects due to specific outlying items. Second, as women in general (and not celebrities only) are regarded to be experienced users of shoes (Belk, 2003), the presentation of shoes as products should prevent any confounding effects of expertise on the fame manipulation. From the 480 pictures of shoes two sets of 240 stimuli were created. One set was used for the fMRI session and a behavioral memory test performed after scanning; the other set was only used as filler items in the following behavioral memory test. Stimuli set presentation was counterbalanced, so that across subjects all stimuli appeared equally often as a filler in the memory task as they were used in the fMRI session. All photographs were similar in terms of overall complexity, contrast, brightness and pixel width. Pixel height varied for the pictures of shoes due to the height of the shoes: boots gave larger pixel height than flat shoes.

fMRI Paradigm

In the scanner, subjects were shown 20 blocks with a female celebrity and 20 blocks with a non-famous female. These blocks appeared in random order and each block consisted of seven trials. During the first trial of each block, a face appeared randomly on the right or left side of the screen with a name presented next to it. For the famous faces, the actual first and last name of the celebrity was given. For the non-famous faces, names were created by combining general first and last names. As both Dutch and international celebrities were shown to the subjects, the names of the non-famous females corresponded to typical Dutch or foreign female names as well.

During the six following trials of each block, the female face remained on the screen, and instead of the name a shoe appeared next to the face (see Figure 1).

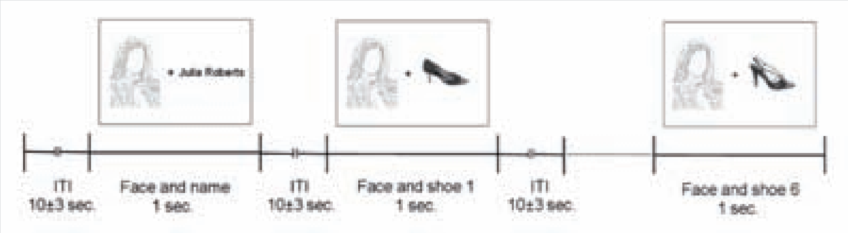


Figure 1. Temporal layout of the stimulus presentation in the fMRI task. Shown here is a block of trials with a female celebrity. During the first trial of each block a female face was presented together with a name. At the 6 following trials the face was paired with a shoe. Subjects were instructed to indicate whether or not they thought this shoe was owned by the female whose face was presented next to the shoe. All trials were separated by a varying intertrial interval (ITI). In this figure a sketch of a celebrity is presented instead of a real photo as used in the study, due to potential copyright restrictions.

The presentation of shoes was randomized so that there were no fixed shoe-face combinations across subjects. In total, subjects were shown 120 trials in which a shoe was paired with a celebrity face and 120 trials in which a shoe was paired with a non-famous face.

While being scanned, subjects were instructed to indicate by appropriate button press whether they thought that the shoe on the screen was owned by the female shown next to it or not. This orientation task aimed to focus subjects' attention and to promote subjects to link the two stimuli together. As a cover story subjects were instructed that 50 percent of all 240 shoes shown were identical to shoes truly owned by the presented famous and non-famous females. This implicated that, on average, for each presented female face there were three shoes possessed by this female (since every female face was shown in combination with six shoes). The aim of this instruction was to balance response behavior between trials showing a celebrity face and trials showing a non-famous face. Subjects were explained that for the shoes possessed by celebrities we selected pictures showing shoes that were highly similar to shoes celebrities had been wearing on press photos. Shoes owned by non-famous females were told to be selected by these females themselves. In addition, to enhance motivation, subjects were instructed to pay close attention to the shoes as their memory performance would be assessed and rewarded (with a maximum of doubling the standard compensation) in a following behavioral session. Subjects responded by pressing with their right middle or index finger on a response box. Mean intertrial interval (ITI) was 10 s (range 7-13 s) and stimuli duration was 1s. Total scan time was approximately 55 minutes.

Behavioral measures

After scanning, subjects performed two behavioral tasks, one regarding the shoes and one regarding the faces. Subjects initially did a recognition memory test and a purchase intention assessment of the previously seen shoes. During the recognition memory test, subjects were exposed to a sequence of pictures containing a random mixture of the 240 shoes processed inside the scanner, only this time without the presentation of a face photograph, and 240 new previously unseen shoes. Subjects were offered two response options (i) picture seen before and (ii) picture not seen before. Purchase intention of the shoes was measured by asking subjects to make an estimate of purchase incidence and indicate it on a scale from 0 to 100 percent (in steps of 10). To assess the recognition memory performance we compared the overall proportion of hits (percentage of previously seen shoes that was correctly identified as recognized: hits / (hits + misses) * 100) with the overall proportion of false alarms (percentage of new shoes that was falsely identified as recognized: false alarms / (false alarms + correct rejections) * 100). Recognition performance was above chance if the proportion of hits was larger than the proportion of false alarms.

During the second behavioral task, subjects evaluated all 20 famous and 20 non-famous faces seen in the fMRI session on physical attractiveness and familiarity. Attractiveness ratings were made on an 11-point scale ranging from 0 to 100 (in steps of 10) with 0 standing for ‘not attractive’ and 100 indicating ‘very attractive’. Familiarity of the faces was measured using a binary response scale with the options ‘familiar’ and ‘not familiar’. To make sure all celebrities were liked and none of the celebrities elicited negative emotions, subjects indicated their liking of the celebrities on a scale from 0 to 100 (in steps of 20) with 0 indicating ‘not at all’ and 100 indicating ‘very’. All trials in the behavioral tasks were presented in a self-paced manner with a stimulus duration of 1 second.

MRI acquisition parameters

Functional images were acquired with a 1.5T Siemens Sonata scanner with ascending slice acquisition and a T2*-weighted echo-planar imaging (EPI) sequence (TR 2.29 s, TE 30 ms, flip angle 70˚, slice matrix 64 × 64 mm, slice thickness 3.0 mm, slice gap 0.5 mm, FOV 224 mm). Anatomical scans were acquired with a T1-weigthed MP-RAGE sequence (176 sagittal slices, volume TR 2.25 s, TE 3.93 ms, flip angle 15˚, slice matrix 256 × 256, slice thickness 1.0 mm, no gap, FOV 256 mm).

fMRI data analysis

Data were preprocessed and analyzed using standard software (SPM5, Wellcome Department of Cognitive Neurology London). The first 5 volumes of each subjects' EPI sequence set were discarded to allow for longitudinal relaxation time equilibration. The remaining images were realigned to the first volume. Functional images were corrected for motion and differences in slice time acquisition. Next, images were normalized to the Montreal Neurological Institute (MNI) template using parameters defined from the normalization of the anatomical scan to the MNI template and images were smoothed with a Gaussian kernel of 8 mm full-width at half-maximum to reduce noise. Motion parameters were stored and used as so-called nuisance variables in the general linear model (GLM) analysis.

A random-effects analysis within the framework of the general linear model was applied to model event-related responses. Four regressors were defined for each subject based on the onsets of the relevant trials: '*Celebrity Face', 'non-Famous Face', 'Shoe with Celebrity Face'*, and, *'Shoe with non-Famous Face'*. Regressors were modeled with a canonical hemodynamic response function and a general linear model analysis was used to create contrast images summarizing differences in brain activity across the *Shoe with Celebrity Face* and *Shoe with non-Famous Face* conditions as well as differences in brain activity across the *Celebrity Face* and *non-Famous Face* conditions. With these images, two group average contrast SPM maps were created: The Object contrast map showed what brain activity was underlying the processing of an object in the context of a famous face (*Shoe with Celebrity Face* > *Shoe with non-Famous Face*) and the Face contrast map showed what brain activity was underlying the processing of a famous face without the presence of an object (*Celebrity Face* > *non-Famous*

Face). To see whether different brain areas were involved in the processing of an object in the context of a famous face and in the processing of a famous face alone, we performed an additional statistical test comparing the brain activity present in the Object contrast map with the activity pattern present in the Face contrast map (p<.05 uncorrected). This exclusive masking procedure revealed only activity in the Object contrast map that did not overlap with the brain areas involved in the Face contrast map. All statistical analyses were thresholded at the cluster-level with a p<.001 uncorrected.

Results

Behavioral results

Manipulation check

Although the pictures of famous and non-famous females were selected based on equal attractiveness ratings, post-scan results revealed that the famous females (M = 65.1%, s.d. = 7.3%) were perceived as being slightly more attractive than the non-famous females (M = 60.5%, s.d. = 7.8%) ($t_{(22,1)}$ = 2.7, p = .014). To eliminate a confounding effect of physical attractiveness on the fame manipulation, four faces (24 trials per subject) were removed from further analyses. Removal of the two famous faces that received the highest score on attractiveness together with the two non-famous faces that received the lowest score on attractiveness resulted in equal attractiveness ratings (M_{famous} = 64.0%, s.d. = 7.6%; $M_{infamous}$ = 61.4%, s.d. = 7.9%; $t_{(22,1)}$ = 1.5, p = .15). The mean attractiveness rating of the 36 remaining faces was 63% (s.d. = 6.4%) and significantly higher than 50% ($t_{(22,1)}$ = 9.5, p < .001), indicating that both the celebrity and the non-famous females were perceived as being more attractive females than average.

All famous faces received likeability ratings above 50% (M = 66%, s.d. = 8.8; $t_{(17,1)}$ = 7.7, p < .001) so no aversive reactions toward the presentation of celebrities were expected. Post-scan measures on familiarity revealed that only in 1% of the total number of trials subjects did not recognize a celebrity as being famous or incorrectly perceived a non-famous face as being famous. Trials containing incorrectly judged famous or non-famous faces were removed from further behavioral analysis. However, as only few faces were incorrectly perceived as being famous or non-famous, trials containing these faces were not removed from the data used for brain analysis.

Fame did not affect response times of the responses given in the orientation task performed during scanning: subjects responded equally fast when indicating whether the presented female was the owner of a shoe if the presented female was a celebrity or a non-famous person ($t_{(22,1)} = .93$, $p = .36$). In addition, we checked the effects of fame on the responses given in the orientation task and found that subjects indicated that they less often thought a shoe was owned by a celebrity (M = 40.5%, s.d. = 8.5%) than by a non-famous female (M = 51.9%, s.d. = 8.8%) ($t_{(22,1)} = 7.9$, $p < .001$). At first glance, this difference may seem surprising as the subjects were explicitly instructed that, on average, 50 percent of the shoes were truly owned by the female presented next to the shoe. However, this result supports our hypothesis that subjects indeed have more associations linked to a famous than to a non-famous face: The more knowledge subjects have about a person (in our case, a celebrity), the less often they think a particular shoe matches with this person.

Effect of fame on recognition memory

Recognition memory performance remained clearly above chance level as the overall proportion of hits (hits / (hits + misses) * 100 = 49.8%, s.d. = 13.5%) was significantly larger than the proportion of false alarms (false alarms / (false alarms + correct rejections) * 100 = 25.5%, s.d. = 12.4%) in the post-scan recognition memory test ($t_{(22,1)} = 15.8$, $p < .001$, $M_{\text{Recognition performance}} = 24.3\%$, s.d. = 7.7%). As expected, subjects demonstrated better memory for shoes presented in combination with a famous face (M = 28.6%, s.d. = 1.0%) than with a non-famous face (M = 19.9%, s.d. = 7.0%) ($t_{(22,1)} = 5.5$, $p < .001$). This is in line with results observed in earlier studies showing that celebrity endorsers have a positive effect on product memory (e.g. Friedman and Friedman, 1979; Petty et al., 1983).

Effect of fame on purchase intention

Contrary to our expectations, post-scan scores on purchase intention were not significantly different for shoes presented together with a famous face (M = 40.1%, s.d. = 8.4%) and shoes that were presented in combination with an non-famous face (M = 39.9%, s.d. = 8.1%) ($t_{(22,1)} = -0.3$, $p = .79$). However, fame did affect the purchase intention if shoes were categorized based on the responses that were given in the orientation task during scanning. Shoes of which subjects indicated they were *not* owned, received higher purchase intentions if they were presented together with a celebrity (M = 36.4%, s.d. = 8.6%) than when they were shown with a non-famous female (M = 34.6%, s.d. = 8.8%) ($t_{(22,1)} = -2.1$, $p = .05$). This result shows that only the shoes that were not perceived as being owned received a higher explicit purchase intention after initial presentation in a context of fame.

fMRI results

The effect of fame on product processing

When analyzing brain responses time-locked to the presentation of a shoe next to a face, we found differential activity in the medial part of the right orbitofrontal cortex between shoes presented with a famous face and shoes presented with a non-famous face (*Shoe with Celebrity Face* > *Shoe with non-Famous Face*) (see Figure 2 and Table 1). Masking this result with an exclusive mask that was generated of the Face contrast map (*Celebrity Face > non-Famous Face*) did not change the activity found in the medial orbitofrontal cortex. This supported the conclusion that activity in this area was related to the learning of associations between a famous face and a product and that it was not related to the processing of faces alone as the areas in which activity was related to the processing of faces were excluded in this analysis after masking.

The effect of fame on face processing

To reveal brain activity related to the processing of a celebrity face, we analyzed the data time-locked to the onset of the trial presenting a face together with a name. Contrasting the trials in which the face and name of a celebrity was shown with trials in which the face and name of a non-famous female were shown revealed significant activations in brain areas associated with the retrieval of episodic [the angular gyrus, precuneus and medial prefrontal cortex] (Maguire, 2001; Wagner et al., 2005) and semantic [the superior frontal area and middle temporal gyrus] knowledge (Simons and Spiers, 2003; Wiggs et al., 1999) (see Figure 3 and Table 1). All activations in this contrast appear to be predominantly lateralized in the left hemisphere, a pattern typical for semantic memory-related activity (Mummery et al., 1999).

We did not find any activation in the medial temporal lobe, a region typically involved in the retrieval of episodic memories (Burgess et al., 2002). This suggests that either the explicit memories related to the famous face were well

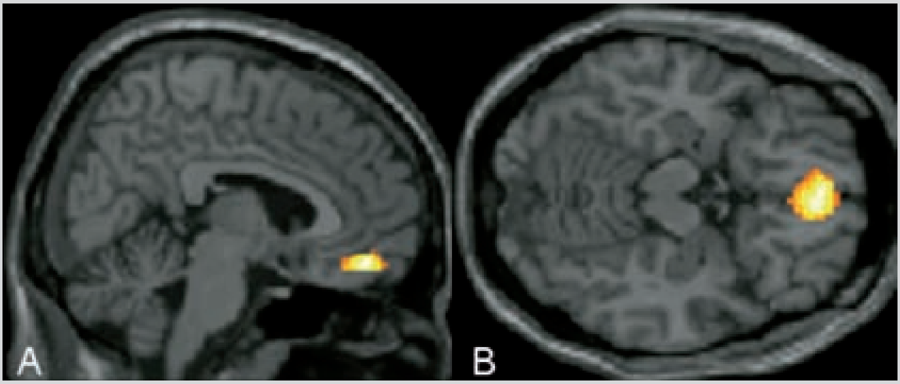


Figure 2. Brain map showing the medial orbitofrontal cortex involved in the processing of products in the context of fame (Shoe with Celebrity Face > Shoe with non-Famous Face), *p* <.001 uncorrected, (A) x = 6; (B) z = -16.

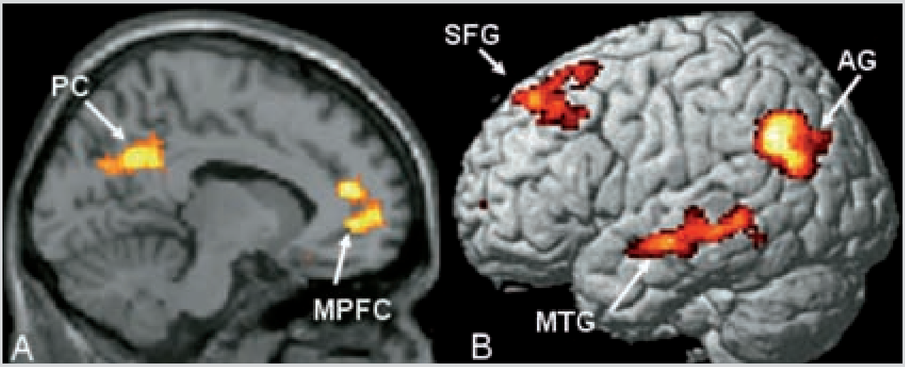


Figure 3. Brain regions involved in the processing of famous faces (Celebrity Face > non-Famous Face), *p* <.001 uncorrected. (A) Medial view of the left hemisphere (parasagittal slice): PC = Precuneus; MPFC = Medial prefrontal cortex; x = -8. (B) Lateral view of the left hemisphere (3D reconstruction): SFG = Superior frontal gyrus; AG = Angular gyrus; MTG = Middle temporal gyrus.

Table 1. Significant areas of activation associated with the effect of fame on product processing (Shoes with Celebrity face > Shoes with non-Famous face) and on face processing (Celebrity face > non-Famous face). HEM = hemisphere, BA = Brodmann area.

Brain region	HEM	x	y	z	Nr. of voxels	z-score (max)
Shoes with Celebrity Face > Shoes with non-Famous Face						
Medial orbitofrontal cortex, BA 11	R	6	46	-16	343	4.8
Celebrity Face > non-Famous Face						
Anterior cingulate cortex, BA 10	L	-8	48	0	625	5.0
Superior frontal area, BA 9	L	-18	38	48	612	4.9
Precuneus	L	-8	-58	32	696	4.7
Angular gyrus, BA 39	L	-44	-62	38	1070	4.6
Middle temporal gyrus, BA 21	L	-56	-44	-2	609	4.1

consolidated in prefrontal areas and retrieved independently of the medial temporal lobe (Takashima et al., 2006) or the memories were not vivid (Ryan et al., 2001) or associative enough (Eldridge et al., 2000) to increase activity in this area. In addition, the processing of famous faces did not activate the striatum or any other brain regions related to the processing of rewards. Apparently, the passive viewing of celebrities was not experienced as more rewarding than viewing equally attractive non-famous faces, indicating that earlier exposures to famous faces did not influence subjects' affective response towards these celebrities.

The effect of fame on purchase intent for not-owned shoes

Behavioral results showed that purchase intention was enhanced by fame if subjects thought that a celebrity or non-famous attractive female did not own the shoes. However, contrasting the condition *Not-owned Shoes with Celebrity Face* with the condition *Not-owned Shoes with non-Famous Face* did not reveal any significant neural activations. This null finding is likely due to a lack of statistical power because of the reduced number of relevant trials per condition (only the not-owned trials were included).

Discussion

The results of our study are consistent with the general finding that celebrities are more effective endorsers than non-famous individuals. The enhanced memory performance for items that were encoded in the context of a famous individual can neither be explained by increased attractiveness of the celebrity nor by a higher level of perceived expertise, but only by the persuasiveness of fame itself. As predicted, we observed increased activity in the orbitofrontal cortex during the encoding of celebrity-product pairings. This result provides strong support for the idea that the mechanism underlying celebrity endorsement is a transfer of positive affect from celebrity to product as the orbitofrontal cortex has been suggested to be important for the learning of associations between neutral and valenced stimuli (Rolls and Grabenhorst, 2008). In particular, we found enhanced activity in the medial part of the orbitofrontal cortex, which supports the hypothesis that celebrities give rise to positive emotions as the medial orbitofrontal cortex has consistently been associated with the encoding of the subjective liking of stimuli (Beer et al., 2008; Grabenhorst et al., 2008; Plassmann et al., 2008; Rolls et al., 2009). Although, the orbitofrontal cortex has been shown to respond to beautiful faces (Ishai, 2007; O'Doherty et al., 2003), the activity in the present study is unlikely to represent the reward activity related to the physical attractiveness of the famous faces, as the famous and non-famous faces included in our fMRI experiment were rated as equally physically attractive.

In addition, we performed an exclusive masking analysis to investigate whether the activity underlying the processing of products in the context of a famous face differed from the activity underlying the perception of a famous face alone. This analysis showed that the brain areas activated by passively viewing famous faces were not significantly activated during the trials in which a famous face was shown in combination with a product. In other words, the medial orbitofrontal cortex did not simply process the presence of a famous face during the presentation of celebrity-object pairings, but instead encoded the presentation of an object in the context of fame. Overall, our results support the hypothesis that the neural activity found in the medial orbitofrontal cortex represents a transfer of affect from celebrity to product.

