INVESTIGATING THE NEURAL MECHANISMS OF SOCIAL VALUES VIA HORMONES AND NEUROIMAGING

by

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To Holly, for her forbearance and faith.

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by

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Recent research on the social functions of the neuropeptide hormones oxytocin and vasopressin has increasingly shown them to be dependent on context, but the nature of the contexts in which their behavioral and neural effects are elicited remains unclear. Despite rising interest, it has been particularly difficult to determine when oxytocin or vasopressin may increase trust and parochial prosocial behaviors or if they may enhance egalitarian behavior at all. This study examined the influence of these hormones on behavioral and blood oxygen level-dependent (BOLD) responses in two social tasks, each performed by participants during three separate functional Magnetic Resonance Imaging (fMRI) sessions conducted within a placebo-controlled, double-blinded procedure. In one task, faces were judged on how trustworthy and how dominant they appeared, and the other task asked for single sentence descriptions of real-world activities to be evaluated on how worthwhile they were and how likely subjects were to participate in them. Each activity was categorized according to four motivational contexts conceptualized in the Basic Human Values Theory, a model of core values. Two of these contexts capture the distinction between parochial and egalitarian prosocial behavior as relating, respectively, to the

values of Benevolence and Universalism. Compared to placebo, vasopressin did not effect either facial judgment. Oxytocin did not affect trustworthiness ratings but did increase ratings of facial dominance compared to placebo. Oxytocin did not influence activity ratings when compared to placebo, but vasopressin increased how worthwhile Universalism activities were perceived to be. The hormones affected BOLD signal more in the activities task than the facial judgments. In particular, a dissociation was seen for the hormones across evaluations of Benevolent activities with oxytocin enhancing BOLD in the left anterior insula and posterior inferior frontal gyrus compared to vasopressin. This may indicate a role for oxytocin in enhancing the processing of emotional and semantic meaning in parochial prosocial contexts. This study presented the first evidence of oxytocin increasing the perception of facial dominance and of vasopressin promoting egalitarian prosocial behavior. I also provide evidence that oxytocin enhances mental processing in parochial rather than egalitarian contexts.

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LIST OF ABBREVIATIONS

ACC – Anterior Cingulate Cortex

ANOVA – Analysis of Variance

BHVT – Basic Human Values Theory

BOLD – Blood-Oxygen-Level Dependent

DLPFC – Dorsolateral Prefrontal Cortex

DMPFC – Dorsomedial Prefrontal Cortex

F – F-test value

FWE – Family-Wise Error

fMRI – Functional Magnetic Resonance Imaging

GLM – General Linear Model

IFG – Inferior Frontal Gyrus

M - Mean

MCC – Middle Cingulate Gyrus

mm – millimeters

MNI – Montreal Neurological Insitute

MPFC – Medial Prefrontal Cortex

ms - milliseconds

OFC – Orbitofrontal Cortex

OXY – Oxytocin

PCC – Posterior Cingulate Cortex

PSC – Percent Signal Change

PVQ – Portrait Values Questionnaire

ROI – Region of Interest

s – seconds

sd – standard deviation

SPM – Statistical Parametric Mapping

STG – Superior Temporal Gyrus

TPJ – Temporoparietal Junction

VAS - Vasopressin

VMPFC – Ventromedial Prefrontal Cortex

WFU – Wake Forest University

CHAPTER 1

INTRODUCTION

In the past decade, neuroscientists have learned much regarding how the brain compares the rewarding properties of a variety of stimuli and outcomes during goal-directed decision making (Rangel & Hare, 2010). As this knowledge continues to grow, neuroeconomists and decision neuroscience researchers have begun collaborating with social neuroscientists to learn how subjective social preferences are represented in the brain during incentivized decision making. The clear majority of these studies involve tasks that contrast choices with potentially greater monetary gains versus choices with a potentially better social outcome for the individual and the other parties involved. Thus far, they have revealed brain regions that communicate with and potentially influence the primary reward processing areas of the brain, such as the such as the temporoparietal junction (TPJ), dorsomedial prefrontal cortex (DMPFC) and anterior insula, and have developed theories regarding what socio-affective processes (e.g. empathy and reciprocity) the activity in these regions might represent in these circumstances (see Fehr & Camerer, 2007 for a list of study articles). When these reward and social processing areas show a high level of concurrent activity the result is a strong tendency towards the socially beneficial choice over the more financially beneficial choice.

One outstanding question that is typically overlooked is whether the information communicated between reward and emotion processing areas and regions such as the TPJ, DMPFC and insula represents individuals' social preferences. Brosch and Sanders (2013) proposed that values, a class of high order subjective preference, influence neural representations of reward value in the striatum and orbitofrontal cortex (OFC), perhaps by increasing the

prioritization placed on information received from regions involved in social cognition. Their use of the term "values" is noteworthy. Social neuroscientists rarely mention the values construct as it is found in social psychology, or the corresponding values theories, despite their consistent use of the word "values" to describe the degree of worth a person assigns to a given social outcome. This is surprising because the social terms modeled in values theory such as cooperation, fairness, generosity, etc. (see Rokeach, 1973), are common in the social neuroscientific literatures that explore social preferences, demonstrating high overlap of conceptual topics between these disciplines. Social neuroscientists borrow these terms, along with many tasks, from social psychology or behavioral economics but rarely employ a framework by which they might begin to understand how differences in the biological substrates of different social behaviors might suggests relationships between the different concepts we use to describe them.

In values theory, these terms are grouped within broad frameworks that seek to explain universal human goals with a small set of values concepts. For example, the values theory that my dissertation will draw upon, the Basic Human Values Theory (BHVT), was developed by applying multidimensional scaling techniques to surveys on values terms taken by individuals in over 70 countries (Schwartz & Bilsky, 1990). This work revealed ten human values that are intended to comprehensively represent basic concepts related to subjective social preferences that are universal across humanity. Applying concepts from values theory could grant much needed theoretical definition to the mental operations observed to be associated with specific social contexts during subjective choice neuroimaging tasks.

If, as Brosch and Sanders proposed (2013), social information received by reward processing areas from the social processing regions is granted priority to influence choices, the potential mechanism could take the form of either a top-down mechanism driven by those social regions, or by a bottom-up mechanism in which affective regions grant attentional saliency and affective weight to social information. My dissertation project will approach this topic with the premise that the mechanisms that might make the varied social prioritizations possible are bottom-up mechanisms and those different prioritizations or preferences may be selectively associated with specific chemical signals. I make this assumption based on extensive evidence that the peptide neuromodulators oxytocin (OXY) and vasopressin (VAS) strongly influence social motivation and the salience of social information in animal and human studies (Averbeck, 2010; Bartz, Zaki, Bolger, & Ochsner, 2011; Burkett & Young, 2010).

OT and VAS have received much attention from researchers recently for their potential as a piece of the puzzle of explaining the biological basis of humans' unique prosocial and even altruistic capabilities. Values have been shown to be related to the frequency of experienced emotion and to influence attentional salience and valence of goal-relevant stimuli (Nelissen, Dijker, & De Vries, 2007; Feather, 1995), indicating that they may be related to emotion and salience processing in areas of the brain such as the amygdala, rostral anterior cingulate gyrus (RACC), and anterior insula in which OXY and/or VAS receptors have been found (Allman, Watson, Tetreault, & Hakeem, 2005; Boccia, Petrusz, Suzuki, Marson, & Pederson, 2013). Early evidence from both genetic studies and pharmacological administration of OXY and VAS also suggest that these hormones influence behaviors related higher-order values and increase brain activity in some of the mentioned brain areas during these tasks. For example,