Memory retrieval and attention

The present study predicted that the positive affect induced by a celebrity endorser could result from the retrieval of explicit and/or implicit knowledge. Investigation of the neural activity underlying the processing of a famous face showed increased activation in brain areas commonly involved during semantic and episodic retrieval tasks. This indicates that the perception of a celebrity face results in the retrieval of explicit memories. Interestingly, we did not find any evidence for the retrieval of implicit memories as there was no increase in neural activity in areas associated with the processing of reward when contrasting famous faces with non-famous faces. We only found activity in a reward-related region, the medial orbitofrontal cortex, during the presentation of a famous face *together* with an object. The medial orbitofrontal cortex was not activated during the presentation of a famous face alone, which suggests that the medial orbitofrontal cortex did not encode the positive affect associated with the retrieval of implicit memories related to a famous face, but instead represented the learning of associations between an initially neutral product and a positively valenced face.

The idea that explicit memories are retrieved during the perception of a celebrity endorser is supported by the behavioral responses subjects gave during the orientation task in the scanner. In this task, we found that subjects less often thought that a shoe was owned by a celebrity than by a non-famous female. In light of the present imaging results this makes sense: the more subjects knew about a female whose face was presented, the less likely they found a shoe to match this female. Furthermore, the spontaneous retrieval of memories during exposure to famous faces is in line with the general idea that well-known persons produce automatic retrieval of person-identity information from long-term memory (Bruce and Young, 1986).

In the current study, the persuasiveness of celebrities did not depend on arousal-driven-attention. The processing of famous and non-famous faces did not evoke differential neural activity in attention-modulated areas such as the visual or inferotemporal cortex and reaction times on the orientation task were equal for both famous and non-famous conditions. This result seems to be in contradiction with the finding of Pleyers and colleagues (2009), who showed that a decrease in attention has a negative effect on the learning of associations between products and positively valenced stimuli. However, in the present study subjects were performing a task in the scanner that was explicitly designed to prevent them from losing attention during the lengthy experiment. Therefore, subjects probably paid equal attention to trials mimicking celebrity endorsements and trials presenting non-famous endorser. Nevertheless, the absence of attentional effects in the present imitation of celebrity endorsement implies that enhanced attention is not essential for celebrity advertisements to be effective.

Purchase intention

In the current study, purchase intentions were not higher for products presented in the context of fame than for products associated with an unknown female. In contrast to the study on celebrity expertise by Klucharev and colleagues (2008), our results show that a single exposure to a celebrity-product pairing was insufficient to affect explicit attitudes. Our imaging results suggest, however, that during this single exposure, positive affect *is* transferred from the celebrity to the product as activity in the medial orbitofrontal cortex is enhanced during the presentation of a product in the context of fame. The fact that we found an effect of fame on the brain but not on subjects' attitudes indicates that fame does increase the liking of objects but that this effect is too small to measure at the explicit level. This interpretation is important for consumer researchers as it suggests that the absence of significant changes in explicit purchase intention measures does not necessarily imply that the liking of a product is unaffected by the experimental manipulation.

Finally, there was one other interesting effect in the present behavioral results that deserves further attention. Although fame did not affect the purchase intention of all shoes presented, fame did affect the purchase intention if shoes were categorized based on the responses that were given in the orientation task during scanning. Shoes of which subjects indicated they were not owned, received higher purchase intentions if they were presented together with a celebrity than when they were shown with a non-famous female. This result indicates that only the shoes that were not perceived as being owned by a more-than-average-attractive female (recall that both famous and non-famous faces received attractiveness ratings higher than 50%), received a higher explicit purchase intention after initial presentation in a famous context. It appears that a context of fame during encoding works particularly persuasive for products that subjects regarded as part of their consideration set, i.e. items that are not specifically associated with almost physically perfect models but instead can be owned by individuals like the subjects themselves.

To summarize, we have shown that the encoding of an object in the context of fame elicits activation in the medial orbitofrontal cortex. This result supports the hypothesis that, during celebrity endorsement, positive affect is transferred from presenter to product. Our research clearly demonstrated that this positive affect originates from the retrieval of semantic and episodic memories as brain regions implicated in the retrieval of explicit memories were activated during celebrity face perception. Furthermore, our results suggest that neither attentional processing nor the retrieval of implicit memories is required for a celebrity advertisement to be effective. Future studies should investigate whether the observed mechanism underlying the persuasive effect of fame can be generalized to the male population.

4.

PEER INFLUENCE

Abstract

People often conform to the behavior of others with whom they identify. However, it is unclear what mechanisms underlie this type of conformity. Here, we investigate the processes mediating in-group conformity by using functional magnetic resonance imaging (fMRI). Participants completed a perceptual decision-making task while undergoing fMRI, during which they were exposed to the judgments of both in-group and out-group members. Results show that in-group conformity involves the striatum, subgenual anterior cingulate cortex, hippocampus and posterior superior temporal sulcus (pSTS). Furthermore, we found that the activity in the pSTS positively correlated with in-group trust. These findings suggest that in-group conformity is mediated by both signals associated with emotion and reward, as well as by the ability to take the perspective of others. The contribution of this data to the generation of new hypotheses regarding the brain basis of social conformity is discussed.

Based on Stallen, Smidts & Sanfey (2013). Peer influence: Neural mechanisms underlying in-group conformity. *Frontiers in Human Neuroscience,* 7(50), 1-7.

Introduction

People are often influenced by others with whom they identify. They buy clothes similar to those of their peers, visit restaurants because their colleagues go there, and download music their friends listen to. By adopting the tastes of others, people show they belong to a specific group. This social factor, whereby people follow the behavior or advice of others they associate with, has been labeled *in-group influence*. In-groups are defined simply as others with whom one identifies, with common in-groups comprised of people of the same age, gender, ethnicity or religion, in addition to groups of one's friends, family members, colleagues or class mates (Turner, 1991). Several reasons may explain why consumers are so susceptible to the influence of others, such as the need for accurate information, the need for social approval or affiliation, or the need to maintain a positive self-concept (Cialdini & Goldstein, 2004; Deutsch & Gerard, 1955). For instance, the need for accurate information is thought to be important in situations of fear or uncertainty, when people can use the behavior of their group as a guideline to understand a situation. Conformity can also underlie the need for social approval, where people want to be liked by people similar to them, or when they want to behave correctly in a socially normative sense. Additionally, in-group conformity may be driven by the need to maintain a positive self-concept, as conforming to others may enhance or repair one's self-esteem. These suggested motives underlying conformity are of course interrelated often (David & Turner, 2001), and while the various theories may provide reasons for why in-group conformity occurs, they typically do not explain what processes are mediating this effect.

The aim of the present study was to gain greater insight into the processes underlying in-group conformity. To examine the mechanism of in-group conformity, we used functional magnetic resonance imaging (fMRI), a modern neuroscientific method that provides a non-invasive measure of neural activity by assessing regional changes in blood oxygenation (blood oxygen level dependent (BOLD) response). Using fMRI enables us to make inferences about the processes that underlie in-group conformity, which is difficult to assess using behavioral measures alone. To investigate the basic underlying processes, we measured in-group conformity using an artificial group manipulation and using a domain that was neither relevant for identity signaling nor related to actual choice. Examining the processes driving in-group conformity under minimal conditions provides insights into the fundamental mechanisms underlying this effect.

Although the application of neuroimaging methods in decision-making research has increased in popularity during the last decade, only recently have neuroscientists started to identify the brain networks implicated in social influence, for example examining the influence of experts (Campbell-Meiklejohn, Bach, Roepstorff, Dolan, & Frith, 2010; Klucharev, Smidts, & Fernandez, 2008), the persuasiveness of celebrities (Stallen et al., 2010), the mechanisms of racial bias (Beer et al., 2008; Gonsalkorale, Sherman, Allen, Klauer, & Amodio, 2011; Van Bavel, Packer, & Cunningham, 2008), the influence of majority behavior on individual decision-making (Berns, Capra, Moore, & Noussair, 2010; Berns et al., 2005; Klucharev, Hytonen, Rijpkema, Smidts, & Fernandez, 2009; Mason, Dyer, & Norton, 2009), and, most relevant to the current investigation, the influence of in-group membership on both money allocation (Volz, Kessler, & von Cramon, 2009) and helping behavior (Hein, Silani, Preuschoff, Batson, & Singer, 2010). Volz and colleagues (2009) investigated the neural implementation of social identity theory, which assumes that each individual has both a personal and a social identity, and that the way information is processed depends on which identity of the individual is salient at the time of decision-making (Tajfel & Turner, 1986). The results of Volz and colleagues (2009) support social identity theory by demonstrating that the social self is derived from the same cognitive processes as the individual self, as activation of both types of identities resulted in similar neural patterns in the prefrontal and parietal network. A second study on in-group influence by Hein and colleagues (2010) investigated the neurobiological basis of the decision to help either an in-group or out-group member in pain. Their results showed that seeing an in-group member in pain evoked more empathy-related responses in the brain than seeing an out-group member in pain, and demonstrated that the degree of this empathy-related response predicted in-group favoritism in actual helping behavior at a later point in time. Importantly however, none of these studies on social influence in the brain examined the processes that underlie conformity to the in-group.

Procedure

Participants and design

Twenty-eight healthy right-handed participants (mean age 20.7 years) took part in the experiment. All were free of neurological or psychiatric illness, head trauma or drug abuse, and none were taking medication. Written informed consent was obtained according to the local medical ethics committee, and participants were compensated financially. Data from three participants were discarded due to technical problems, and one participant was excluded because he guessed the study aim. This resulted in 24 subjects for final analyses (12 males). We used a repeated measures design with the identity of the group member (in-group or out-group member) as a single within-subject factor.

Materials and Methods

Upon arrival, participants' group membership was manipulated using a minimal group paradigm approach (Tajfel, Billig, Bundy, & Flament, 1971). In the task, adapted from Volz et al. (2009), 5 perceptual illusions, such as the young girl-old woman illusion, were shown for 2 seconds each, After each illusion, two possible answers were displayed on the screen and participants were asked to choose between them. Then, participants were informed that they had been categorized as people who either focus on the foreground of visual illusions, people who focus on the background, or as people who could not be classified into either of these two categories. Unbeknownst to participants, everyone was classified as a foreground perceiver (in-group). The other two groups (background and unclassified) will be referred to as the out-group. We manipulated group membership artificially instead of using real, existing groups, as this allowed us to control the (minimal) information participants had about their in-group and out-group members, and hence ensured that the hypothesized in-group conformity effect could not be explained by factors other than group membership, such as for example perceived differences in expertise in perceptual decision-making.

Decision-making task

After the perceptual illusion task, participants completed the decision-making task while undergoing MRI (see Figure 4). First, participants were instructed to look at a dot pattern on a computer screen for 1.5 seconds. The number of dots on display ranged from 5 to 30 (*M* = 15, *SD* = 7.5), and the participants' goal was to estimate the number of dots as accurately as possible. After the brief presentation of the dots, participants were instructed to think about their

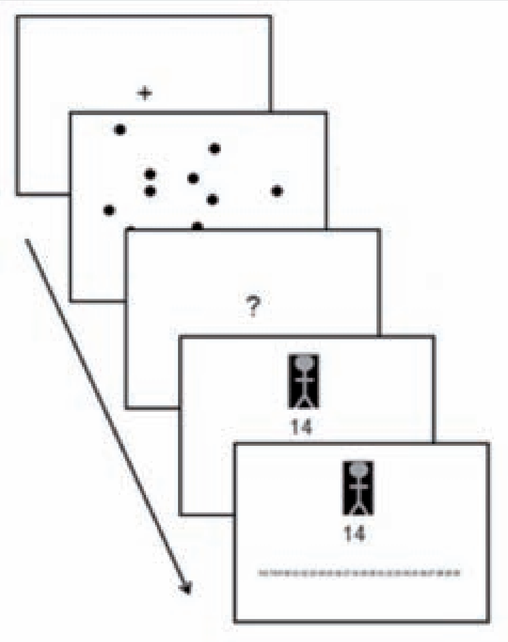


Figure 4. Trial outline with duration times in seconds. Group membership of the other participant was indicated by the color of the cartoon.

estimate (duration jittered between 2.5 and 6 seconds). Next, the estimate of a previous participant was displayed. This estimate came from either a member of the same group as the participant, that is, a foreground perceiver (in-group member) or from a member of a different group (out-group member). Group membership of the other participant (foreground perceiver, background perceiver or unclassified perceiver) was indicated by a colored cartoon of either yellow, purple or blue. Colors were counterbalanced to ensure no confound between the color of the cartoon and group membership. After presentation of the estimates, a response screen appeared. This screen was identical to the previous screen on which the estimate was presented, except for a response bar displayed at the bottom of the screen. This bar consisted of a row of numbers from 5 to 30, on which participants were instructed to indicate their estimate.

Responses were indicated by scrolling to the number of their choice and pressing a confirmation button. The estimates provided by in-group and out-group members were predetermined by a computer script and, unbeknownst to the participant, were always correct. Finally, to enhance motivation, participants were told that the group who performed best would win an (unspecified) prize, with the winning group notified at the end of the study. The presentation of a fixation screen (duration jittered between 3.5 to 5 seconds) signaled the start of a new trial. Participants performed 214 trials. To maintain attention, 6 self-paced breaks were included. The total scanning session took approx. 55 minutes.

MRI acquisition parameters

Functional images were acquired with a 1.5T Siemens Sonata scanner, using an ascending slice acquisition and a T2*-weighted echo-planar imaging (EPI) sequence (TR 2.29s, TE 30 ms, flip angle 70°, slice matrix 64×64 mm, slice thickness 3.0 mm, slice gap 0.5 mm, FOV 224 mm). Anatomical scans were acquired with a T1-weighted MP-RAGE sequence (176 sagittal slices, TR 2.25s, TE 3.93ms, flip angle 15°, slice matrix 256×256, slice thickness 1.0 mm, no gap, FOV 256mm).

Dependent variables

Behavioral questionnaires

To test the group manipulation, participants answered a questionnaire at the end of the experiment. This measured the level of identification (‘I feel connected to the blue/yellow/purple team’), trust (‘I trust people from the blue/yellow/purple team’) and the degree of positive associations (‘I have positive associations with the blue/yellow/purple team’) towards other participants. Responses ranged from 1 (not true at all) to 7 (very true).

Conformity

Conformity was assessed by calculating the percentage of trials on which participants gave the same judgments as the in-group or out-group member.

Brain imaging analyses

Data were preprocessed and analyzed using a standard software package (SPM8, Wellcome Department of Cognitive Neurology London). The first 5 images of each participant’s EPI sequence were discarded to allow for longitudinal relaxation time. The remaining images were realigned to the first imaging volume. Functional images were corrected for motion and differences in slice time acquisition. Next, images were normalized to the Montreal Neurological Institute (MNI) template using parameters defined from the normalization of the anatomical scan to the MNI template, and images were smoothed with a Gaussian kernel of 8mm full-width at half-maximum to reduce noise. Motion parameters were stored and used as nuisance variables in the general linear model (GLM) analysis. A random-effects analysis within the framework of the general linear model was applied to model event-related responses (Friston, Frith, Frackowiak, & Turner, 1995).

Four regressors were defined for each participant based on the onsets of the relevant trials: '*Conformity to In-group'*, '*Conformity to Out-group'*, '*Non Conformity to In-group*', and '*Non Conformity to Out-group'*. Brain responses were time-locked to the presentation of the estimate of either the in-group or out-group member. Regressors were modeled with a canonical hemodynamic response function and a general linear model analysis was used to create contrast images summarizing differences in brain activity across the *Conformity to In-group* and *Non Conformity to In-group* trials, as well as differences in brain activity across the *Conformity to Out-group* and *Non Conformity to Out-group* trials. To test hypotheses regarding brain areas that were uniquely involved in conformity to an in-group member, we masked the brain activity present in the In-group contrast map (*Conformity to In-group* > *Non Conformity to In-group*) with the Out-group contrast map (*Conformity to Out-group* > *Non Conformity to Out-group*) (p < .05 uncorrected) (e.g. Pochon et al., 2002). This exclusive masking procedure revealed activity in the In-group contrast map that did not overlap with the brain areas involved in the Out-group contrast map (p < .001, uncorrected, 10-voxel minimum). To assess whether there was a relationship between brain activity underlying conformity and the self-report measures assessed, we correlated individual beta values of the reported brain activity with participants' scores on the scales measuring identification, positive associations, and trust towards in-group and out-group members.

Results

Manipulation check

In line with the group manipulation, participants identified more strongly with in-group members (*M* = 4.7, *SD* = 1.0) than with out-group members (*M* = 3.2, *SD* = 1.0), *t* (23) = 5.4, *p* < .001 (paired t-test). There were no differences in identification between the two out-groups, that is, participants identified equally with out-group members that were classified as background perceivers (*M* = 3.3, *SD* = 1.1) or that were not classified (*M* = 3.2, *SD* = 1.2), *t* (23) = .6, *ns*. Consistent with an in-group preference, participants had more positive associations with in-group members (*M* = 5.8, *SD* = .6) than with out-group members (*M* = 4.9, *SD* = .9), *t* (23) = 4.3, *p* < .001, and participants reported greater trust in in-group members (*M* = 4.9, *SD* = 1.1) than in out-group members (*M* = 4.1, *SD* = 1.0), *t* (23) = 3.3, *p* < .005.

Behavioral conformity

Participants conformed more often to in-group judgments than to out-group judgments. The percentage of trials in which participants' judgment matched the estimate of the group member was higher when seeing the estimate of an in-group member (*M* = 67.8%, *SD* = 9.4%) than an out-group member (*M* = 65.4%, *SD* = 9.2%), *t* (23) = 2.8, *p* < .01.

Neural correlates of in-group conformity (Table 2)

When examining brain areas exclusively involved in conformity to the in-group, we found a significant increase in activity in right caudate, subgenual anterior

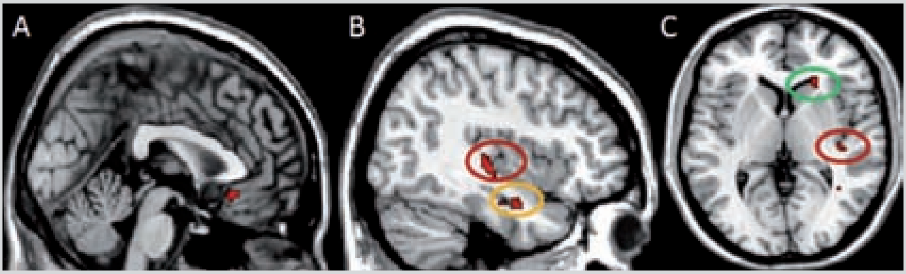


Figure 5. Brain regions involved in in-group conformity, *p* < .001 uncorrected. (A) subgenual ACC, x = 0; (B) pSTS/ insula (circled in red) and hippocampus (circled in yellow), x = 40; (C) pSTS/ insula (circled in red) and caudate (circled in green), z = 4.

Table 2. Significant areas of activation associated with conformity towards in-group members. MNI coordinates of peak activity. HEM = hemisphere; BA = Brodmann area; pSTS = posterior superior temporal sulcus; SubACC = subgenual anterior cingulate cortex.

Brain region	HEM	BA	x	y	z	Nr. of voxels	z-score (max)
Hippocampus	R	20	36	-10	-18	101	4.6
pSTS/ Insula	R	48	40	-20	0	68	4.6
SubACC	-	11	0	26	-8	28	3.7
Caudate	R	47	22	29	4	21	3.6

cingulate cortex (subACC), right hippocampus, and in the intersection of the right posterior insula and the posterior superior temporal sulcus (pSTS) (see Figure 5). Furthermore, we found that the activity in the posterior insula/pSTS positively correlated with participants' scores on the trustworthiness of in-group members ($r = .53$, $p < .01$). Thus, the more trustworthy participants' judged their in-group, the higher the activity in this region.

Discussion

To examine the basic processes that mediate in-group conformity, we explored the neural mechanisms underlying this effect. Activity in the caudate was selectively enhanced when participants conformed to the in-group, supporting the hypothesis that the striatum plays an important role in social influence (Campbell-Meiklejohn, et al., 2010; Klucharev, et al., 2009; Zaki, Schirmer, & Mitchell, 2011). The striatum, located in the center of the brain, is a major input station for midbrain dopamine neurons and plays a primary role in the processing of rewards, including primary rewards such as liquids, foods, and sexual stimuli (Berns, McClure, Pagnoni, & Montague, 2001; O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003; Redouté et al., 2000), as well as to money (Knutson, Westdorp, Kaiser, & Hommer, 2000) and more abstract rewards such as reputation or status (Izuma, Saito, & Sadato, 2008; Zink et al., 2008). The finding that the striatum is involved in in-group conformity, in conjunction with conformity-related activations in other low-level processing areas such as the subACC, an area implicated in the experience of affective states (Drevets et al., 1997), and the hippocampus, an area important for the retrieval of spatial memories (such as possibly the dot display) (e.g. Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000), suggests that in-group conformity is mediated by basic value signals in the brain. These results are in line with previous findings suggesting that the involvement of the subACC is related to the positive affective experience of social inclusion, as this brain region has been implicated in social acceptance (Somerville, Heatherton, & Kelley, 2006), and also shown to be more active for individuals low in rejection sensitivity (Burklund, Eisenberger, & Lieberman, 2007). Taken together, these findings may suggest that people conform more to in-group members than to out-group members because the behavior of in-group members is more strongly associated with the experience of positive affect and reward.

Greater activity for in-group conformity was also found in a region bordering the pSTS and the posterior insula, with peak activity in the posterior insula but extending further into pSTS. The pSTS is an area often implicated in the cognitive capacity of perspective taking, typically termed Theory of Mind (Frith & Frith, 2006). The concept of Theory of Mind is defined as the understanding that others have their own individual perspective on the world, which may differ from your own. Finding that the BOLD response in the pSTS is selectively enhanced for in-group conformity is interesting, as this could imply that participants took the perspective of the other more when the other was an in-group member than an out-group member. This hypothesis supports previous work suggesting that people mentalize more about in-group than out-group members (Freeman, Schiller, Rule, & Ambady, 2010; Harris & Fiske, 2006; Heatherton, 2011). Moreover, activity in the pSTS correlated with participants' self-report measures on the perceived trustworthiness of the in-group, again indicating that those who reported strong feelings of trust towards their in-group were more in-tune with the mental state of their in-group member.

Future research could productively test the hypotheses that in-group conformity is fundamentally mediated by positive affect and the ability to perspective-take, as these interpretations here are based on previous research linking activity in specific brain regions to basic cognitive functioning. In general, the ability to assess with certainty the cognitive processing reflected by specific brain activity is challenging due to the multiple functions brain regions typically engage in (Poldrack, 2006). Follow-up behavioral and neuroimaging studies can reveal how different contexts, such as participant population and decision-making domain, may modulate the basic mechanisms of in-group conformity reported here. For instance, the conformity effect reported here is quite small, likely due to the minimal conditions under which in-group conformity was tested. However, when using natural groups, such as friends or sports teams, and when measuring conformity in a decision-making domain more closely related to identity formation, such as consumption choice for clothing, music, hairstyle or food (Bearden & Etzel, 1982; Berger & Heath, 2007, 2008), the present in-group conformity bias would likely be stronger. In-group conformity in contexts more relevant to identity formation may not only be mediated by basic mechanisms of positive affect and perspective taking as reported here, but by the activation of social identity processes as well. A candidate brain region for these processes is the dorsal medial prefrontal cortex, as previous research has found this area to be implicated in the activation of self and group identity and to correlate with a behavioral in-group bias (Volz, et al., 2009). In addition, our findings encourage the study of in-group conformity across different age ranges. We found in-group conformity to be mediated by increased activity in the subACC, an area known to be involved in social inclusion (Burklund, et al., 2007; Somerville, et al., 2006) and positive affect (Kim et al., 2003; Sharot, Riccardi, Raio, & Phelps, 2007) in adults. However, in adolescents the subACC has been found to correlate with social exclusion (Masten et al., 2009). This may predict that while in-group conformity in adults is possibly primarily driven by positive affect associated with social inclusion, in-group conformity in adolescents may be driven more by negative affect associated with social exclusion.

Conclusion

The present findings complement behavioral work on group influence (e.g. Asch, 1951; Cialdini & Goldstein, 2004; Jetten, Spears, & Postmes, 2004) and expand on recent studies on the neural bases of both conformity (Berns, et al., 2010; Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001; Campbell-Meiklejohn, et al., 2010; Klucharev, et al., 2009; Mason, et al., 2009; Zaki, et al., 2011), and in-group influence (Hein, et al., 2010; Volz, et al., 2009). The current study is a first step towards understanding the nature of actual in-group conformity behavior, and provides a first insight into what mechanisms drive this effect. Our data indicate that both positive associations linked to in-group members, as well as the ability to take the perspective of the in-group, play an important role in in-group conformity. Understanding why group membership has such a profound influence on decision-making provides a window into one of the basic motivations underlying human social behavior.

5.

THE HERDING HORMONE

Abstract

People often conform to others with whom they associate. Surprisingly however, little is known about the possible hormonal mechanisms that may underlie in-group conformity. Here, we examined whether conformity towards one's in-group is altered by oxytocin, a neuropeptide often implicated in social behavior. After administration of either oxytocin or placebo, participants were separated into one of two groups and asked to provide attractiveness ratings of unfamiliar visual stimuli. While viewing these stimuli, participants were shown ratings for each stimulus provided by both in-group and out-group members. Results demonstrated that on trials in which the ratings of the in-group and out-group were incongruent, participants given oxytocin conformed to the ratings of their in-group, but not out-group. Participants in the placebo condition did not show this in-group bias. These findings indicate that oxytocin administration can influence subjective preferences, and support the view that oxytocin's effects on social behavior are context-dependent.

Based on Stallen, de Dreu, Shalvi, Smidts, Sanfey (2012). The herding hormone: Oxytocin stimulates in-group conformity. *Psychological Science*, 23(11), 1288-1292.

Introduction

Humans and non-human primates alike adjust their behavior and beliefs towards others in their social circles (Cialdini & Goldstein, 2004; Whiten et al., 2005). In humans, conformity can affect judgments ranging from low-level perceptual line-length estimates (Asch, 1951) to more complex behaviors such as energy conservation (Schultz et al., 2007) and jury verdicts (Davis, 1973). To explain these well-documented tendencies, cultural evolutionary models conjecture that conformity has adaptive value under a wide range of conditions (Henrich & Boyd, 1998). By conforming to common behaviors and shared opinions of one's own group or community (henceforth "in-group"), members benefit from the wisdom of the group as a whole and thus increase survival likelihood at both the personal and the group level.

If in-group conformity indeed has adaptive value, it seems likely that there are evolved biological mechanisms that may facilitate and sustain in-group conformity. Here, we hypothesize that in-group conformity is mediated by oxytocin, a neuropeptide produced in the hypothalamus which functions as both hormone and neurotransmitter (Bartz et al., 2011; Donaldson & Young, 2008). Well-known for its role in reproduction and pair-bond formation (Gainer & Wray, 1994), numerous studies have demonstrated that oxytocin also plays a pivotal role in motivating affiliation and pro-social behavior. For instance, experiments with animals have found that the manipulation of oxytocin binding in the rat brain modulates caring behavior towards pups (Olazábal & Young, 2006), and that the neural distribution of oxytocin receptors correlates with the intensity of pair bonding in voles (Insel & Shapiro, 1992). In humans, intranasal administration of oxytocin reduces distress, enables the behavioral expression of trust, and additionally appears to motivate cooperation and generosity (Baumgartner et al., 2008; Declerck et al., 2010; Kosfeld et al., 2005; Zak et al., 2007).

Although there is a robust relationship between oxytocin and pro-sociality, it is becoming evident from the literature that the effect of oxytocin on social behavior is not indiscriminately positive but that situational and individual factors critically moderate the effects of oxytocin on pro-social behavior (Bartz et al., 2011; Kemp and Guastella, 2011). For instance, oxytocin appears to increase trust towards partners only when cues about untrustworthiness are absent (Mikolajczak et al., 2010), enhances cooperation only when one's partner is known (Declerck, et al., 2010), and also motivates negative feelings such as envy and schadenfreude following losses in interpersonal competition (Shamay-Tsoory et al., 2009). Similarly, oxytocin's effects on trust and cooperation depend on group membership –people given oxytocin as compared to placebo are more cooperative towards in-group members than towards out-group members (De Dreu et al., 2010), and are less willing to sacrifice in-group, but not out-group, members when presented with hypothetical moral choice dilemmas (De Dreu et al., 2011).

This emerging insight that oxytocin plays an important role in group affiliation, and therefore may encourage parochial cooperation and in-group favoritism, raises the possibility that oxytocin may stimulate in-group conformity. However, whether oxytocin's effects on in-group favoritism are sufficiently powerful to actually influence individuals' subjective preferences remains an important open question. Here, we examined this possibility by assessing whether oxytocin (i) stimulates conformity, and (ii) induces in-group conformity in particular. We employed a minimal-group setting paradigm, which utilizes a neutral decision domain and allows the participant's opinion to be voiced anonymously. By using this basic setting, we can test the most fundamental conditions for an in-group conformity effect, as the design eliminates both reputation concerns for the participant as well as the possibility of gaining positive public recognition by conforming to other group members.

Therefore, after administration of either oxytocin or placebo participants were assigned to arbitrary groups based on trivial criteria, and we hypothesized that oxytocin would lead to greater in-group conformity. Demonstrating that oxytocin influences in-group conformity in particular, even under these most basic conditions, would illustrate that the effects of oxytocin are sufficiently strong to influence actual preference, and additionally provide valuable support for earlier findings suggesting that oxytocin tunes the individual specifically towards the in-group.

Materials and Methods

Design and participants

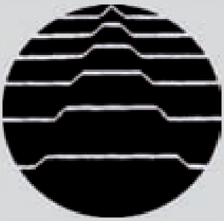
To examine effects of oxytocin on in-group conformity we recruited males (*N*=74; 37 oxytocin) for a double blind, randomized, placebo-controlled between-subject design. To avoid pharmacological effects other than those caused by oxytocin, the placebo contained all active ingredients except for the neuropeptide. Participants received €10 (~$13 US), and provided informed consent before the experiment. Exclusion criteria were significant medical or psychiatric illness, medication, smoking more than five cigarettes per day, or drug/alcohol abuse. Participants were instructed to refrain from smoking or drinking (except for water) for 2 hours before the experiment, and were tested between noon and 4 pm. The experiment was approved by the University of Amsterdam ethics committee and complied with American Psychological Association guidelines. Five participants (3 oxytocin, 2 placebo) were excluded because they failed to follow instructions correctly (>10 trials with response times <1s), and therefore analyses were conducted on 69 participants (mean age=21.1 years, *SD*=2.9 years). Exclusion of these participants did not affect the results.

Experimental procedure

Each experimental session tested six participants at a time, with participants seated in individual cubicles to prevent any form of communication. They self-administered the medication (Syntocinon spray, Novartis; three puffs per nostril, each with 4 IU of oxytocin or placebo) under experimenter supervision. The experimenter then left the cubicle, and participants completed a series of unrelated tests. Instructions guaranteed complete anonymity.

Effects of oxytocin typically emerge after 30–40 min (Baumgartner, et al., 2008; De Dreu, et al., 2010; De Dreu, et al., 2011; Kosfeld, et al., 2005), and therefore after 38–42 minutes (dependent on how quickly participants completed the unrelated tasks) the computer switched to the main experiment. First, participants learned that they would perform a task involving the participant's own group (denoted as "Team Y6"), and another three-person group (denoted as "Team X4"; labeling was counterbalanced, had no effects, and is further ignored). Group assignment was based on the order in which participants signed up for the experiment, and participants were told that most, though not necessarily all, group members were currently present in the laboratory (De

Symbol 14



Team X4

X4 – person 1	Rating	10
X4 – person 2	Rating	…
X4 – person 3	Rating	9

Team Y6

Y6 – person 1	Rating	2
Y6 – person 2	Rating	3
Y6 – you	Rating	… (*Type here your rating between 1 and 11*)

Figure 6. Sample trial. On each trial, participants saw a symbol and ratings of that symbol's attractiveness by out-group members [omit (Team X4)] and in-group members [omit (Team Y6)]. Participants were then asked to provide their own rating. Ratings were made on a scale ranging from 1, *not attractive at all*, to 11, *very attractive*, and participants were shown one, two, or no ratings from each team, depending on the trial. In this example, two out-group members (Team X4) rated the symbol as being attractive while two in-group members (Team Y6) rated the symbol as being unattractive.

Dreu, et al., 2010). Finally, they were told that they would not know who was in either group and that responses would remain anonymous.

Then, participants were told that they would be asked to rate a series of symbols, using a scale of *1=not attractive at all* to *11=very attractive*[1]. The task was self-paced. While viewing the symbols, participants also saw the ratings for that symbol from the members of their own team as well as from the members of the other team, if available at that time (on some trials no ratings were provided, and on other trials either one or two were given to both examine whether the number of ratings affected the strength of the conformity bias, and to enhance the impression that ratings were in real-time—see Figure 6 for a sample trial). Trials of interest were those in which in-group and/or out-group members either liked (high ratings of 8—11) or disliked (low ratings of 1—4) the symbol. Trials with intermediate ratings (from 5—7) were used as filler trials to prevent participants from guessing the study aim, and trials in which participants received no rating information ('blank trials') were used to assess whether oxytocin affected general attractiveness judgments. Following this task, participants completed the Positive and Negative Affect Scale (PANAS; Watson et al., 1988) to assess potential mood effects of oxytocin.

Results

To determine whether participants showed a general conformity effect, we first analyzed the congruent trials in which two in-group and two out-group members both liked or disliked the symbol. This 2 (treatment: placebo/oxytocin) x 2 (rating: in-group high, out-group high / in-group low, out-group low) mixed-model ANOVA, with treatment as between-subject factor and rating as within-subject factor, showed a main effect of rating, $F(1,67)=16.44$, $p<.001$, but no interaction between treatment and rating, $F(1,67)=1.79$, $p=.185$. This finding demonstrated that participants gave significantly higher ratings when both in-group and out-group members liked the symbol, and lower ratings when both in-group and out-group members disliked the symbol ($M_{\text{in\_out-group high}}=6.51$, $SD_{\text{in\_out-group high}}=1.36$; $M_{\text{in\_out-group low}}=5.51$, $SD_{\text{in\_out-group low}}=1.65$), thus confirming the presence of a general tendency to conform to others' judgments (Cialdini and Goldstein, 2004).

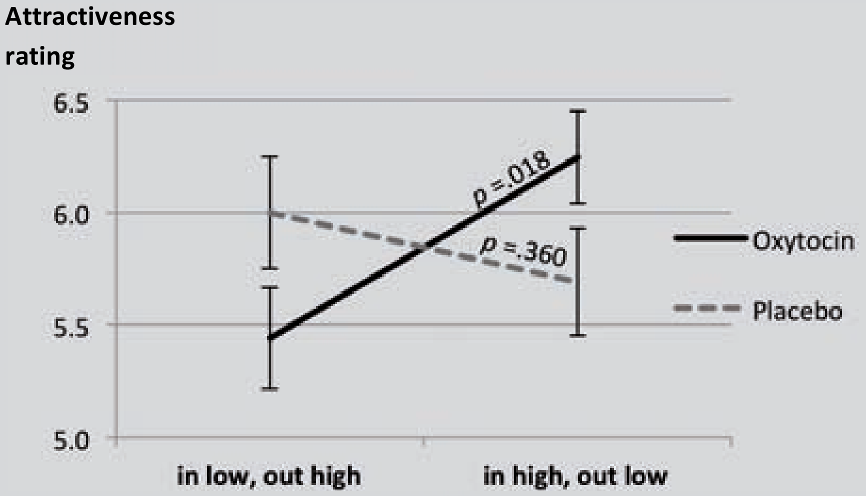


Figure 7. Mean ratings of the attractiveness of symbols as a function of groups' ratings and participants' condition. Results are shown for incongruent trials; that is, when the in-group and out-group gave opposite ratings. Errors bars indicate standard error of the mean.

To test our hypothesis that oxytocin affected in-group conformity in particular, we analyzed the incongruent trials–trials where the in-group and out-group gave opposite ratings, that is, when the in-group liked the symbols but the out-group did not and *vice versa*. These trials included those in which two members of each group gave ratings, as well as those in which ratings were given by just one in-group member and one out-group member. A 2 (treatment: placebo/oxytocin) x 2 (rating: in-group high–out-group low /in-group low–out-group high) x 2 (number of members: 1 in-group, 1 out-group/ 2 in-group, 2 out-group) mixed-model ANOVA with treatment as a between-subject factor and rating and number of members as within-subject factors, revealed only a significant interaction between rating and treatment, *F*(1,67)=5.76, *p*=.019. Figure 7 shows that oxytocin stimulated conformity when in-group and out-group members gave contrasting ratings, independent of the number of ratings provided.

Specifically, participants given oxytocin expressed preferences that were closer to those of the in-group, $t(33)=2.50$, $p=.018$ ($M_{\text{in-group low, out-group high}}=5.44$, $SD_{\text{in-group low, out-group high}}=1.27$; $M_{\text{in-group high, out-group low}}=6.25$, $SD_{\text{in-group high, out-group low}}=1.4$), while participants given placebo did not, $t(34)=.93$, $p=.360$ ($M_{\text{in-group low, out-group high}}=6.00$, $SD_{\text{in-group low, out-group high}}=1.47$; $M_{\text{in-group high, out-group low}}=5.69$, $SD_{\text{in-group high, out-group low}}=1.42$). This supports the hypothesis that oxytocin stimulates in-group conformity.

Analysis of ratings on trials where no ratings were provided showed no effect of oxytocin, $t(67)=.78$, $p=.437$ ($M_{\text{oxy}}=5.37$, $SD_{\text{oxy}}=1.91$; $M_{\text{plac}}=5.75$, $SD_{\text{plac}}=1.83$), indicating that oxytocin did not result in a particular response bias. Furthermore, participants' responses on the PANAS showed no effect of oxytocin on either positive affect, $F(1,67)=.25$, $p=.83$ ($M_{\text{oxy}}=3.3$, $SD_{\text{oxy}}=1.27$; $M_{\text{plac}}=3.22$, $SD_{\text{plac}}=1.22$), or negative affect, $F(1,67)=.33$, $p=.80$ ($M_{\text{oxy}}=2.41$, $SD_{\text{oxy}}=1.18$; $M_{\text{plac}}=2.47$, $SD_{\text{plac}}=1.08$). Finally, oxytocin did not influence response latencies, $F(1,67)=.26$, $p=.614$ ($M_{\text{oxy}}=5.08$ seconds, $SD_{\text{oxy}}=1.97$ seconds; $M_{\text{plac}}=4.85$ seconds, $SD_{\text{plac}}=1.96$ seconds).

Discussion

The present results demonstrate that oxytocin stimulates in-group conformity. When asked to rate novel visual stimuli on attractiveness, and when the participant's in-group and out-group exhibited opposing preferences, individuals given oxytocin expressed preferences that were closer to those of the in-group than the out-group. The selective in-group bias was absent in the placebo condition, and independent of the number of ratings shown. This finding provides novel evidence that oxytocin is involved in influencing people's preferences about actual stimuli, complementing earlier work demonstrating that oxytocin alters perceptions of more abstract concepts such as generosity, trust and fairness. The results also support the notion that the effects of oxytocin on social behavior are context-dependent (Bartz et al., 2011; Kemp and Guastella, 2011). In line with past work demonstrating that oxytocin's effect on trust are reduced when the other is described as untrustworthy (Mikolajczak, et al., 2010), is unknown (Declerck, et al., 2010) or is a member of an out-group (De Dreu, et al., 2010), we find here that the effects of oxytocin on conformity are limited to the in-group and do not include preferences of the out-group.

Our results raise some interesting questions regarding what processes underlie oxytocin's influence on in-group conformity. One explanation of the selective in-group conformity bias under oxytocin may be that this neuropeptide stimulates conformity to in-group members by enhancing in-group identification processes (De Dreu, et al., 2011), as previous work has shown that the perception of shared group membership is both essential and sufficient to establish in-group favoritism (Deutsch & Gerard, 1955; Tajfel et al., 1971). Thus, participants in our study may have identified more with their in-group after receiving oxytocin rather than placebo. An additional question is to what extent oxytocin's effects on in-group conformity depend on social comparison processes with out-group members. Here, we find that oxytocin induces conformity towards the in-group only when the two groups provide opposing ratings, but not when both have similar views. Therefore, oxytocin may play a critical role in mediating in-group identification processes, particularly when the situation involves intergroup comparisons and when group conformity functions to distinguish oneself from members of other groups. This possibility aligns well with previous work suggesting that a primary function of in-group biases is to signal group membership and establish intergroup differentiation (Jetten et al., 2004). Future studies could in particular examine whether oxytocin's effects on conformity are driven by increased in-group affiliation, or rather whether oxytocin also leads people to move away from the out-group—this is an important question, but these processes cannot be disentangled with the present data.

The minimal group setting employed here was designed to be as modest a manipulation as possible. It is thus not surprising that we did not observe in-group conformity in the placebo condition—previous studies have shown that in-group conformity is stronger when individuals engage in face-to-face interactions and when responses are made public and not in minimal group settings with anonymous private reporting (such as employed here) (Bond, 2005; Deutsch & Gerard, 1955). Accordingly, future research focusing on inter-group settings with reduced anonymity, increased reputation concerns, and potentially stronger in-group identification, appears therefore likely to uncover increased conformity under oxytocin versus placebo.