polymorphisms on VAS receptor AVP1a were related to increased generosity in a donations task and increased prioritization of two prosocial values: Benevolence and Universalism (Knafo, et al., 2008). Intranasal administration of OXY has also been demonstrated to result in increased donations in similar tasks (Kosfeld, Heinrichs, Zak, Fischbacher, Fehr, 2005; Israel, Weisel, Ebstein, & Bornstein, 2012; Baumgartner, Heinrichs, Vonlanthen, Fischbacher, Fehr, 2008; Mikolajczak, Gross, Lane, Corneille, de Timary, & Luminet, 2010), however, the effects have not been tested along with assessments of values. Doing so may prove useful because the effects of OXY during specific conditions of prosocial tasks results in behavior that illustrates the distinction between the Benevolence and Universalism values. This is due to a difference between the two values regarding what groups of people they primarily serve. Individuals high in Benevolence seek to build relationships with and increase the welfare of individuals within one's in-group. Individuals high in Universalism seek to increase the welfare of all and particularly look to elevate those who are in some way disadvantaged (Schwartz, 1992). These two prosocial values effectively conceptualize the recent controversial findings regarding the possibility that OXY may specifically promote prosocial behavior only toward in-group individuals (for review, see de Dreu, 2012). This suggests the possibility that values may help resolve discrepancies and disputes within the literature by helping to better define the dissociable social functions for specific brain areas or for different neuromodulators, such as hormones.

My dissertation project examines both the lower-level perceptual effects and higher-order social appraisal effects of OXY and VAS within a single study. The two hormones, as well as a placebo, are administered via nasal spray in a double-blinded, within-subjects crossover design that compares participants' behavioral and BOLD responses on two tasks. In one novel task

participants assess verbal descriptions of activities related to either prosocial or self-interested values. In the other task participants r/ate the trustworthiness or dominance of photographed faces. The two prosocial values studied are Benevolence and Universalism and the two self-interested values that conceptually and empirically oppose these prosocial values are Power and Achievement (Schwartz, 1992). Achievement is defined by a concern for competence according to social standards of success. Individuals high in Power are less concerned with gaining success on merit and are more motivated by social status, authority, and the desire to control resources and other people. These values are often negatively correlated with the prosocial values on assessments of individual value priorities, as well as in many empirical studies on that relate values to behaviors or attitudes (e.g. Schwartz, 1996).

Social values have a long history across the social sciences for modeling both the breadth of human social goals and general individual differences in motivation. In appropriate contexts, values have significant and pervasive, but indirect effects on social behaviors ranging from adherence to vegetarian diets (Adams, 1990; Lea, 2001; Sims, 1978), to volunteer commitments (Lydon & Zanna, 1990; Hitlin, 2003) and attitudes such as political party affiliation (Caprara, Schwartz, Capanna, Vecchione, and Barbaranelli, 2006; Schwartz, 1996). I propose that the conceptual properties by which values are defined correspond well with the patterns of brain activity observed during incentivized social decisions. Furthermore, several aspects of neuropeptide functioning in the central nervous system including the duration of their effects, the regions their neurons connect with and the location of their receptors could allow them an indirect, neuromodulatory role in incorporating the social contexts related to core values into decision making.

1.1 The Problem of Values

Prominent personality and social psychologist Gordon Allport claimed that "values are the dominating force in life, and all of a person's activity is directed toward the realization of his values" (Allport, 1961, p. 543). Despite the ubiquity of values in our lives and the acknowledgment of their importance in research across the social sciences (Maio, 2010; Williams, 1968), values fell out of common usage by anthropologists and sociologists in the mid-20th century (Hitlin & Piliavin, 2004), and were perhaps the construct most effectively dismissed by psychologists during behaviorism (see Rohan, 2000).

There are several likely reasons for values being a neglected topic of study. Social values have long been seen as an unwieldy set of constructs due to their subjectivity and the difficulty in measuring them (Hitlin & Piliavin, 2004; Williams, 1968). Prior to the recent establishment of comprehensive theoretical frameworks such as the BHVT there was little collaboration between researchers with different approaches or conceptualizations of values and a general lack of discussion relating values to broader social theories. Thus, other constructs that overlapped conceptually or functionally with values, and were perceived to suffer fewer obstacles for empirical study, became favored (Hitlin & Piliavin, 2004).