Future work combining brain-imaging methods with oxytocin administration could usefully reveal whether effects on in-group conformity are mediated via in-group identification processes, or whether other mechanisms may also play a role. For example, neuroimaging studies have linked in-group identification to the medial prefrontal cortex, with sub-regions in this area differentially involved when thinking about self and others, respectively (Mitchell et al., 2006). In addition, a possible route via which oxytocin might mediate in-group conformity is through activation of the striatum, which is one of the brain areas found to be associated with in-group conformity in chapter 4. The striatum plays an important role in reward-dependent learning and both the ventral and dorsal striatum are known to contain oxytocin receptors (Skuse & Gallagher, 2009). Importantly, previous studies have demonstrated that the striatum is heavily involved in social influence (Campbell-Meiklejohn, Bach, Roepstorff, Dolan, & Frith, 2010; Klucharev, Hytönen, Rijpkema, Smidts, & Fernández, 2009). One possibility therefore is that oxytocin promotes in-group conformity by activating the striatum, which in turn enhances the rewarding value of in-group membership, and, consequently, promotes in-group conformity. Indeed, recent work on the effects of oxytocin on cooperation in the Prisoner's Dilemma Game found that oxytocin augmented the caudate response to reciprocated trust, suggesting that oxytocin increases the reward value of reciprocated cooperation, and that oxytocin may facilitate learning whether to trust others or not (Rilling et al., 2012). However, to what extent oxytocin's effects on in-group conformity are mediated by positive reinforcement learning signals in the striatum remains an important open question that could be addressed by future work combining oxytocin administration with the experimental paradigm as used in chapter 4.

To conclude, the current results extend previous findings regarding oxytocin's effects on in-group favoritism (De Dreu, et al., 2010; De Dreu, et al., 2011) into the domain of social influence. Although group membership here was artificially manipulated, neutral stimuli were presented, and participants' evaluations were kept anonymous, the effect of oxytocin was sufficiently powerful to influence actual preferences and induce in-group conformity. Thus, oxytocin not only promotes in-group favoritism, but may even stimulate individuals to conform to the behavior and beliefs of others in their group. The finding that oxytocin stimulates conformity towards in-group members, but not out-group members, provides useful insights into the nature of this hormone, and will help in developing a more refined theory of the effects of oxytocin on human social judgment and behavior.

Note

1. Symbols used in the current study were chosen from a broader set used by van der Lans et al. (2009), who rated these stimuli on familiarity, distinctiveness, and neutrality. We selected a subset of 45 symbols that were ranked by Van der Lans's participants from the Netherlands as unfamiliar, non-distinctive, and neutral in terms of likeability.

Part 2

Whereas the first part of this thesis examines the impact of social influence on decision-making, the second part of this thesis focuses on the role of social norms, as our decisions are not only influenced by others but also by our beliefs about what behavior is morally right as well as by our perceptions about what behavior is typically approved of and disapproved of by others. To this end, chapter 6 gives an overview of the neural processes that underlie the decision to cooperate with others and describes how expectations and emotions elicited by the social context influence cooperation. Chapter 7 examines the role of oxytocin in social norm enforcement.

6.

THE COOPERATIVE BRAIN

Abstract

Cooperation is essential for the functioning of human societies. To better understand how cooperation both succeeds and fails, recent research in cognitive neuroscience has begun to explore novel paradigms to examine how cooperative mechanisms may be encoded in the brain. By combining functional neuroimaging techniques with simple but realistic tasks adapted from experimental economics, this approach allows for the discrimination and modeling of processes that are important in cooperative behavior. Here, we review evidence demonstrating that many of the processes underlying cooperation overlap with rather fundamental brain mechanisms, such as, for example, those involved in reward, punishment and learning. In addition, we review how social expectations induced by an interactive context and the experience of social emotions may influence cooperation and its associated underlying neural circuitry, and we describe factors that appear important for generating cooperation, such as the provision of incentives. These findings illustrate how cognitive neuroscience can contribute to the development of more accurate, brain-based, models of cooperative decision-making.

Based on Stallen & Sanfey (2013). The cooperative brain. *The Neuroscientist*, Jan 8 [Epub ahead of print].

Introduction

Picture yourself in a rural village surrounded by meadows open to herdsmen to graze their cows. It is in each herder's interest to put every new cow he acquires onto the land, even if this means that the pasture will be damaged by overgrazing in the long-run. After all, more cows means more income for the herdsman and the disadvantage of less food per cow is spread among all the other herdsmen. But therein is the problem. If all herdsmen act this way, the meadows will be depleted to the detriment of all.

Hardin, 1968

The above scenario has become famous as a parable outlining the inherent conflict between self-interest and cooperation. Cooperative actions by individuals help the collective, but a selfish individual can benefit even more by not cooperating and instead pursuing his own private interests. Modern examples of 'the tragedy of the commons' can be found in countless domains, from relatively trivial instances such as littering, vandalism, and illegal downloading of media, to more consequential situations such as the use and overuse of environmental resources. For instance, oceans are not owned by individuals and provide a common resource of fish. However, as the amount of fishing increases year after year, the fish population loses its ability to restore itself, resulting in an overall diminution of the fish stock. So while the individuals who overfish benefit from greater supply, the collective suffers from a depleted resource. Similarly, the release of carbon dioxide has resulted in high concentrations of greenhouse gases that are harmful for everyone in the long term. Therefore, in order to prevent depletion of common resources, such as oceans or clean air, and to ensure the availability of public goods, such as medical care or inexpensive music on the internet, cooperation is required.

A growing number of studies in both the field and in the laboratory demonstrate that people are imperfect cooperators – they tend to cooperate only if others do so, and there is a substantial minority of people who never cooperate, instead 'free-riding' at the cost of others (Fischbacher, Gachter, & Fehr, 2001) (Figure 8). This suboptimal pattern of behavior causes unstable cooperation levels and often results in the disappearance of positive collective action over time. Thus, people must often be persuaded to sacrifice self-interest for the collective benefit. But how is cooperation induced? What processes are important in encouraging cooperation within a group?

In this review, we will outline the basic processes that underlie cooperation, such as reward and learning mechanisms, and discuss what is known about the neural bases of these processes. In addition, we review how expectations induced by either the social context or social emotions may influence cooperation, also noting the associated underlying neural circuitry, and we describe factors important for generating cooperation, such as the provision of incentives. We conclude by discussing how a broad perspective in understanding the mechanisms of cooperation may help in developing more effective ways of promoting cooperative behavior. Understanding at a fundamental level how cooperation both succeeds and fails can provide valuable clues as to how interventions could be structured to maximize cooperative interactions in important social policy contexts.

Recent laboratory research in cognitive neuroscience has begun to explore novel paradigms that offer fruitful avenues to examine how cooperative processes may be encoded in the brain. Most of this research is embedded within the field of Neuroeconomics/Decision Neuroscience, an interdisciplinary effort to better understand the fundamentals of human decision-making. Within this field, researchers are building models of decision-making that incorporate both the psychological processes that influence decisions, how these processes are constrained by the underlying neurobiology, and also developing formal models of these decisions, an approach developed from economics.

Game Theory

An early effort to formally model how cooperation and noncooperation can occur emerged from Game Theory (Von Neumann & Morgenstern, 1947), a collection of rigorous models attempting to understand and explain situations in which decision-makers must interact with one another, such as bidding in auctions and salary negotiations. Consequently, these models were applied to large-scale social scenarios, in particular strategic decision-making during the Cold War era. For example, theorists were influential in applying formal Game Theoretic principles to the Vietnam War (Schelling, 1960). However, a fundamental flaw of this approach, as was painfully evident from efforts to

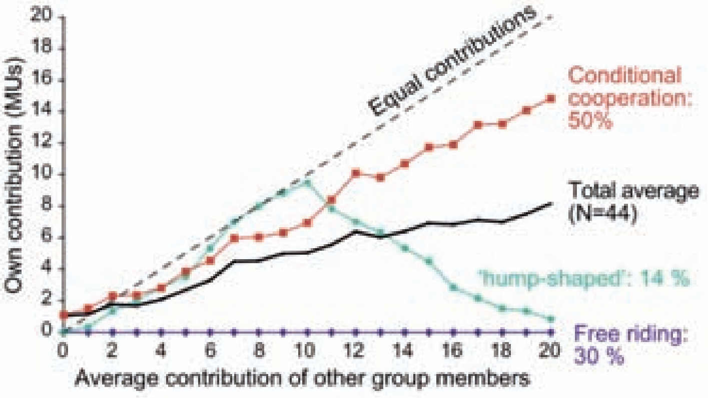


Figure 8. People's willingness to contribute to a public good is typically conditional on the average contribution of others. Here, 44 individuals interacted anonymously with each other (Fischbacher et al., 2001), with participants raising their contributions to the public good only if the average contribution of the others increased (conditional cooperation - 50%, red). However, about one third of the participants never contributed anything (free-riding: 30%, purple), or only contributed if the average contribution of others was low (hump-shaped: 14%, green). The remaining 6% of the participants in the experiment exhibited irregular contribution behavior. Reprinted with permission from Fischbacher et al., (2001) and Fehr and Fischbacher (2004)[2].

formulate policy based on these theoretical principles, is that actual observed decision behavior typically deviates, often quite substantially, from the predictions of the model. Ample research has shown that players typically do not play according to the purely self-interested strategies predicted by Classical Game Theory (Camerer 2003). In reality, decision-makers are influenced by a wide range of psychological factors, which can enhance, though sometimes reduce, cooperative behavior. For example, people are typically both less selfish and more willing to consider factors such as reciprocity and equity than the classical model predicts. They care about status and social hierarchies, often seek vengeance, but are also affected by factors such as empathy and guilt. So, in order to develop policy principles that can accurately predict both the development, and ideally the enhancement, of cooperation, the formal models require elaboration with detailed information regarding the psychological principles that guide decisions in social interactions.

The emergence of a Neuroeconomic approach to examining interactive decision-making offers real promise for the development of such models. This nascent research field combines psychological insight and brain imaging with realistic social tasks that allow for the exploration of cooperation in a controlled laboratory environment. In contrast to standard behavioral studies, the combination of Game Theoretic models with the on-line measurement of brain activity during decision-making allows for the discrimination and modeling of processes that are hard to separate at the behavioral level. Within this Neuroeconomic approach, tasks have been designed that ask people to decide about monetary divisions in an interactive setting, with money used both as a reward in itself, and also as a proxy for other ‘rights’ that affect cooperation (land, political power, etc). These tasks are well-suited to be used in combination with brain imaging methods and produce a surprisingly rich pattern of decision-making, allowing a wide range of questions to be answered about motivations to engage in cooperative behavior.

The games used in these experiments are generally simple and offer compelling social scenarios (see Figure 9). The Public Goods Game (Fehr & Gachter, 2000) (PGG) is the most commonly used game to study cooperation. In this game, four participants at a time are provided with a monetary endowment, and each individual then decides how much of this endowment they wish to keep for themselves and how much they want to contribute to a public pot. The experimenter multiplies the total contributions in the pot by a factor (typically 1.6), and this ‘public good’ is then distributed equally among all players, irrespective of their contribution. Additionally, each participant retains the part of their endowment that was not shared. After all participants have indicated their decisions, outcomes are revealed and a new round starts. In a similar fashion to societal public goods such as clean air or medical care, the defining characteristic of a public good in the PGG is that all participants consume an equal share of the good, even those who did not bear the cost of providing the good. So, while the group as a whole is best off if all participants contribute equally, each individual has a competing incentive to free-ride, that is, to contribute nothing to the good, and the Public Goods Game nicely captures this conflict between self-interest and group cooperation in a controlled laboratory setting.

Other economic games are also useful in examining different aspects of cooperation. In the Trust Game (Berg, Dickhaut, & McCabe, 1995) (TG), a player (the Investor) decides how much of an endowment to invest with a partner (the Trustee). Once transferred, the experimenter multiplies this money by a factor of 4. Then, the Trustee has the opportunity to return some of this increased pot of money back to the Investor, but, importantly, need not return anything. If the Trustee honors trust and returns money, both players usually end up with a higher monetary payoff than originally endowed. However, if the Trustee abuses trust and keeps the entire amount, the Investor takes a loss. As the Investor and Trustee interact only once during the one-shot version of the game, Game Theory predicts that a rational Trustee will never honor the trust given by the Investor. The Investor, realizing this, should never place trust in the first place, and so will invest zero in the transaction. Despite these grim theoretical predictions, a majority of investors do in fact send some amount of money to the Trustee, and, again contrary to predictions, this trust is generally reciprocated.

The well-studied Prisoner's Dilemma game (PDG) (Poundstone, 1992) is similar to the TG, except that both players now simultaneously choose whether or not to trust each other, without knowledge of their partner's choice. In the PDG, each player chooses to either cooperate or not with their opponent, with their payoff dependent on the interaction of the two choices. The largest payoff to the player occurs when he or she defects and their partner cooperates, with the worst outcome when the decisions are reversed. Mutual cooperation yields a modest payoff to both players, while mutual defection provides a lesser amount to each. The classical Game Theoretic prediction for the PDG is mutual defection, which, interestingly, is a worse outcome for both players than mutual cooperation, but again, in most iterations of the game players exhibit much more trust than expected, with mutual cooperation occurring about 50% of the time. These latter two games model two-person situations in which players must decide to what degree they can increase their payoff by relying on a cooperative partner.

Finally, the Ultimatum Game (Guth et al., 1982) (UG) is often used to examine responses to fairness. Here, two players must divide a sum of money, with the Proposer specifying the division. The Responder then has the option of accepting or rejecting this offer. If the offer is accepted, the sum is divided as proposed. If it is rejected, neither player receives anything. The UG therefore models decisions about resource allocation on the part of the proposer, as well as responses to fairness and inequity by the responder. If people are motivated purely by self-interest, the responder should accept any offer, and, knowing this, the proposer will offer the smallest nonzero amount. However, once again, this Game Theoretic prediction is at odds with observed behavior across a wide range of societies, with rejections of unequal offers standardly observed. Thus, people's choices in the UG do not conform to a model in which decisions are driven by financial self-interest.

While utilizing these tasks, researchers have also employed a variety of neuroscientific methods to investigate the respective underlying brain systems, including functional neuroimaging, the study of brain-damaged neurological patients, transcranial magnetic stimulation, pharmacologic manipulations, genetic association studies, and studies of psychiatric patients, as well as lesion and single-cell recording studies in nonhuman primates. Here, we will focus on how brain imaging studies, in particular those using functional Magnetic Resonance Imaging (fMRI), can yield insights into the processes underlying cooperation. The following sections will provide an overview of how external incentives may motivate cooperation, and examine the basic neural mechanisms underlying cooperation, in particular the role of reward and learning. Thereafter we review some more recent work which demonstrates that social context and social emotions have important roles to play in determining how and when we cooperate, and we outline the possible neural pathways via which these factors affect cooperation.

Incentives

To encourage cooperation in social dilemma situations, and of course to reduce the likelihood of free-riding, authorities frequently reward cooperators (for example, by providing awards or tax benefits) or punish non-cooperators (for

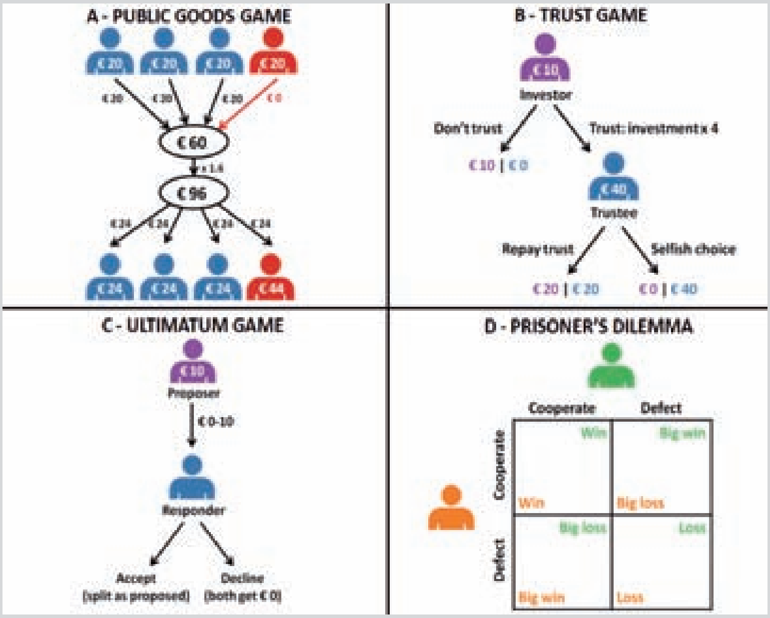


Figure 9. Outline of Game Theoretic tasks that are most commonly used to examine motivations involved in cooperative behavior. A) Public Goods Game. Four players are provided with equal monetary endowments. Each individual decides how much of this endowment to contribute to the public pot. The experimenter multiplies all contributions by a factor of 1.6 and the result is equally divided among all players. Note that the player on the right is a 'free-rider'. This player enjoys the benefit of the group donations, while not contributing anything. B) Trust Game. One player, the Investor, decides how much of his endowment to invest with a partner, the Trustee. The experimenter multiplies the transferred investment by a factor of 4. The Trustee has the option to return some of the final investment amount to the Investor but does not need to. C) Ultimatum Game. One player, the Proposer, specifies how to divide a sum of money. The other player, the Responder, then has the option of accepting or rejecting this offer. If the offer is accepted, the sum is divided as proposed. If it is rejected, neither player receives anything. D) Prisoner's Dilemma Game. Two players simultaneously choose to either cooperate or defect with the other. The largest payoff to a player occurs when they defect and their partner cooperates, while conversely the worst outcome occurs when they cooperate and their partner defects. Mutual cooperation yields a modest payoff to both players, with mutual defection providing a still lower amount to each.

example, by levying fines or supplementary taxes). Indeed, experimental evidence has shown that incentives are quite effective in promoting increases in cooperation. For instance, a large amount of studies have demonstrated that stable cooperation levels are rarely attained in a Public Goods Game. In the standard version of this game, there is usually substantial cooperation across the initial rounds of the game, but over time cooperation drops, and by the final few rounds cooperation is typically at a very low level (Fehr & Fischbacher, 2004a). This is generally attributed to the diminishing "shadow of the future" in these later rounds, that is, the lowered likelihood of negative future consequences for non-cooperation. However, the addition of a punishment or reward mechanism to the standard game increases cooperation considerably (Balliet, Mulder, & Van Lange, 2011). In Public Good Games with incentive options, participants are provided with the opportunity to either punish or reward the other players in each round. Whether a punishment or a reward is administered depends on the specific experimental manipulation, but the relevant award is usually made immediately after being informed about the group's contributions on that round. In these experiments, punishments and rewards are typically dispensed anonymously, and, importantly, are costly to the participant, as well as having a real effect on the target player. So, every monetary unit spent in order to punish (reward) decreases (increases) the income of the targeted player by 2 to 4 units. When a reward or a punishment can potentially be meted out, cooperation generally does not decrease, and may even increase over time. Moreover, full cooperation levels are commonly observed even in the concluding rounds of the game (Fehr & Gachter, 2000) (Figure 10). Although there are fewer studies on rewards than punishments, both types of incentives appear to be equally effective in inducing cooperation (Balliet et al., 2011).

Surprisingly, though there is now a substantial body of research demonstrating clear effects of incentive mechanisms on cooperative behavior, relatively little is known to date about how the brain may encode this type of cooperation. One study has examined the neural systems involved in incentive mechanisms though in a slightly different context, that of fairness norms (Spitzer, Fischbacher, Herrnberger, Grön, & Fehr, 2007). Participants played a variant of the Ultimatum Game known as the Dictator Game with punishment and non-punishment conditions. As expected, participants transferred more units to their partner in the punishment condition than in the non-punishment condition,

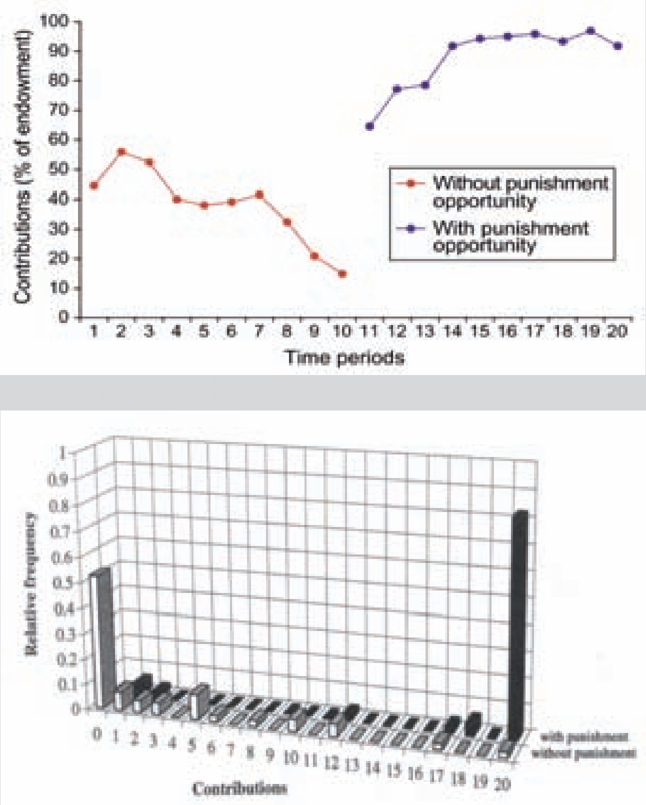


Figure 10. Fehr and Gächter (2000) demonstrated that the addition of a punishment option to the Public Goods Game considerably increased cooperation levels. Top graph: In the absence of a punishment opportunity (periods 1-10) cooperation levels dropped. However, after the introduction of a punishment mechanism there was an immediate increase in cooperation (period 11). During the remaining rounds, cooperation increased, until there was almost 100% cooperation in the final period. Bottom graph: Distribution of the average contributions in the final period of a Public Goods Game played by the same participants, with and without punishment option. In the punishment condition, 82.5% of the participants cooperate, contributing their entire endowment. In the no-punishment condition, 53% of the participants free-ride in the final period. Reprinted with permission from Fehr and Gächter (2000) and Fehr and Fischbacher (2004)[3].

indicating that participants complied more with the norm of fairness under the threat of punishment. Brain areas in which activations were observed in the punishment condition were the dorsolateral prefrontal cortex (DLPFC), orbitolateralfrontal cortex (OLFC) and caudate (see Figure 11 for an overview of all brain areas referred to in this review). The authors suggest these findings reflect the involvement of processes that evaluate social threat and implement cognitive control in cooperative decision-making under potential punishment. These findings provide an initial glimpse into the neural systems that may be involved in changes in social decision-making under incentive conditions. However, whether this mechanism underlies the effect of external incentives in general, including the effect of rewards, remains an open question, and future research could usefully examine the neural mechanisms via which incentives modify cooperative behavior.

Reward

As described in the preceding section, there is limited knowledge about how the brain encodes external motivations of cooperation, however, there is a growing literature on how cooperation is internally motivated, and the associated neural mechanisms. One of the most consistent findings across studies on the neural mechanisms of cooperative behavior is that cooperation is highly associated with activation in brain areas known to be involved in reward-based learning (Decety and others 2004; Rilling and others 2002; Rilling and others 2004a). For instance, these studies have shown that reciprocated cooperation in the Prisoner’s Dilemma and Trust Game is associated with activity in the ventral striatum and ventromedial prefrontal cortex (VMPFC), brain regions that have been consistently found to be activated by both social and monetary rewards (McClure, York, & Montague, 2004). Relatedly, viewing the faces of individuals who had previously cooperated in a Prisoner’s Dilemma Game, as compared to faces with whom the player had no history, elicited enhanced neural activity in the reward-related areas such as the striatum, nucleus accumbens, and orbitofrontal cortex (Singer and others 2004). Though there are obvious dangers in making inferences about the cognitive processes reflected by activation in specific brain regions (Poldrack, 2006), these findings suggest that by labeling mutual cooperation as rewarding in and of itself, that is, independent of whatever monetary gain was obtained by the cooperative action, people are motivated to resist the temptation to selfishly accept but not reciprocate favors.

For example, a PDG study (Rilling and others 2004a) demonstrated increased ventral striatum and ventromedial prefrontal activity for mutual cooperation decisions, even when controlling for the amount of the money earned by the decision itself. Indeed, when contrasting play with either a human or a computer partner in the Prisoner's Dilemma Game, it was found that activation in these regions was strongest when participants interacted with another human, even when the two types of partners played identical strategies. These studies provide further support for the hypothesis that cooperation with other people is inherently rewarding, with this interpretation also in line with theories from both evolutionary psychology and developmental science that argue that cooperation is rewarding per se, and that, although the material pay-off from cooperation may be delivered at a later remove, the psychological reward seems to be immediate.

Learning

When interacting with others who frequently reciprocate one's cooperative behavior, people typically continue a pattern of cooperation, whereas interacting with non-cooperators decreases cooperation markedly (Fehr & Fischbacher, 2004a). This behavior is consistent with the notion that one of the best predictors of an individual's trustworthiness is their behavior in previous interactions (Axelrod & Hamilton, 1981; King-Casas et al., 2005), that is, we are of course more likely to invest trust in someone who has shown to be cooperative than to trust someone who has previously betrayed us. Indeed, experiments have demonstrated that repeated interactions with a partner influence participants' subjective ratings of this partner's character in both Prisoner's Dilemma (Singer and others 2004) and Trust Games (Delgado et al., 2005), and, importantly, subsequently moderate the participants' investment behavior towards this partner (Chang, Doll, van't Wout, Frank, & Sanfey, 2010). These findings indicate that people learn about the cooperative nature of another player based on the history of that partner's behavior, and that this social learning provides the basis for future cooperation (or non-cooperation).

Brain imaging work on the learning of cooperative behavior suggest that cooperation is facilitated by a mechanism similar to reward-dependent learning based on the computation of basic reward-prediction errors (Rilling and others 2004a). Reward-prediction errors are signals reflecting the discrepancy between

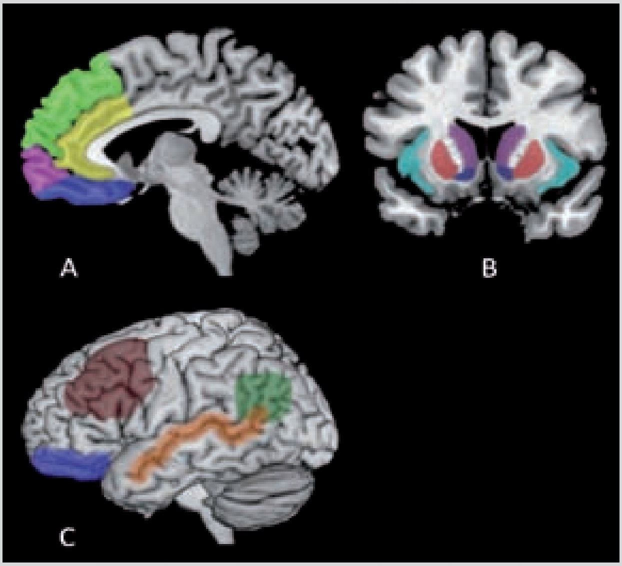


Figure 11. Overview of brain areas associated with cooperation. Colors indicate schematic locations. A) Green: Dorsal Medial Prefrontal Cortex (DMPFC); Yellow: Anterior Cingulate Cortex (ACC); Pink: Ventromedial Prefrontal Cortex (VMPFC); Blue: Orbital Frontal Cortex (OFC). MNI coordinate: x = -5. B) Turquoise: Insula; Red: Putamen; Purple: Caudate; Dark blue: Nucleus Accumbens (NACC). The Striatum comprises the Putamen, Caudate and NACC. MNI coordinate: y =13. C) Blue: OFC; Brown: Dorsolateral Prefrontal Cortex (DLPFC); Orange: Superior Temporal Sulcus (STS); Dark green: Temporal Parietal Junction (TPJ).

the predicted probability of a reward and its actual outcome (Fiorillo, Tobler, & Schultz, 2003). Changes in neural activity related to reward prediction errors are thought to be critical for reinforcement learning (Schultz et al., 1997), and may motivate behavioral change, such that, over time, behavior that is more rewarding than predicted will be adopted more easily, whereas behavior that is less rewarding than predicted will be reduced (Tricomi, Delgado, & Fiez, 2004). Indeed, neuroimaging data from the Prisoner's Dilemma Game showed that mutual cooperation in this game was associated with a positive BOLD response in reward-processing areas, whereas non-reciprocated cooperation was associated with a negative BOLD response, suggesting that reciprocated cooperation involves a positive reward prediction error (i.e. an outcome is more rewarding than expected), and non-reciprocated cooperation involves a negative reward prediction error (i.e. an outcome is less rewarding than expected) (Rilling and others 2004a). Additionally, similar reinforcement signals have been found to positively reinforce cooperation in the Trust Game (King-Casas et al., 2005). In this study, an iterated version of the Trust Game was used in which homologous regions of two participants' brains were scanned simultaneously. Results showed that the head of the caudate nucleus received information about the fairness of the decision of the other, and encoded the intention to reciprocate the other's trusting decision. In line with the idea that people build a model of their partner's behavior to predict the other's next move, this temporal transfer of the neural signal correlated with future increases in trust, and activity in the caudate decreased over time as feedback from one's partner became more reliable. This shift of activity in the caudate suggests that this area keeps track of the reputation of one's partner by a mechanism that resembles reinforcement learning, showing that people learn about the cooperativeness of their partner over time (King-Casas et al., 2005). Taken together, these findings indicate that the modulation of the BOLD response in dopaminergic regions during (non-) cooperative interactions reflects the learning of who will and will not reciprocate our trust, thereby helping us to decide with whom to cooperate, and whom to avoid.

Social context

In everyday situations, individuals' willingness to cooperate is not only based on actual interactions with others, but may also be influenced by additional information that is gathered from the specific social context. For instance, research has demonstrated that trustworthiness judgments are influenced by factors other than direct experience with a partner. In a Trust Game, more trust was placed in partners who were described as having a praiseworthy character than in partners with a neutral or bad moral character (Delgado et al., 2005). Also, participants typically invest more money when partners look trustworthy, with this trustworthiness assessed by an independent group of raters, indicating that participants believed that certain facial cues were predictive of the reciprocation of trust (van't Wout and Sanfey 2008; Chang and others 2010) (Figure 12). These findings suggest that initial impressions may function as a risk signal, which in turn influences the amount of money an individual expects to be sent back. Importantly however, implicit judgments, such as those derived from personality or facial information, actually interact with experienced trustworthiness. When repeatedly interacting with the same partners in a Trust Game, both facial expressions and actual game experience influenced participants' behavior, so that partners who were initially judged as most trustworthy, and who actually turned out to be most trustworthy, were entrusted with most money (Chang et al., 2010).

A possible mechanism via which implicit and explicit social signals may influence cooperative decision-making is via the development of context-specific expectations. That is, based on initial impressions or previous experience, people may develop expectations about the trustworthiness of their partner, and in turn use these context-specific expectations as a behavioral reference point (Chang et al., 2010). For instance, prior information about partners' personality traits influences learning about the trustworthiness of another, with this reflected in reduced caudate activation when learning about the game behavior of previously described morally good and bad partners (Delgado et al., 2005). Similarly, expectations may reflect a social norm about what other people would do in a given situation. For instance, rejection rates of unfair offers in the Ultimatum Game increase when participants are provided with information about how other people respond (Bohnet & Zeckhauser, 2004), but decrease when participants believe an unfair offer is 'typical' (Sanfey 2009). Additional support for the role of expectations in everyday decision-making comes from a study in which a computational model of expectations is developed and used to identify the brain networks involved in the tracking of social expectation violations (Chang and Sanfey 2011). Here, participants played a Ultimatum Game in the role of the responder while undergoing fMRI. Prior to scanning, expectations were elicited by asking participants to report their beliefs about the kind of offers they expected to encounter. Results demonstrated that the Anterior Cingulate Cortex (ACC) was integral in tracking the violations of these expectations. The ACC has previously been associated with other processes related to the detection of expectation violations such as the signaling of social norm deviation (Klucharev et al., 2009), the weighting of social prediction errors (Behrens, Hunt, Woolrich, & Rushworth, 2008), and responses to unfairness in

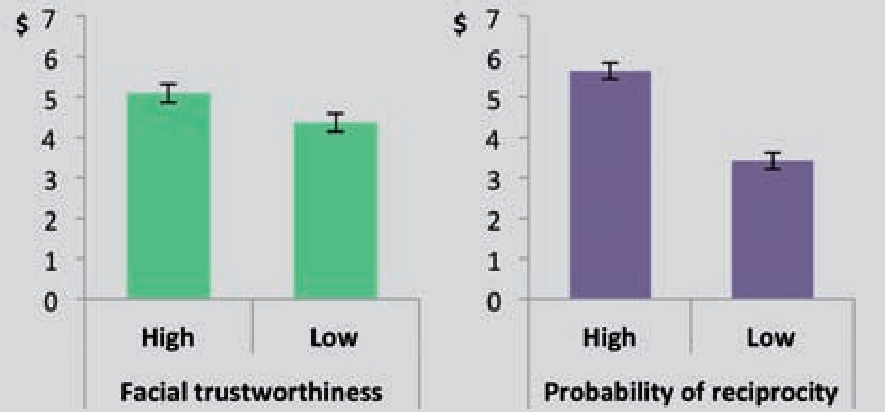


Figure 12. Chang and colleagues (2010) studied the impact of both facial trustworthiness and previous direct experience on the amount of trust people place in a partner (in $). In this experiment, participants played a repeated Trust Game in the role of Investor, while both the facial trustworthiness (high or low) as well as the probability of reciprocation (high: 80% or low: 20%) of the partner was systematically manipulated. Left graph: In the first trial of the Trust Game, participants invested more money partners who looked more trustworthy as compared to those who looked less trustworthy. Right graph: Participants overall gave more money to partners who reciprocated 80% of the time as compared to participants who reciprocated 20% of the time.

the Ultimatum Game (Sanfey and others 2003), suggesting that this area plays a critical role in the calculation of conflict between individual preferences and social norms. These findings are in accordance with the proposal that the ACC is involved in the processing of both negative affect and cognitive control (Shackman et al., 2011), and indicates that people generate a specific neural signal when others violate their expectations, which in turn may serve as an emotional indicator motivating people to enforce a social norm.

Social emotions

Both psychological and neuroscience data have extensively demonstrated that emotions play an important role in decision-making (Loewenstein and Lerner 2003; Phelps 2009). Surprisingly however, there is little experimental research examining what specific emotions are recruited in cooperative decisions. One potential emotion underlying the decision to cooperate is the anticipation of guilt. That is, a motivation for cooperating is that we would expect to feel guilty if we did not reciprocate generous behavior. Initial evidence for this guilt hypothesis comes from studies examining the social behavior of patients with damage to the VMPFC, who are impaired in decision-making, learning, and planning (e.g. Damasio, 2003; Koenigs and others 2007; Koenigs and Tranel, 2007). Based on these studies, one hypothesis is that damage to the VMPFC impairs concern for other people, and that the abnormal behavior following damage to this region may, at least in part, result from an inability to experience guilt. To address this hypothesis, Krajbich and colleagues used a formal economic model incorporating measures of envy and guilt to analyze the behavior of VMPFC patients (Krajbich, Adolphs, Tranel, Denburg, & Camerer, 2009). They found that VMPFC patients were less trustworthy and transferred less money in Ultimatum, Trust, and Dictator games, than healthy control participants. Moreover, the model showed that VMPFC patients are relatively insensitive to guilt, thereby demonstrating that the expression of guilt, and perhaps more generally the elicitation of imagined outcomes, plays an important role in cooperative decision-making, and that the VMPFC may be central to the implementation of these processes.

To test whether the anticipation of guilt can indeed motivate cooperative behavior, researchers used a formal model of guilt aversion in conjunction with brain imaging data to identify the brain mechanisms that mediate cooperation while participants deciding whether or not to reciprocate trust in the Trust Game (Chang, Smith, Dufwenberg, & Sanfey, 2011). In this model, the construct of guilt was formalized as the deviation between the player's belief about what their partner expects them to do and the amount of money this player actually returned, and posited that cooperation depends on the avoidance of the expected negative affective state associated with guilt. Results showed increased activity in the VMPFC, dorsolateral prefrontal cortex (DLFPC) and nucleus accumbens (NACC) when Trustees chose to abuse trust and maximize their gains. These findings are in line with previously mentioned patient work showing that the VMPFC plays an important role in the experience of guilt, and further suggests that the insensitivity to guilt in these patients may result from the inability to form accurate expectations about the social behavior of others.

When Trustees chose to match the Investor's expectations, and thus tried to minimize their anticipated guilt, Trustees exhibited increased activity in the insula, supplementary motor area (SMA), ACC, DLPFC, and parietal areas, including the temporal parietal junction (TPJ) (Chang et al., 2011). The insula, SMA and ACC have been associated with a number of negative states, such as guilt, anger, and disgust, as well as social and physical pain (Calder and others 2000; A.R. Damasio and others 2000; Shin and others 2000; Eisenberger and others 2003; Singer and others 2004). Therefore, these results demonstrate that not fulfilling the expectations of another may result in the experience of negative affect, which in turn can motivate cooperation. Consistent with this interpretation, participants who reported they would have experienced more guilt had they returned less than they believed their partner expected them to return, showed increased activity in the insula and SMA when they matched expectations. Thus, people who are more guilt sensitive show increased activity in the network associated with negative affective states, providing further support for the argument that the anticipation of guilt may be used as a guide to cooperative decision-making. The DLPFC in turn may function to override the affective feelings originating in the insula, as this area is known for its role in executive processing, and has been shown to play a key role in the implementation of fairness related behaviors (Knoch et al., 2006; van't Wout et al., 2005).

Social ties

In addition to the specific emotion of guilt, a variety of affective states elicited by emotional bonds, or social ties, may also influence cooperation (Van Winden et al., 2008). For example, people cooperate more with others they like, they feel close to, or with whom they have something in common (Bohnet & Zeckhauser, 2004; Komorita & Parks, 1995). Moreover, group membership has a strong influence on cooperation, and people are more likely to cooperate with in-group than out-group members (Huffman and others 2006). One potential mechanism underlying the influence of social ties on cooperation that may underlie the above behavioral findings is the generation of empathy (Huffman and others 2006; De Dreu 2012). That is, social ties may foster greater empathy between individuals, which in turn may enhance cooperative behavior. This notion is supported by brain imaging studies showing that empathic neural responses in the insula and ACC are modulated by the behavior of others (Singer and others

2004). For instance, when watching another individual getting a painful shock, empathy-related activation in pain areas, including the insula and ACC, was notably absent when this individual had previously shown non-cooperative behavior in a Prisoner's Dilemma Game (Singer et al., 2006). Moreover, these empathic pain-related activations in the insula were stronger when participants witnessed an in-group member receiving shocks as compared with an out-group member (Hein, Silani, Preuschoff, Batson, & Singer, 2010). Additional evidence for the view that increased empathic concern moderates the influence of social bonds on cooperation comes from recent pharmacological studies using oxytocin, a hormone implicated in many aspects of human social cognition, including trust, in-group favoritism and empathy (for a review see Bartz and others 2011). Intranasal administration of oxytocin increases cooperative behavior in particular with ingroup members (De Dreu et al., 2010), suggesting that oxytocin may amplify trust and empathy towards relevant others and, in turn, motivate cooperation.

Closely related to the capacity to empathize is the ability to understand the mental states of others, traditionally referred to as theory of mind. The neural circuitry of theory of mind has been well-studied and areas implicated in this process include the dorsal medial prefrontal cortex (DMPFC), as well as regions within the parietal and temporal lobes, such as the TPJ, and posterior part of the superior temporal sulcus (STS) (McCabe and others 2001; Gallagher and Frith 2003; Rilling and others 2004b). Indeed, cooperative decisions reliably engage brain systems implicated in theory of mind processes, suggesting that this ability to perspective-take plays an important role in cooperation. For instance, a study examining the Trust Game showed that DMPFC activity is high during the initial stages of building trust with another, with this activity decreasing once trust is firmly established (Krueger et al., 2007). This suggests that, in conjunction with brain systems involved in reward-based learning, this region may encode the degree to which another player is trustworthy or not, this providing vital information in the decision to cooperate. Similarly, the receipt of partner feedback in both Prisoners Dilemma and Ultimatum Games has been found to reliably engage brain systems implicated in theory of mind such as the DMPFC and pSTS, with each of these areas activated more strongly when playing with a human than a computer partner (Rilling and others 2004b). To investigate the role of the DMPFC in cooperation in more detail, Yoshida and colleagues applied a computational model of dynamic belief inference to neuroimaging data of a stag-hunt game (Yoshida, Seymour, Friston, & Dolan, 2010). In the stag-hunt game each of two players has to decide whether to hunt for a valuable stag or a less valuable rabbit, without knowing the choice of the other. To hunt the stag, both players must cooperate, while each player can acquire the rabbit by himself. Combining this game with a computational model allowed the assessment of both the neural correlates of the sophistication of players' strategic thinking as well as the degree of uncertainty regarding their opponents' level of sophistication, where here sophistication was defined by the degree of belief inference (first-order, second-order, etc.). Different regions in the prefrontal cortex were involved in the implementation of these two separate components of belief, with activity in the DMPFC greater when players were more uncertain about their opponents level of inference, suggesting that this area has a specific role in encoding the uncertainty of belief inference (Yoshida et al., 2010). In contrast, the players' sophistication itself was associated with activation in the DLPFC, an area important for executive processing (Smith and Jonides 1999).