1.2 BHVT Structure and Assessment Measures

The circumplex model of the BHVT concepts (see figure 1) and the subsequent assessment measures for the model were derived from survey responses by people in multiple countries who rated the personal importance of values concepts (Schwartz, 1992; Schwartz 2006), many of which were drawn from the work and measures of Rokeach (Rokeach, 1973). Responses were analyzed using multidimensional scaling to spatially represent the data. The ten

higher-order value types then emerged based on the observed relationships between the item-level value terms. These relationships also allow the generation of hypotheses based on the relative conceptual similarity of adjacent values and dissimilarity of values lying on opposing sides of the circumplex model (e.g. Universalism versus Power). These hypotheses are captured by four axial value orientations which show the value-types most closely related and are named in a manner that gives reference to the values-type they tend to be negatively correlated with (e.g. Self-Enhancement versus Self-Transcendence, which I will refer to respectively as self-interested and prosocial throughout this manuscript). Two primary assessment measures have been used to assess BHVT values: the Schwartz Values Questionnaire and the Portrait Values Questionnaire (Schwartz, 2006). The PVQ is currently preferred because the items are presented as a personal attribution, which is more concrete than the abstract definitions of the SVS (Schwartz, et al., 2001). See Appendix for the full PVQ questionnaire.

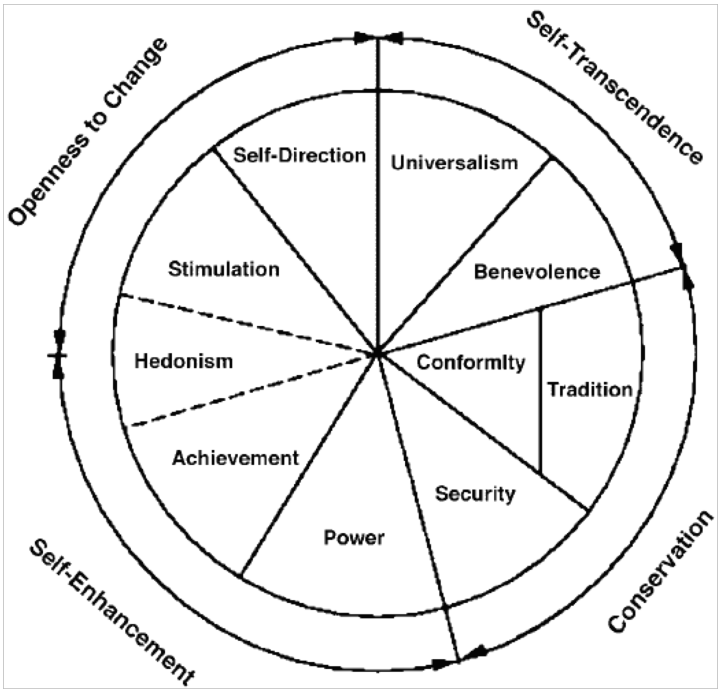


Figure 1. Circumplex model of the 10 values proposed by the Basic Human Values Theory.

1.3 Values and Behavior

Values affect behavior despite their abstract nature. Behaviors associated with values that are highly important to an individual can be made to better align with those values when one's cognitive awareness of those values is increased (Verplanken & Holland, 2002). There is significant evidence that values influence attitudes. For instance, different kinds of discriminatory attitudes towards women have been observed to correlate with different values (Feather & Mckee, 2012). Specifically, hostile sexism was correlated with Power, benevolent sexism correlated with the value of Security, and both kinds were negatively correlated with Universalism and Benevolence. Among other studies, relationships have been observed between values and political affiliation (Caprara, et al., 2006; Schwartz, 1996). This influence on attitudes becomes pronounced when an object or topic presents a conflict between two or more values, resulting in a conflicted or ambivalent attitude (Maio, 2010). For example, someone who highly prioritizes both Tradition and Universalism may have difficulty formulating a clearly positive or negative attitude towards homosexuality. Values research has, perhaps, been most successful in linking values to various lifestyle factors. Universalism is linked with adherence to vegetarian diets (Adams, 1990; Lea, 2001; Sims, 1978). Prioritizing self-interested values, among a few others, is related to an increase in household energy consumption (Abrahamse & Steg, 2011).