This result suggests that the DLPFC is involved in the strategic processes required for the implementation of social goals governing mutual cooperation. This study is a good template for demonstrating how utilizing both formal mathematical models of high-level cognitive behavior in conjunction with brain imaging measures can add much useful knowledge to our understanding of the processes involved in cooperative social decision-making. These innovative approaches only recently adopted within decision neuroscience offer much promise for more detailed understanding of how humans cooperate, and how this process fails on occasion.

Conclusion

As we have attempted to demonstrate, neuroscience can provide important biological constraints on the processes involved in decisions involving cooperation, and indeed the research reviewed here is revealing that many of the processes underlying these complex social decisions may overlap with rather fundamental brain mechanisms, such as those involved in reward, punishment and learning. Though still occupying a small sub-field, the cross-disciplinary nature of these Neuroeconomic studies are innovative, and combining insights from Psychology, Neuroscience, and Economics has the potential to greatly increase our knowledge about the psychological and neural basis of cooperation. Participants in these studies are generally directly embedded in meaningful social interactions, and their decisions carry real weight in that their compensation is typically based on their cooperative decisions. Importantly, observed decisions in these tasks often do not conform to the predictions of classical Game Theory, and therefore more precise characterizations of both behavioral and brain mechanisms are important in adapting these models to better fit how decisions are actually made in an interactive environment. Further, the recent use of formal modeling approaches in conjunction with psychological theory and fMRI offers a unique avenue for the study of social dynamics, with the advantages of this approach being twofold. Firstly, it ensures that models of cooperative behavior are formally described, as opposed to the rather ad-hoc models that are typically constructed. And secondly, by assessing whether these models are neurally plausible, it provides a more rigorous test of the likelihood that these models are good representations of how people are actually making decisions about whether or not to cooperate.

Finally, as we mentioned earlier, there is the potential for this work to ultimately have a significant practical impact in terms of understanding how interactive decision-making works. While this is useful general knowledge to disseminate to the public, a more important potential gain is related to public policy. Results gleaned from laboratory studies in experimental economics have been found to generalize to behavior in the field (Carpenter & Seki, 2011; Karlan, 2005), suggesting that these tasks can be usefully employed to inform as to how real-world decisions regarding cooperative behavior are taken. More comprehensive knowledge of the neural processes underlying cooperation could in turn generate useful hypotheses as to how policy interventions could be structured, for example in relation to tax compliance, medical decision-making, investment behavior and social norms. Typically, these policy decisions are based on the standard economic models of behavior that often do not accurately capture how individuals actually decide. The development of more accurate, brain-based, models of cooperative decision-making has the potential to greatly help with these policy formulations as they relate to our interactive choices. Knowing what signals commonly trigger both cooperation and noncooperation can assist in designing policy to better achieve desired societal aims.

Notes

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7.

THE JUSTICE JUICE

Abstract

The hormone oxytocin has long been considered primarily important for pro-social behavior. However, recent studies are beginning to suggest that oxytocin does not necessarily lead to indiscriminately pro-social behavior, but rather that it may play a broader role in social behavior. The aim of this study was to explore the possible effects of oxytocin on social norm enforcement. If oxytocin does indeed play a key part in the promotion of social behavior in general, then does administration of oxytocin foster the choice to punish social norm violators? And might oxytocin lead to a greater willingness to compensate victims of social norm violations? To investigate the role of oxytocin in social norm enforcement, we conducted a between-subject, double-blind, placebo-controlled experiment in which participants played three versions of a newly developed monetary game, named 'The Justice Game'. These versions were: a second-party punishment game, a third-party punishment game and a third-party compensation game. Results demonstrated that oxytocin did indeed significantly increase sensitivity to social norm violations, specifically, that participants in the oxytocin group showed a greater willingness to administer corrective punishments to those who violated a social norm than those in the placebo group. This effect was present in both of the punishment games, demonstrating that the effects of oxytocin on social norm enforcement extend into the domain of altruistic punishment. Oxytocin did not affect the willingness to compensate victims of social norm violation. Together, our findings support the hypothesis that oxytocin's effects on pro-social behavior are context-dependent.

Based on Stallen, Smidts, Heijne, Couwenberg, de Dreu & Sanfey (in preparation). The justice spray: Effects of oxytocin on social norm enforcement.

Introduction

Research on the hormone oxytocin and its associated role in human social behavior has increased exponentially during the last years, with recent studies showing that intranasal administration of oxytocin promotes pro-social behaviors, such as trust (Baumgartner et al., 2008; Kosfeld et al., 2005), generosity (Zak et al., 2007), cooperation (Declerck, Boone, & Kiyonari, 2010), attachment security (Buchheim et al., 2009; Feldman, 2012), the recognition of faces (Guastella, Mitchell, & Mathews, 2008; Rimmele, Hediger, Heinrichs, & Klaver, 2009; Savaskan, Ehrhardt, Schulz, Walter, & Schächinger, 2008), mental states (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007), and biological motion (Kéri & Benedek, 2009), and reduces social stress (Ditzen et al., 2009; Heinrichs, Baumgartner, Kirschbaum, & Ehlert, 2003). The finding that oxytocin plays such a key role in the promotion of positive social behaviors has generated considerable excitement in the media, and the 'love hormone' has now become a frequent topic in the popular press.

However, in contrast to the belief that oxytocin works as a 'magic trust elixir', more recent research is beginning to suggest that oxytocin plays a more complex role in social behavior than initially assumed. These studies showed that oxytocin does not necessarily lead to indiscriminately pro-social behavior, but that its positive effects depend on contextual and personality characteristics to some degree (Bartz, Zaki, Bolger, & Ochsner, 2011; Guastella & Macleod, 2012). For instance, it has been found that the positive effects of oxytocin on trust disappear when cues about trustworthiness of a potentially trusted other are absent (Mikolajczak et al., 2010), when the other is unknown (Declerck et al., 2010), or when the other is an out-group member (De Dreu et al., 2010). Similarly, oxytocin has been found to promote conformity to the in-group, but not the out-group (Stallen, De Dreu, Shalvi, Smidts, & Sanfey, 2012), and to improve empathic abilities for less socially proficient individuals, though these abilities are not affected in those who are more socially skilled (Bartz et al., 2010). Furthermore, some studies even point to potential negative effects of oxytocin, such as increased envy and schadenfreude (Shamay-Tsoory et al., 2009), and enhanced out-group derogation (De Dreu et al., 2010; De Dreu, Greer, Van Kleef, Shalvi, & Handgraaf, 2011), indicating that oxytocin may enhance 'anti-sociality' as well. Together, these findings suggest a hypothesis that, instead of solely promoting pro-social behavior, oxytocin may facilitate the integration of social information more generally (Bartz et al., 2011). By increasing the salience of social cues, oxytocin can thereby influence the processing of socially relevant information (Guastella & Macleod, 2012). This social-salience hypothesis can explain why situational differences shape the effects of oxytocin, as increasing the salience of social cues is likely to have varying downstream cognitive effects as a function of what kind of information is attended to. Moreover, this hypothesis can simultaneously account for both the positive and negative effects of oxytocin, as increased attention towards socially relevant cues can be expected to magnify pro-sociality when dealing with known, close others, such as in-group members, but instead diminish pro-sociality in situations of uncertainty, or when interacting with out-group members for example (Bartz et al., 2011).

To test the hypothesis that oxytocin facilitates the processing of social information more general, we explored whether oxytocin administration increased individuals' sensitivity to social norm violations. Social norms play a central role in human behavior and have a large influence on individual decision-making, with these norms defined as standards of behavior that are based on widely shared beliefs about how one should be behave in a given situation (Fehr & Fischbacher, 2004a). Violations of social norms typically evoke strong emotional responses in the 'victims' of the violations, for example the anger typically experienced when somebody skips in front of you in a queue even if this would only add seconds to your waiting time. Interestingly, these violations can also lead to emotional responses from third-parties observing the situation from afar, such as when you observe a bus driver closing his doors intentionally on a late-arriving passenger. As a result, people are willing to punish social norm violators and compensate victims of norm violators. Importantly, this often occurs even when people incur costs themselves, when they have not been harmed directly by the violation, and even in situations in which they do not receive any direct benefits by punishing the violator or compensating the victim (Fehr & Fischbacher, 2004b; Bicchieri & Chavez, forthcoming). For instance, people often make the effort to sign petitions urging authorities to file criminal charges against thieves or murderers, and donate money to victims of dictator regimes.

Given the key role of social norms in everyday behavior, we expected oxytocin to increase people’s sensitivity to social norm violations. In the present study, we therefore investigated individuals’ response to the violation of norms concerning distributional fairness. If another person takes resources away that belong to you, then does administration of oxytocin foster the decision to punish this person? We also examined whether this effect of oxytocin would extend into the domain of altruistic punishment and compensation. That is, does oxytocin lead to a greater willingness to punish someone if this person did not take resources from you, but from someone else? And will oxytocin increase the willingness to compensate victims of such a third-party norm violation? Based on the hypothesis that oxytocin increases the saliency of social cues, we predicted that participants who received oxytocin would respond more strongly to this type of unfairness than participants in the placebo group, accordingly showing increases in (altruistic) punishment towards social norm violators, and increased compensation towards the victims of social norm violations.

Materials and Methods

Design and participants

We recruited 55 males (28 oxytocin) for a double blind, randomized, placebo-controlled between-subject experimental design. Participants provided informed consent before the experiment, and received a standard payment of €35 for participating in the experiment plus an additional bonus payment of between €7 and €15 based on their decision behavior. Thus, participants earned on average €47 (*SD*=€1.29) in the experiment. Exclusion criteria for participation were significant medical or psychiatric illness, medication, smoking more than five cigarettes per day, or drug/alcohol abuse. Participants were instructed to refrain from smoking, eating and drinking (except for water) for 3 hours before the experiment, and were all tested in the afternoon to prevent effects of circadian rhythm. The experiment was approved by the Radboud University ethics committee. One participant (in the oxytocin group) was excluded because he reported not participating seriously, and therefore analyses were conducted with a group of 54 participants (mean age=21.2 years, *SD*=2.4 years, 27 oxytocin and 27 placebo).

Experimental procedure

Upon arrival at the lab, participants provided informed consent and received instructions about the task. They completed several practice trials, and were given a quiz at the end to check whether instructions were understood correctly. Next, they self-administered the medication (Syntocinon spray, Novartis; 24 IU; three puffs per nostril, each with 4 IU of oxytocin or placebo) under experimenter supervision. To avoid pharmacological effects other than those caused by oxytocin, the placebo contained all active ingredients with the exception of the neuropeptide. While in the MRI scanner, participants also completed one unrelated task before beginning the present task. About 40 minutes (*M*=41.5, *SD*=21.7) after substance administration (depending on how quickly participants completed the previous task), participants started with the experiment of interest. This timing conforms to other studies showing that effects of oxytocin are present between 30-60 min after intranasal administration (Baumgartner, et al., 2008; De Dreu, et al., 2010; De Dreu, et al., 2011; Stallen et al., 2012; Kosfeld, et al., 2005).

Justice Game

To examine the role of oxytocin in social norm enforcement, we developed a new interactive decision task we termed the Justice Game. The Justice Game involves 2 players, one of whom is randomly assigned the role of Taker. At the start of the game both the Taker and the Partner each receive an endowment of 200 chips. The Taker is then given the opportunity to take chips from the Partner and add these chips to his own endowment, or alternately he can leave the distributions as they are. The Taker can take a maximum of 100 chips from the Partner. However, after the Taker has indicated his decision, the Partner is given the option of punishing the Taker by spending chips of his own. For each chip the partner spends, the income of the Taker is reduced by 3 chips. Thus, punishment in this task is both costly and effective. The Partner can use maximum of 100 chips from his endowment for punishment purposes.

Participants played three versions of the Justice Game: second-party punishment games, third-party punishment games, and third-party compensation games. The second-party punishment games were identical to the Justice Game as described above, with participants always assigned to the role of Partner. In third-party punishment games, participants were assigned the role of Observer, where they watched a Taker decide whether to take chips from another participant playing the role of Partner. In this role, the Observer also received an endowment of 200 chips at the beginning of each game. Following the decision of the Taker to either take or not, the Observer had the option of punishing the Taker for his action towards the Partner. Observers could use a maximum of 100 chips from their endowment for punishment purposes. Each punishment chip spent by the Observer decreased the income of the Taker by 3 chips. Observers did not know whether the Partner punished the Taker or not. Finally, third-party compensation games were identical to the third-party punishment games, except that in third-party compensation games the Observer now had the option of compensating the Partner (as opposed to punishing the Taker). One chip spent by an Observer in third-party compensation games increased the income of the Partner by 3 chips.

Participants played 48 trials of each of the three versions of the Justice Game, resulting in 144 trials in total. The identity of Takers was never revealed to the participants, and on each trial they were paired with different Takers. Thus, all games were anonymous, independent, and single-shot. To control the number of trials of interest for neuroimaging analyses, Takers' choices were preprogrammed. Participants were led to believe that Takers' decisions represented the decisions of previous participants who had been assigned the role of Taker, and whose final payment was dependent on the choices participants made in their role of Partner and Observer. Half of the trials were preprogrammed to be 'fair' trials, in which the Taker did not take any chips from the Partner. The other half of the trials consisted of 'unfair' trials in which the Taker took 25, 50, 75, or 100 chips from the Partner. For each game type, there were 24 fair trials and 24 unfair trials, with 6 trials of each unfair trial type (i.e. 6 trials in which a Taker took 25 chips, 6 trials in which a Taker took 50 chips, etc.). To assure participants experienced punishment and compensation to be real and consequential, 6 trials were randomly selected for payment, and participants were remunerated accordingly at the end of the experiment.

For an example of the trial outline, see Figure 13. After the presentation of a fixation screen (2-5 seconds), a start screen (2 seconds) appeared indicating the beginning of a trial. This screen displayed the initial endowments of both the Taker and the Partner (200 chips each). Next, a screen was shown that revealed the decision of the Taker, i.e. the number of chips the Taker took from the Partner (4 seconds). Games and trial types were randomized within each experiment, with a colored box at the top of each screen indicating the current

Fixation Start amount Taker's action Decision

Figure 13. Trial outline. Example of a second-party punishment game. In this sample trial a Taker takes 100 chips from his Partner.

game type. The specific colors used for the boxes of the three game types were counterbalanced across participants. We avoided directly using the terms 'punishment' and 'compensation' to prevent influencing individuals' actual fairness norms. Instead, games were introduced as 'You-Other' games (second-party punishment games), 'Other-Other, You: Take' games (third-party punishment games), and 'Other-Other, You: Give' games (third-party compensation games). At the conclusion of each trial, participants indicated the amount they wished to punish or compensate respectively on a response scale, which consisted of a row of numbers from 1 to 100, in steps of 10. Responses were indicated by scrolling to the number of their choice and pressing a confirmation button, and had to be provided within 6.5 seconds. The starting position of the scrolling cursor was determined randomly at the beginning of each trial. To ensure participants' attention, 3 self-paced breaks were included in which participants were offered the opportunity to break from the task for a few minutes and then to continue when ready. We assessed participants' expectations about the task by asking them to report the number of chips they expected a Taker to typically take from a Partner. This measure was taken before the administration of oxytocin/placebo, and at the conclusion the experiment (about 1,5 hrs after treatment, *M*=1h30 min, *SD*=6 min).

Results

Average amount of chips paid for punishment and compensation

To determine whether oxytocin affected participants' overall response to social norm violations, we first analyzed whether oxytocin administration altered the mean amount of chips participants used for punishment and compensation of the second-party punishment, third-party punishment and third-party compensation games respectively. We focused here on the unfair trials (i.e. trials in which the Taker actually took chips from the Partner). For each of the three game types, we conducted a 2 (treatment: placebo/oxytocin) x 4 (number of chips taken: 25 /50 /75 /100 chips) mixed-model analysis of variance (ANOVA), with treatment as a between-subject factor and the number of chips taken by the Taker as a within-subject factor. Greenhouse-Geisser corrections were used to correct for violations of sphericity.

All three ANOVAs showed main effects of the number of chips taken by the Taker (second-party punishment game: $F(2,95)=55.31$, $p<.001$; third-party punishment game: $F(2,82)=43.25$, $p<.001$; third-party compensation game: $F(2,86)=34.09$, $p<.001$), but no interactions were found between treatment and the number of chips taken, and there were no between-subject effects. The absence of significant treatment effects for all three game types indicates that oxytocin administration did not influence the mean amount of chips participants spent on punishment or compensation. However, the significant main effects on punishment behavior as a function of the number of chips taken confirms that participants experienced the Taker's behavior as unfair and were willing to incur costs to punish and compensate, as the more chips were taken, the more chips were spent on compensation and punishment (second-party punishment game: $M_{25\text{ chips}}=20.82$, $SD_{25\text{ chips}}=18.71$, $M_{50\text{ chips}}=32.37$, $SD_{50\text{ chips}}=23.57$, $M_{75\text{ chips}}=42.54$, $SD_{75\text{ chips}}=28.01$, $M_{100\text{ chips}}=56.52$, $SD_{100\text{ chips}}=34.77$; third-party punishment game: $M_{25\text{ chips}}=11.07$, $SD_{25\text{ chips}}=10.74$, $M_{50\text{ chips}}=20.21$, $SD_{50\text{ chips}}=16.28$, $M_{75\text{ chips}}=25.57$, $SD_{75\text{ chips}}=21.86$, $M_{100\text{ chips}}=36.86$, $SD_{100\text{ chips}}= 30.49$; third-party compensation game: $M_{25\text{ chips}}=7.15$, $SD_{25\text{ chips}}=9.27$, $M_{50\text{ chips}}=11.44$, $SD_{50\text{ chips}}=10.51$, $M_{75\text{ chips}}=16.32$, $SD_{75\text{ chips}}=13.66$, $M_{100\text{ chips}}=20.86$, $SD_{100\text{ chips}}=18.07$; see Figure 14).

To assess if the mean number of chips participants spent differed across game types, we conducted a 2 (treatment: placebo/ oxytocin) x 3 (game type: second-party punishment game/ third-party punishment game/ third-party compensation game) multivariate repeated-measures analysis of variance with treatment as between-subject factor and game type as within-subject factor. Results showed a main effect of game type ($F(2,51)= 24.05$, $p<.001$), demonstrating that participants behaved differently across the three versions of the games. No interaction or between-subject treatment effects were present.

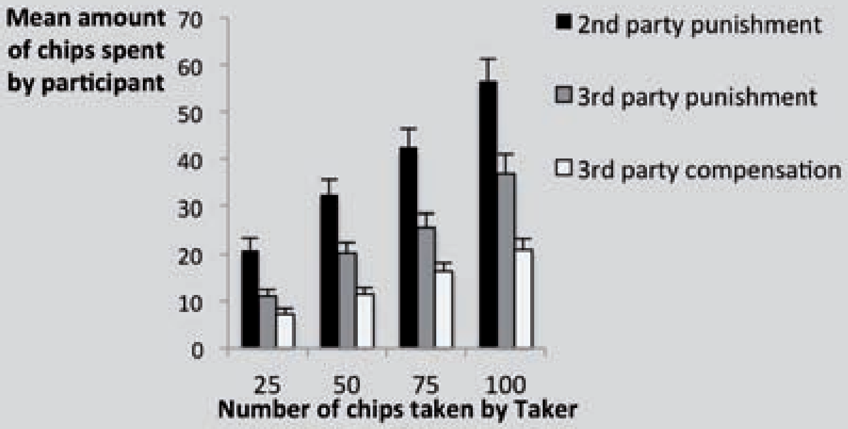

Figure 14. Mean amount of chips spent as a function of the number of chips taken by the Taker. The more chips are taken by the Taker, the more chips are spent on punishment and compensation. This effect is present in all three game types. Error bars indicate standard error of the mean.

Subsequent pairwise comparisons between punishment conditions reveal that participants spent more chips to punish in the second-party punishment game (*M*= 38.07, *SD*= 23.55) than in the third-party punishment game (*M*= 23.52, *SD*= 18.47) (*t*(53)=5.99, *p*<.001, Bonferroni-corrected). In addition, comparing across third-party games, participants spent more chips to punish than to compensate (*M*= 13.93, *SD*= 11.63) (*t*(53)=3.88, *p*<.001, Bonferroni-corrected). Thus, participants responded most strongly if they themselves were treated unfairly, and, when in the role of Observer, were more willing to punish a norm violator themselves than to compensate a victim of social norm violation.

Frequency of punishment and compensation

Though there were no differences between oxytocin and placebo in terms of the overall mean number of chips spent, we were also interested in whether the treatment may have affected the pattern of punishment/compensation behavior. To this end, we next examined whether oxytocin affected the *frequency* of punishment and compensation (i.e. the percentage of trials in which participants chose to spent chips). For each of the three game types, we conducted a 2 (treatment: placebo/ oxytocin) x 4 (number of chips taken by Taker: 25 /50 /75 /100 chips) x 10 (number of chips spent per punishment or compensation: 10/20/30/40/50/60/70/80/90/100) multivariate repeated-measures ANOVA, with treatment as a between-subject factor, and both the number of chips taken as well as the number of chips spent per punishment/compensation as within-subject factors.

Analysis of the frequency of punishment in second-party punishment games showed significant main effects of the number of chips spent per punishment (*F*(9,44)= 7.77, *p*<.001) and of the number of chips taken (*F*(3,50)= 6.17, *p*=.001). These main effects demonstrate that participants did not always spend the same number of chips, and that, across treatments, more chips taken by the Taker led to more frequent punishments. Furthermore, there was also a significant interaction effect between the number of chips spent per punishment and the number of chips taken (*F*(27,26)= 3.45, *p*=.001), showing that more chips taken by the Taker, increased the frequency of high punishments in particular. These findings confirm that participants experienced punishments as being costly and consequential and suggest that the taking of chips indeed was experienced as a violation of a fairness norm. Importantly however, we also found a significant interaction effect between treatment and number of chips spent per punishment (*F*(9,44)= 2.10, *p*=.050), showing that oxytocin administration influenced the frequency of the various levels of punishment possible (see Figure 15). Specifically, participants in the oxytocin group administered low punishments more often than participants in the placebo group, and conversely placebo players administered high punishments more often. No other significant interactions were present and there was no main effect of treatment.

Similarly, analysis of the third-party punishment games also showed main effects of the number of chips taken by the Taker (*F*(3,50)= 2.95, *p*=.041), and number of chips spent per punishment (*F*(9,44)= 9.24, *p*<.001), and a significant interaction effect between these factors (*F*(27,26)= 24.05, *p*=.016). However, in contrast to the second-party punishment games, there was no significant interaction effect present between treatment and number of chips spent per punishment (*F*(9,44)= 1.37, *p*=.230). Instead, there was a significant three-way

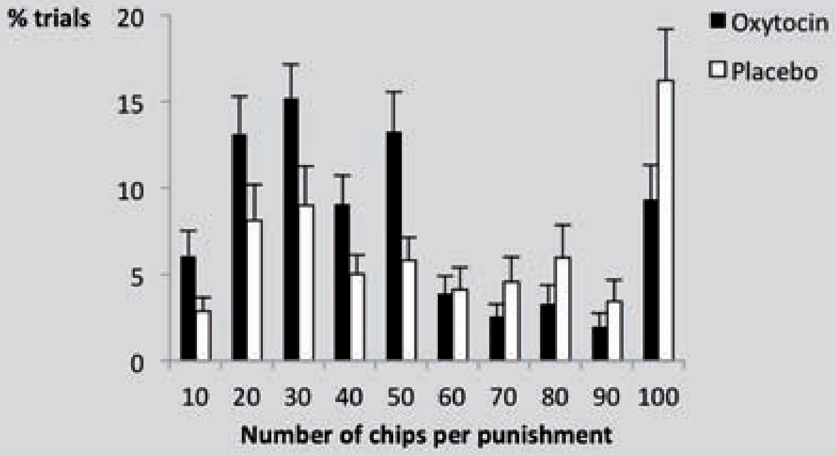

Figure 15. Frequency of punishment in the second-party punishment games. Participants in the oxytocin group administered smaller punishments (10-50 chips) more often than participants in the placebo group.

interaction between treatment, the number of chips taken by the Taker, and the number of chips spent per punishment (*F*(27,26)= 2.34, *p*=.017) (see Figure 16). This interaction shows that the effect of oxytocin on how often low punishments were administered was stronger the more chips the Taker took from the Partner. Thus, while in the second-party punishment games the effect of oxytocin on the frequency of punishment was independent of the number of chips taken, in the third-party punishment games the effect of oxytocin was dependent on the Taker's behavior. This three-way interaction effect was absent in the placebo group. There were no further significant interaction effects in the third-party punishment games, and there was no main effect of treatment.

Analysis of the third-party compensation games demonstrated only a significant main effect of the number of chips taken by the Taker (*F*(3,50)= 4.74, *p*=.006), a significant main effect of the number of chips spent per punishment (*F*(9,44)= 10.03, *p*<.001), and a significant interaction effect between these factors (*F*(27,26)= 2.41, *p*=.013), confirming that the frequency of compensation was dependent on both the behavior of the Taker and size of the punishments. The absence of any treatment effects shows that, in contrast to the hypothesis that oxytocin motivates positive pro-social behavior, oxytocin administration did not affect the frequency of compensation of victims of social norm violations.

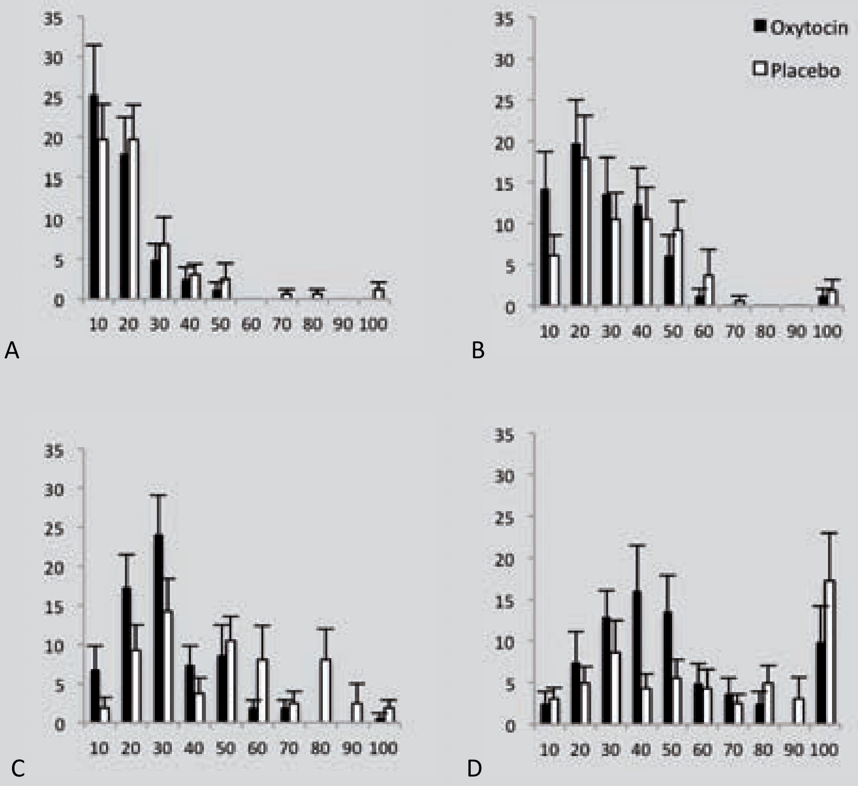

Figure 16. Frequency of punishment in third-party punishment game. Y-axis = percentage of trials. X-axis: number of chips spent per punishment. A) Taker takes 25 chips; B) Taker takes 50 chips; C) Taker takes 75 chips; D) Taker takes 100 chips. Error bars indicate standard error of the mean. The figure shows that the more chips the Taker takes, the stronger the effect of oxytocin on the administration of lower punishments.

Discussion

The present results demonstrate that participants engaged in a social interactive game following oxytocin administration were more sensitive to social norm violations. While oxytocin had no effect on the mean amount of punishment or compensation in response to social norm violations, oxytocin did alter the pattern of punishment behavior. More specifically, participants in the oxytocin group were more likely to administer smaller punishments (i.e. 10-50 punishment chips on a scale of 100) in response to norm violations than participants in the placebo group. The finding that oxytocin increases the willingness to administer low punishments in particular, suggests that oxytocin may underlie a corrective response to a perceived norm violation of fairness, such as 'giving someone a slap on the hand' if taking things that do not belong to him. That is, oxytocin seems to impact more 'cognitively' based, vigilant punishment behavior, as opposed to influencing an affective response to a transgression, for example one based on anger or fear.

Importantly, this corrective punishment effect was present in both second- and third-party punishment games. This demonstrates that the effects of oxytocin on social norm enforcement also extend into altruistic punishment, as the third-party punishment games were structured in such a way that participants were not directly harmed themselves by the Taker's action and neither received any direct benefits by administering a costly punishment, nor could punishments be used to teach the Taker a lesson. Importantly, in the third-party punishment games the effect of oxytocin on the frequency of punishment was additionally dependent on the degree of social norm violation. This shows that, while oxytocin's effect on social norm enforcement was always present in second-party games, only when other individuals were also 'hurt' substantially, oxytocin stimulated the punishments of social norm violators as well.

Interestingly, oxytocin did not influence the frequency of compensation behavior. This finding may suggest that oxytocin's response to social norm violations is limited to stimulating corrective punishment of social norm violators, and that oxytocin is not causally involved in the willingness to compensate victims of a norm violation. However, overall, the frequency of compensation was quite low for both the oxytocin and placebo group, suggesting that the absence of an oxytocin effect on compensation could be due to a floor effect as well. Whether oxytocin really has no effect on the willingness to compensate, or whether the null finding reported here is due to the experimental set-up used, is an interesting question that future research might help to answer.

A potential mechanism via which oxytocin may stimulate corrective punishment is by the modulation of expectations. That is, by increasing people's expectations about fairness, oxytocin may make individuals more optimistic about the behavior of others, and in turn, increase the willingness to administer corrective punishments when these optimistic expectations are not met. Future work could usefully examine whether oxytocin influences people's expectations as at present only a few studies have addressed this question, with mixed findings to date. For instance, a study on the role of oxytocin in trust decisions found that oxytocin increased trust behavior, but did not affect individuals' expectations about the trustworthiness of others (Kosfeld et al., 2005). In contrast, another study examining the effect of oxytocin on in-group trust found that oxytocin administration had a positive effect on beliefs about the trustworthiness of in-group, though not out-group, members (De Dreu et al., 2010). To investigate to what extent oxytocin can moderate people's expectations, we are currently analyzing how oxytocin affects the neural mechanisms involved in the tracking of expectation violations. Neuroimaging studies have shown that the violation of social expectations typically activates a brain network including the anterior cingulate cortex (ACC), insula and dorsolateral prefrontal cortex (DLPFC) (Chang & Sanfey, 2011; Chang et al., 2011). If oxytocin indeed influences individuals' beliefs about social norms, then oxytocin would be expected to modulate these neural correlates of expectation violations. For instance, if oxytocin increases one's expectations of fairness, then oxytocin administration should increase activation in the ACC, insula and DLPFC when individuals' expectations are violated. The expectation violation signal in these brain areas may in turn serve as a motivating signal to bias social norm enforcement.

To gain more insight into the mechanisms by which oxytocin influences social decision-making, a better understanding about the effects of oxytocin on brain activity may be helpful. For instance, a brain area potentially involved in mediating the effect of oxytocin on social norm enforcement is the amygdala. The amygdala is known to play a key role in the detection and processing of socially relevant information (Adolphs, 2010), and animal models indicate that this area is involved in how oxytocin affects social behavior (Ferguson, Aldag, Insel, & Young, 2001; Huber, Veinante, & Stoop, 2005). Indeed, several neuroimaging studies examining the influence of oxytocin on neural activation in humans have shown that oxytocin moderates activity in this brain area (Baumgartner et al., 2008; Domes et al., 2010; Domes, Heinrichs, Gläscher, et al., 2007; Gamer, Zurowski, & Büchel, 2010; Kirsch et al., 2005; Petrovic, Kalisch, Singer, & Dolan, 2008), with most studies indicating that amygdala activity is down-regulated by oxytocin. However, recent studies now indicate that oxytocin can also in fact increase amygdala activation (Domes et al., 2010; Gamer et al., 2010; Hurlemann et al., 2010; Rilling et al., 2012). The finding that oxytocin has differential effects on the amygdala suggests that oxytocin may facilitate the processing of relevant information by either suppressing or enhancing amygdala activity, depending on the context. This idea, that context is an important factor in assessing how oxytocin alters brain functioning and as a consequence behavior, is one that is increasingly influential in recent conceptualizations of oxytocin function (Bartz et al., 2011). It would be interesting to investigate whether oxytocin's effects on social norm enforcement are mediated by the amygdala, as this particular neural involvement would provide support for the hypothesis that oxytocin increases sensitivity to social norm violations, and corroborate previous work showing that the role of oxytocin in mediating complex social behavior involves the amygdala.

A potential alternative interpretation of the results reported here is that instead of increasing sensitivity to fairness norms, oxytocin may have influenced individuals' aversion to inequity (Bolton & Ockenfels, 2000; Fehr & Schmidt, 1999), a theory from behavioral economics that posits that people prefer situations in which everyone has the same amount. That is, in this context, oxytocin made players particularly sensitive to the fact that after a Taker seized chips, the two players had unequal amounts remaining. However, although the explanation of inequity aversion is appealing because of its simplicity, we believe the present data to fit better with a social norm account, for three reasons. Firstly, if oxytocin increased inequity aversion then oxytocin administration would be expected to affect both punishment and compensation behavior equally, as both are effective mechanisms for returning the two players to a state of equality. However, we do not find such an effect, with oxytocin having no impact on compensation behavior. Secondly, we found that oxytocin actually increased participants' expectations regarding fairness, which cannot be explained by inequity aversion and which instead provides a plausible mechanism via which oxytocin may moderate social norm enforcement. Finally, a recent study examining the effect of oxytocin on rejection rates in an Ultimatum Game showed that oxytocin did not increase the rejection rate of unfair offers (where rejection leads to both players receiving nothing, hence equity) in the absence of any other alternative offers (Radke & De Bruijn, 2012). The rejection rate of unfair offers is likely to reflect individuals' sensitivity to inequity aversion (Falk, Fehr, & Fischbacher, 2003), and therefore the absence of an effect of oxytocin on this measure suggests that oxytocin does not influence inequity aversion.

To conclude, the finding that oxytocin enhances social norm enforcement fits well with other studies showing that oxytocin influences social behavior, such as trust (Baumgartner et al., 2008; Kosfeld et al., 2005), generosity (Paul J Zak et al., 2007), cooperation (Declerck et al., 2010), and empathy (Bartz et al., 2010). Yet, while most studies reported oxytocin to promote positive pro-social behavior, our findings confirm more recent studies showing that oxytocin plays a role in 'negative' behaviors as well. Here, we show that oxytocin can in fact facilitate increased punishment of unfair others, but does not increase compensation. Furthermore, this effect is present even when the unfair act is directed towards another person and the punishment itself is costly to the player. The finding that oxytocin promotes social norm enforcement by increasing the willingness to administer corrective punishments shows that oxytocin plays a more general role in social behavior than previously assumed, and provides important support for the hypothesis that oxytocin facilitates the processing of social information in general. Future work is required to determine the exact mechanisms by which oxytocin affects social norm enforcement.

8.

DISCUSSION

This thesis

This thesis describes how our decisions are influenced by the social context. Both Chapter 2 and Chapter 6 review fundamental work on the neural processes underlying social decision-making. Together, these two chapters show that many of the processes underlying social decision-making overlap with rather basic brain mechanisms, and they demonstrate that the social context has an important role to play in how we make our decisions. The empirical chapters of this thesis (Chapter 3, 4, 5, and 7) each provide a different example of how the social context may influence decision-making and its underlying neural circuitry. In this Discussion, I provide brief summaries of these empirical chapters, and discuss the contribution of this experimental work to both the theoretical literature as well as to the more applied field of consumer decision-making. In addition, the practical impact of the thesis in terms of its potential contribution to policy decision-making is discussed, and suggestions for future research are given.

Chapter 3 – Neural mechanisms of celebrity endorsement

Chapter 3 examined the persuasiveness of celebrity endorsers and found that even a single exposure to a celebrity-product pairing is already sufficient to establish a transfer of positive affect from the celebrity to the product. This chapter illustrates how the application of neuroimaging techniques can increase insight into the processes underlying consumer decision-making, and extends previous neuroimaging work on the persuasiveness of celebrity endorsement (Klucharev, Smidts, & Fernández, 2008). For instance, the use of celebrities as endorsers in product advertising is popular and indeed often effective (Rossiter & Smidts, 2012). However, so far it has been unclear what processes drive the persuasiveness of fame. Chapter 3 shows that an increase in BOLD activity in the medial orbitofrontal cortex underlies the processing of celebrity-product pairings. This finding supports the hypothesis that the effectiveness of celebrities stems from a transfer of positive affect from celebrity to product. Furthermore, additional neuroimaging results suggest that this positive affect is elicited by the spontaneous retrieval of explicit memories associated with the celebrity endorser. These results have important practical implications for advertisers as they show that the retrieval of explicit memories is of central importance to the persuasiveness of celebrity endorsers. Advertisers may use this information and design celebrity advertisements more effectively by facilitating consumers in the retrieval of explicit positive memories (e.g. by adding names of popular movies featuring the endorser).

Chapter 4 – Neural mechanisms of peer influence

Chapter 4 demonstrates that people have a powerful drive to conform to the behavior of their group members. This influence is present even when tested under minimal group paradigm conditions, when measuring conformity using a within-subjects design, and when identity signaling is not an issue, indicating the strength of this decision bias. Neuroimaging findings indicate that this in-group bias is mediated by the ability to take the perspective of another person as well as by signals in the brain related to the valuation of rewards and the experience of emotions. These results extend previous findings on the neural mechanisms of conformity (Klucharev et al., 2009; Klucharev, Munneke, Smidts, & Fernández, 2011), and support the important influence of in-group members on consumer choice (Arndt, 1967; Brown & Reingen, 1987). In addition, these findings emphasize the significance of word-of-mouth as a marketing strategy (Dye, 2000; Hogan, Lemon, & Libai, 2004), which of course has special relevance for the rapidly developing world of social media. By tweeting or by leaving a Facebook message, the experience of a product can spread much faster than through pure face-to-face interaction. In addition, the findings presented in Chapter 4 reinforce the notion that people conform more to others with whom they identify than to those with whom they have nothing in common. This is important for marketers, as use of social media sites is often based on shared interests or activities. Presumably, attitudes or opinions about brands or products will spread rapidly within such groups, making the image of a brand particularly relevant if discussed in large online social network groups (Brown, Broderick, & Lee, 2007; Mangold & Faulds, 2009). Finally, chapter 4 hints at the possibility that a marketing campaign will be particularly effective if the target audience can identify with the endorser of an advertising campaign, as the neuroimaging findings suggest that presenting the endorser as an in-group member may activate affective and reward processes in the brain and thereby facilitate conformity.

Chapter 5 – Oxytocin and in-group conformity

Chapter 5 demonstrates that the influence of in-group members on decision-making is affected by the neuropeptide oxytocin. People who received a nasal spray containing oxytocin were more likely to conform to the opinion of in-group members than others who received a placebo. These results extend previous findings on oxytocin's effects on in-group favoritism (De Dreu et al., 2010, 2011) into the domain of social influence. The finding that oxytocin is involved in affecting people's subjective preferences raises the question as to what mechanism underlies this effect of oxytocin on in-group conformity, and how this mechanism relates to the neuroimaging results described in chapter 4. One explanation is that oxytocin plays an important role in the activation of social identity, that is, the part of individuals' identity that is derived from perceived membership of a relevant social group (Tajfel & Turner, 1986). Classic findings on group influence have shown that the perception of shared group membership is minimally required for in-group conformity to occur, and that the activation of a social identity enhances the need to agree with group opinions (Deutsch & Gerard, 1955). The possibility that oxytocin stimulates conformity to in-group members by enhancing in-group identification processes aligns well with the hypothesis that oxytocin increases sensitivity to social relevant information and in turn motivates social behavioral biases (Bartz et al., 2011). Future research combining oxytocin administration with brain imaging methods could usefully provide insight into the mechanisms underlying oxytocin's effect on in-group conformity.