Prosocial behavior has received attention in the values literature. Values can help sustain commitments, an effect which has most often been demonstrated in studies of volunteerism (Lydon & Zanna, 1990). This relationship between volunteer activity and the values of Universalism and, especially, Benevolence is among the strongest empirical links between

behavior and values (Hitlin, 2003; Omoto & Snyder, 1995). Prosocial behavior has also been operationalized as cooperative or generous behavior in laboratory settings (Sagiv, Sverdlik, and Schwartz, 2011; Schwartz, 1996). Sagiv and Schwartz found in two separate social dilemma games that players who highly prioritized prosocial values were more likely to act cooperatively and to donate a portion of an allotment of money than those who highly prioritized self-interested values. When the cooperative aspect of the game resulted in donation to a charity, Universalism was the most influential prosocial value. When the game was framed as contributing money for a potential participant team payout, Benevolence was the most influential value. In both cases, Power demonstrated the most negative relationship with contributing money. While less work has been done on the value of Power, these observations of its negative relationship with several behaviors also associated with the Universalism and Benevolence values does lend support to the structure of the BHVT model. Additional relationships have been found for self-interested values in applied psychological research. Achievement values have been linked to academic performance (Fries, Schmidt, & Hofer, 2007), and the policy decisions of high-tech entrepreneurs who prioritize self-interested values were seen to be most influenced purely by financial returns (Holland & Shepherd, 2013).

1.4 Relationship of Values to Other Constructs

Attitudes and goals are, like values, key concepts for the behavior of evaluation, but they are defined as mental states representing specific objects, actions or states of being (Rohan, 2000). Values are more generalized than these two constructs in that they are considered to be representations of needs that inform attitudes and goals (Rokeach, 1973; Schwartz, 1992). Needs are often theorized as originating from biological imperatives and values have also been

theorized to be influenced by, or originate from, biological factors (Cavalli-Sforza, 1993; Michod, 1993). Shalom Schwartz explained the universal nature of these values as resulting from their functional significance in maintaining the goals of three universal human requirements: "needs of individuals as biological organisms, requisites of coordinated social interaction, and survival and welfare needs of groups" (Schwartz, 1992).

1.4.1 Distinction between explicit and implicit motives. In the literature on psychological needs, values are referred to by some prominent theorists as explicit motives, and implicit and explicit motives are considered to arise from distinct and independent neurobiological systems (McClelland, 1989; Weinberger and McClelland, 1990). They differ in measurement approach because needs are theorized to be behavioral motivations unavailable to conscious knowledge. Thus, while explicit motives can be assessed by self-report, implicit motives are typically assessed via coding appropriate motive related words in free writing samples (Smith, 1992; Winter, 1999). A recent meta-analysis of studies investigating the relationship between implicit and explicit motives, which included values, found them to be only weakly correlated, although a relationship appeared evident (Köllner, & Schultheiss, 2014). One study showed no correlation between two BHVT values, Benevolence and Power, and two conceptually related implicit motives, need for affiliation and need for power (Hofer, Chasiotis & Campos, 2006). Despite this, they found both Benevolence and need for affiliation to correlate with life satisfaction and found an interaction effect in which Benevolence mediated the degree of the relationship between need for affiliation and life satisfaction.

It may be that explicit and implicit motives are represented in different neural systems and different task demands are required to access the two routes of information processing.

However, whether values should be considered only as explicit motives may not be adequately resolved. Indeed, the study by Hofer, Chasiotis and Campos interpreted these results as indicating congruence between implicit motives and values. I would assert that the interaction in which they observed Benevolence as a mediator for need for affiliation's effect on life satisfaction may demonstrate that the effects of implicit motivations on well-being in general are better realized when those motivations are available to the individual in an explicit form.