Chapter 7 – Oxytocin and social norm enforcement

Chapter 7 outlined a new monetary game I developed (termed 'The Justice Game') which shows that people receiving oxytocin demonstrated a greater willingness to administer corrective punishments to those who violated a social norm than people receiving a placebo. The effect was present even when people were not directly harmed themselves by this norm violation and also when they did not receive any benefits from the administration of punishments (indeed punishment was costly in all cases), showing that the effects of oxytocin on social norm enforcement extend into the domain of altruistic punishment. Importantly, and in contrast to the hypothesis that oxytocin motivates positive pro-social behavior (Zak, 2011), oxytocin administration did not influence the compensation of victims of social norm violations. These findings show that oxytocin plays an important role in social norm enforcement. Furthermore, these results support those of chapter 5, and other recent work on oxytocin showing that administration of this hormone does not necessarily lead to positive pro-social behavior in any context, but rather that oxytocin is involved in a broader range of social behaviors (Bartz et al., 2011), and in particular that oxytocin can stimulate negative behavior as well (e.g. De Dreu et al., 2010; Shamay-Tsoory et al., 2009). Together, these findings provide useful insights into the nature of this hormone, and will help in developing a more nuanced theory regarding the effects of oxytocin on human social cognition and behavior.

Policy impact on consumer decision-making

Examining the neural mechanisms of social influence provides important insights into the fundamental processes underlying decision-making and how these processes are moderated by the social context. However, a more relevant potential gain of a neuroscientific approach to the study of social influence is related to public policy. For example, knowledge of the neural systems underlying in-group influence as described in part 1 of this thesis, could be usefully employed to inform how policy interventions could be designed to promote behavioral change, such as in the field of consumer health decision-making. In addition, further research to the neural mechanisms of cooperation, such as inspired by the work described in part 2 of this thesis, could in turn generate valuable insights into the development of effective policy strategies in relation to the promotion of cooperative behavior.

In-group influence

Given the powerful influence of the in-group, there has been an increasing awareness of the potential use of concepts such as group conformity as a tool to change socially negative behaviors. For example, people often overestimate peers' degree of approval and the prevalence of negative behavior, such as drinking, drug use, violence, littering or cigarette smoking (Baer, Stacy, & Larimer, 1991; Berkowitz, 2010; Donaldson, Graham, & Hansen, 1994; Neighbors, Larimer, & Lewis, 2004; Schultz, 1999). So-called social influence-programs seek to correct these misperceptions by exposing their target groups to the actual attitudes of their peers and the real frequency of the undesirable behaviors. However, despite the initial popularity of these programs, the evidence for their success in establishing behavioral change has been mixed. Over time, many programs failed to change behavior substantially (Clapp, Lange, Russell, Shillington, & Voas, 2003; Peeler, Far, Miller, & Brigham, 2000), and some social influence-programs even increased the undesirable behavior they attempted to reduce (Granfield, 2005; Wechsler et al., 2003).

The mixed findings on the effectiveness of social influence-programs suggest that it is difficult to know exactly how to trigger in-group conformity. For instance, social influence programs may be based on the hypothesis that people are motivated to conform to their in-group because of the positive affect associated with social *inclusion*. Numerous studies suggest that social approval by the group is a basic need, and that conformity to the in-group is a way of enhancing one's chances of group inclusion (Baumeister & Leary, 1995; Deutsch & Gerard, 1955; Moreland & Levine, 1989). Indeed, being part of a group leads to a variety of positive emotions such as happiness, pleasure, and calmness (Baumeister & Leary, 1995), and people hold more positive views towards in-group members than out-group members. However, alternatively, negative affective processes associated with potential social *exclusion* may drive in-group conformity. For example, social exclusion manipulations increase pro-social behavior (Williams, 2007), as well as social conformity in subsequent perceptual decision-making tasks (Williams, Bernieri, Faulkner, Grahe, & Gada-Jain, 2000). Individuals who reported greater fear of negative social evaluations conform more to a group norm (Bearden & Etzel, 1982), and social exclusion led participants to engage in greater nonconscious mimicry of others, especially if they were in-group members (Lakin, Chartrand, & Arkin, 2008), with this mimicry shown to increase affiliation and rapport (Lakin & Chartrand, 2003).

The findings presented in chapter 4 may help in developing more effective social influence campaigns, as the neuroimaging results suggest that conformity towards the in-group may be mediated by both positive affect as well as perspective taking, and less so via negative affective processes such as fear of social exclusion. This indicates that social influence programs may benefit by emphasizing the positive aspects associated with in-group membership rather than stressing the negative feelings associated with social exclusion. In addition, the neuroimaging data suggest that social influence programs will work more effectively when the target is encouraged to imagine the state of mind of the in-group - 'putting themselves in the others' shoes' - and thereby facilitating perspective-taking processes which may result in more trust directed towards in-group information. Obviously, social influence campaigns should try to emphasize socially desirable behavior of the in-group only, as people will conform to negative behaviors of in-group members as well.

Future work could productively directly test the hypotheses raised above, as the interpretations here are based on previous research linking activity in specific brain regions to basic cognitive functioning. As mentioned in the Introduction, it is difficult to be definite about the precise cognitive processes reflected by brain activity, as fMRI data is correlational and brain areas are typically engaged by multiple functions. Therefore, follow-up behavioral and neuroimaging studies can usefully reveal whether social influence programs indeed would benefit more by stressing the positive affect of social inclusion rather than by emphasizing the negative affect of social exclusion.

Cooperation

At present, knowledge about brain functioning is rarely used to help people make better decisions. However, as illustrated above, insight into the neural mechanisms of decision-making may provide valuable clues as to how policy interventions could be structured more effectively. A line of future research that has the potential to have a significant practical impact in terms of public policy is inspired by Chapter 6 of part 2 of this thesis, and involves the study of the effect of incentives on cooperation. Incentives are often effective in promoting cooperation. To encourage cooperation and reduce free-riding in social dilemma situations, authorities frequently reward cooperators (e.g. awards, tax benefits) or punish non-cooperators (e.g. fines, supplementary taxes). However, although a great deal of research has focused on the role of incentives as tools for promoting cooperation, it is currently unclear by which mechanisms rewards and punishments promote cooperative behavior (Balliet et al., 2011). For example, people may cooperate because they derive satisfaction (also termed ‘warm glow’) from doing good (Andreoni, 1990), or because they expect to experience negative affect (e.g. guilt) for non-cooperation (Chang et al., 2011). Previous neuroimaging work has shown that these warm-glow and guilt motives are encoded in different brain areas. For instance, the striatum, an important area in the reward circuit, has been strongly linked to warm-glow (Harbaugh et al., 2007), while the cingulate cortex and insula correlate with the anticipation of guilt (Chang et al., 2011).

Future studies measuring the neural correlates of cooperation in both reward and punishment contexts might examine to what extent cooperation is mediated by warm-glow and the anticipation of guilt respectively, and investigate whether rewards and punishments function as identical reinforcers or rather whether they promote cooperation differently. For instance, cooperation in a reward context may be mainly mediated by the striatum, while cooperation in a punishment context may be mainly mediated by the insula and ACC (or vice versa). This result then can predict that policy strategies using rewards (punishments) as a tool to promote cooperation will be more effective when emphasizing the satisfaction that will be derived from cooperation, while policy strategies using punishments (rewards) will be more effective when emphasizing the guilt to be expected after non-cooperation.

Conclusion

This thesis demonstrates how combining methods and insights from Neuroscience, Psychology, Economics and Marketing can increase understanding of the processes involved in decision-making. Specifically, the collection of studies presented here shows how taking an interdisciplinary approach can increase insight into the way our choices are influenced by the social context, in particular the effects of social influence and social norms. A better understanding of the neurobiological mechanisms underlying social decision-making not only provides useful knowledge about the psychological and neural basis of our behavior, but offers valuable clues as to how people's behavior can be changed as well. An important and exciting challenge for future research is to continue on this path and to use brain-imaging techniques to understand and explain real-world social decision-making and to assist in designing policy to better achieve desired societal aims.

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APPENDIX

Summary

Many of our decisions are influenced by the behavior of others. For instance, people often conform to others with whom they associate. Adolescents start smoking because their peers do, and the Dutch wear orange on King's day because of their shared national identity. In addition, our behavior is often influenced by social norms, that is, unwritten rules based on widely shared values such as fairness, reciprocity, and cooperation. For example, it is inappropriate to smoke at someone else's place without permission, and the Dutch won't like it if you settle down on an already reserved sidewalk spot on King's day to sell stuff from your attic.

The aim of this thesis is to explore how social context influences the neurobiological processes underlying decision-making. To this end, this research takes an interdisciplinary approach, combining methods and insights from Psychology, Marketing, Economics, and Neuroscience. In particular, behavioral responses are collected, and used in combination with both functional magnetic resonance imaging (fMRI) techniques and pharmacological interventions examining the role of the hormone oxytocin in decision-making.

This thesis is divided into two parts. The first part is concerned with the effects of social influence on decision-making, or in other words, how our decisions are influenced by the behavior and beliefs of other people. Specifically, this part of the thesis examines the influence of both celebrity endorsements and peer groups on the neural processes underlying decision-making. Neuroimaging findings indicate that conformity to the group is mediated by the ability to take the perspective of another person, as well as by signals in the brain related to the valuation of rewards and the experience of emotions. In addition, the hormone oxytocin appears to play an important role in conformity behavior. People who received a nasal spray containing oxytocin were more likely to conform to the opinion of in-group members than those who received a placebo.

The second part of this thesis investigates the influence of social norms on decision-making. This section examines the neural processes involved in cooperation and the role of oxytocin in social norm enforcement. Results show

that people receiving oxytocin demonstrated a greater willingness to administer corrective punishments to those who violated a social norm than people receiving a placebo. This effect was present even when people were not themselves directly harmed by this norm violation and did also not receive any benefits from the administration of punishments, showing that the effects of oxytocin on social norm enforcement extend into the domain of altruistic punishment. Together with the finding that oxytocin motivates conformity, these results show that oxytocin is not simply a 'love hormone', as often labelled by the popular press, but rather that oxytocin is involved in a broader range of social behaviors, and that oxytocin can stimulate 'negative' behaviors as well.

A better understanding of the neurobiological mechanisms underlying social decision-making not only provides useful knowledge about the psychological and neural basis of our behavior, but can also generate useful ideas about the application of neuroscience data to practice. A relevant potential gain of taking a neuroscientific approach to the study of social decision-making is related to public policy. For example, knowledge of the neural systems underlying in-group influence, such as smoking due to peer pressure, could be usefully employed to inform how policy interventions could be designed to promote behavioral change. In addition, further research on the neural mechanisms of cooperation could in turn generate valuable insights into the development of effective policy strategies in relation to the promotion of cooperative behavior, such as waste recycling or the reduction of greenhouse gases.

Nederlandse Samenvatting

Veel van onze dagelijkse beslissingen worden beïnvloed door onze sociale omgeving. Zo hebben groepsgenoten bijvoorbeeld een grote invloed op ons gedrag. Jongeren beginnen met roken omdat hun vrienden dat doen en Nederlanders dragen oranje op Koningsdag vanwege het Hollandse groepsgevoel. Ook worden onze beslissingen beïnvloed door sociale normen, oftewel ongeschreven gedragsregels gebaseerd op algemeen veronderstelde waarden, zoals beleefdheid, eerlijkheid en samenwerking. Zo is het bijvoorbeeld ongepast om ongevraagd een sigaret op te steken in andermans huis en is het op de ochtend van Koningsdag niet de bedoeling om je op de stoep te installeren samen met de spullen van je zolder op een kleedje als er al ‘Bezet’ op de grond staat geschreven.

In dit proefschrift wordt ingegaan op de neurale mechanismen die ten grondslag liggen aan de wijze waarop beslissingen worden beïnvloed door onze sociale omgeving. Hierbij worden kennis en methoden gecombineerd uit de psychologie, marketing, experimentele economie, en neurowetenschappen. In het bijzonder wordt er gebruik gemaakt van de beeldvormende hersenscantechniek genaamd fMRI, wat staat voor *functional magnetic resonance imaging*, en van farmacologische interventies met het hormoon oxytocine.

Het eerste deel van dit proefschrift onderzoekt hoe onze keuzes worden beïnvloed door anderen. In dit deel wordt er beschreven welke neurobiologische mechanismen een rol spelen bij de invloed van beroemdheden in reclame en wordt er gekeken naar de invloed van groepsgenoten op onze beslissingen. Conformiteit naar de groep blijkt samen te hangen met een toename in hersenactiviteit in gebieden die betrokken zijn bij het ontvangen van beloningen en de mogelijkheid om jezelf in de schoenen van een ander te verplaatsen. Daarnaast is gevonden dat oxytocine een belangrijke rol speelt bij groepsgedrag. Mannen die dit hormoon kregen toegediend middels een neusspray namen eerder de mening van groepsgenoten over dan mannen die een placebomiddel kregen.

Het tweede deel van dit proefschrift richt zich op de invloed van sociale normen op gedrag. In dit deel worden de neurale mechanismen beschreven die betrokken zijn bij samenwerking en wordt onderzocht of oxytocine je gevoeliger maakt voor de norm van eerlijke verdeling. Het blijkt dat oxytocine een belangrijke rol speelt bij het besluit om anderen te straffen wanneer deze geld niet eerlijk verdelen. Na toediening van dit hormoon zijn mannen namelijk vaker geneigd om kleine, corrigerende sancties toe te dienen aan iemand die geld van een ander pakt en daarmee zijn eigen inkomsten verhoogt. Dit resultaat, samen met de bevinding dat oxytocine ervoor zorgt dat mannen hun mening aanpassen aan die van groepsgenoten, laat zien dat dit hormoon niet simpel een ‘liefdeshormoon’ is zoals vaak gedacht wordt. Oxytocine bevordert niet enkel vrijgevigheid en vriendelijkheid, maar helpt de aandacht re richten op relevante sociale informatie in het algemeen en speelt daarmee een belangrijke rol bij sociaal gedrag in universelere zin.

Door te bestuderen welke neurobiologische mechanismen een rol spelen bij besluitvorming en hoe deze processen worden gemoduleerd door de sociale omgeving geeft dit proefschrift niet alleen inzicht in de werking van het brein, maar levert het ook nieuwe ideeën op betreffende de toepassing van neurowetenschappen in de praktijk. Een nieuwe, en maatschappelijk relevante toepassing van de neurowetenschappen is mogelijk te vinden op het gebied van marketing- of overheidsbeleid gericht op gedragsverandering. Door beter te begrijpen welke neurale processen betrokken zijn bij alledaagse beslissingen, zoals bijvoorbeeld de keuze om te roken als gevolg van groepsdruk, kunnen gedragsinterventies gerichter worden ontworpen dan nu het geval is.

Curriculum Vitae

Mirre Stallen was born in Nijmegen on August 17, 1981. She graduated from high school in 1999, and after a year of travelling began her academic studies at the University of Amsterdam. As an undergraduate she studied Cultural Anthropology for one year and then combined a bachelor in Biomedical Science with a minor in Psychology, receiving her degree cum laude in 2004. She continued her education with a Masters in Cognitive Science, completed in conjunction with internships in both the lab of Dr. Eric-Jan Wagenmakers at the Psychology department of the University of Amsterdam and the lab of Dr. Jennifer Beer at the University of California, Davis. She received her master's degree cum laude in 2006, and then worked for one year as a research assistant in the lab of Prof. Richard Ridderinkhof at the University of Amsterdam. In 2007, Mirre began her PhD studies, which have focused on research in the field of decision neuroscience under the supervision of Prof. Ale Smidts at the Rotterdam School of Management, Erasmus University Rotterdam. The interdisciplinary nature of her project has also involved extensive collaborations with with Prof. Guillen Fernandez and Dr. Alan Sanfey at the Donders Institute for Brain, Cognition and Behavior, Radboud University Nijmegen. Mirre's research has been published in several peer-reviewed journals, such as *Psychological Science* and *The Neuroscientist*, and has been featured widely in the media both within the Netherlands and abroad. She has also presented her work at various international academic conferences, including the annual meetings of both the Society for Neuroeconomics and the Social and Affective Neuroscience Society. Currently, she works as a post-doctoral researcher in the lab of Dr. Alan Sanfey at the Donders Institute, where her research is exploring the psychological and neural processes involved in social cooperation.

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In preparation

Stallen, M., Rossi, F., Heijne, A., Smidts, A., de Dreu, C.K.W. & Sanfey, A.G.. The justice spray: Effects of oxytocin on social norm enforcement.

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Mirre

Dave Moulton's Bike Blog

Why do cyclists shave their legs?
The only explanation you will ever need

It's hotter'n hell, 90 degrees (32 C.) and we are going out for the evening. My wife is wearing long pants.

"Aren't you going to be hot?" I ask. "Why don't you wear a dress or shorts?"

"I can't, I haven't shaved my legs."

End of questioning, no further explanation needed.

My lovely wife doesn't want to be the only one in a roomful of ladies with silky smooth legs, while she is sporting stubble. Even though I would have to get down on my knees with a magnifying glass to find a tiny emerging follicle.

This is exactly the same reason why cyclists shave their legs, No one wants to go out on a group ride and be the only wooly mammoth in the pack.

Even if I am riding alone, I still shave my legs; I never know who I might meet on the road. Shaved legs simply look better on a cyclist. Some call it vanity, frankly I find that an affront to my pride.

I started racing in 1952 and that's when I started shaving my legs. The European professional riders shaved their legs because they were riding the big stage races like the Tour de France and the Giro d'Italia.

Stages were long back then, sometimes in excess of 180 miles. (289.6 km.) They needed some serious massage therapy at the end of each day in order to have the leg muscles supple and relaxed ready to go again the next morning. It is neither comfortable for the cyclist or the masseuse to be massaging hairy legs.

The long, smooth legs in the picture at the top belonged to "Il Campionissimo" Fausto Coppi. I was no different from any other cyclist of the 1950s; we all wanted to emulate the great professional riders of that era. So we shaved our legs.

Shaved legs are faster; it is psychological. Like polishing the engine on a hot rod car; you can't see inside the engine but you polish the outside. The cyclist is the "engine" of his bike; you can't see the heart or the lungs inside, but by making the legs smooth and clean so you see every vein, sinew, and muscle, it is a definite psychological boost.

Professional cyclists today shave their legs for the same reason as their predecessors, and road cyclists of all levels, from amateur racers to weekend warriors follow suit. End of story, there should be no further explanation needed.

Fellow cyclists understand, but non-cyclists question this practice. We come up with all kinds of creative reasons for shaving our legs. We pretend that it is in case we fall and get road rash.

Sure with hair free legs it is easier to clean and dress wounds, but that is not why we shave our legs. A lady known only to me as "Jan" commented on a recent post. "If you fall and get road rash on your legs, wouldn't you also scrape up your arms?" Good point, cyclists rarely shave their arms. (That would be weird.)

If someone asks me, "Why do you shave your legs?" I answer simply, "It's traditional." That is the only answer I need. No one questions it or doubts my word. After all, if something is traditional, who am I to break with tradition?

Professional racing cyclists have been shaving their legs for at least 100 years, that's probably longer than ladies have been shaving their legs. So the practice definitely qualifies as a tradition.

Think of it like the running of the bulls in Pamplona, Spain; when someone asks, "Why would you run down the street in front of a herd of stampeding bulls?"

"It's traditional."
"Oh well, that explains it. No further explanation needed."

Or, “Why are you taking that dead pine tree into your house at Christmas.”

“It’s traditional.”

You see how it works; it doesn’t matter how bizarre or irrational the act, just say, “It’s traditional,” and it is immediately accepted.

It is so easy. No more excuses, no more lies about road rash or guilt feelings over vanity. The answer is, “It’s traditional.”

No further explanation is needed.

http://davesbikeblog.blogspot.nl/2008/06/why-do-cyclists-shave-their-legs-only.html

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SOCIAL CONTEXT EFFECTS ON DECISION-MAKING
A NEUROBIOLOGICAL APPROACH

Many of our daily decisions and choices are influenced by how others behave. Girls buy shoes seen in celebrity ads, teenagers copy music from their facebook friends, and hipster ride fixies* for fashion. Importantly, our decisions are also often influenced by our beliefs about what behavior is morally right, as well as by our perceptions about what behavior is typically approved of or disapproved of by others. To better understand how decision-making is shaped by our social context, this thesis explores how both the behavior of others as well as our perception of social norms can impact the neurobiology of our decisions. The theoretical chapters review cutting-edge work examining the neural systems that underlie social decision-making, and show that many of the processes involved overlap with very basic brain mechanisms. The empirical chapters each illustrate a different example of how the social context influences decision-making and its associated neurobiological circuitry. For instance, this thesis addresses the question why celebrity endorsers are more effective than non-celebrity endorsers, using neuroimaging methods to explore the underlying brain processes. Other empirical chapters investigate the neurobiological processes involved in conformity and social norm enforcement, demonstrating that oxytocin, a hormone often implicated in social behavior, plays a more general role in social behavior than previously assumed. In particular, administration of this hormone was found to stimulate conformity to in-group, but not out-group members, and to increase individual sensitivity to the violation of distributional fairness norms.

** fixed-gear bikes, usually without brakes*

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