Regardless, efforts have been made to connect implicit constructs to biological factors that support theories of a role for hormones in motivating behaviors related to higher-order needs. Need for power has been shown to be influenced by testosterone and to amplify the cortisol response to competitive wins or loses (Schultheiss, Campbell & McClelland, 1999; Schultheiss, et al., 2005; Schultheiss & Rohde, 2002; Wirth, Welsh & Schultheiss 2006). Additionally, Schultheiss, Wirth and Stanton (2004) found Need for affiliation to be related to progesterone, an effect that was curiously maintained even for those women taking oral contraceptives. The authors speculated that this contradiction might be resolved if stimuli that arouse affiliation motivation also elicit a spike in OXY levels which in turn stimulates progesterone release. This may suggest a mechanism for OXY to influence prosocial motivation. However, similar efforts have not been made to see whether such effects might also be seen in studies examining the biological bases of values as a more explicit form of motivation.

The universality of values concepts across humanity, their conception as an extension of needs, their influence on social behavior and the impact they have on well-being all speak to the importance of researching how they may be reflected in human biology. That values are conceptualized as representations of needs may be a clue to their biological basis. Hormones

have a crucial role in maintaining homeostasis by acting as signals that motivate behaviors which promote healthy physiological states (Landgraf & Neumann, 2004). In humans, certain hormones have a role in motivating the maintenance of behaviors and lifestyles that promote mental and physical well-being. Thus, some values may be conceptual descriptions of higher-order needs which hormones have a strong role in regulating.

1.5 Neural Mechanisms of Neuropeptides

Hormones are neuropeptides that have a neuromodulatory role in the central nervous system. Of the 100 neuropeptides OXY and VAS are among the most widely studied (Ludwig, 2011). They are synthesized mainly in the magnocellular cells of the supraoptic and paraventricular nuclei of the hypothalamus and released from the posterior pituitary gland (Stoop, 2012). Parvocellular cells in the paraventricular nucleus contain a much smaller amount of the two hormones and VAS cells are a feature of the suprachiasmatic nucleus (Ludwig & Leng, 2006).

Less is known of the receptor distribution for these neuropeptides across the central nervous system for two primary reasons. First, large variation in receptor locations between species limits the application of animal models to humans (Gimpl & Fahrenholz, 2001). Secondly, there are currently no suitable positron emission tomography radioligands with sufficient receptor specificity for the OXY receptor or the VAS receptor associated with social behaviors (AVP1a) (Baribeau & Anagnostou, 2015). Only three studies to date have sought to localize these receptors either in the brainstem (Loup, Tribollet, Dubois-Dauphin, Pizzolato & Dreifuss,1989), for which there is wide distribution, or the whole brain (Loup, et al., 1991; Boccia, Petrusz, Suzuki, Marson, & Pederson, 2013). Receptor density was high in both studies

for OXY in the lateral septal nuclei and the bed nucleus of the stria terminalis (a primary output region for the amygdala). Other areas observed for one of the studies were the anterior cingulate, retrospenial cortex, central and basolateral amygdala, and low binding in the globus pallius and ventral pallidum. High receptor density was also seen for VAS in the lateral septal nuclei as well as in several thalamic nuclei (Loup, et al., 1991). Low density was seen in the basolateral amygdala and the dentate gyrus.

Even though OXY has been seen to bind to VAS receptors with similar strength to its own receptors (Baribeau & Anagnostou, 2015), this early evidence does not show widespread receptor distribution in the human cortex for either hormone, limiting their direct effects on higher cognition. Despite this, the ability to affect the amygdala, cingulate cortex, thalamus and several reward processing regions supports potentially extensive indirect effects on affiliative motivation, empathy, and/or an influence on the salience of social information.

1.5.1 Relationship to neurotransmitters. The chemical properties of neuropeptides and certain properties of the neurons that release them reveal fundamental differences from neurotransmitters. Hormones are released from large dense-core vesicles rather than the small synaptic vesicles that release neurotransmitters (Ludwig & Leng, 2006). Like neurotransmitters, they may be released from synaptic terminals; however, because the vesicles that release hormones are located on the cell body and dendrites of their neurons in addition to the axon terminals, their actions upon neural circuits are not nearly as region specific. This freedom to act in extracellular space is also aided by the fact that there are no reuptake transporters for neuropeptides (Landgraf & Neumann, 2004), and the half-life in the brain for neuropeptides is approximately 20 minutes, which is orders of magnitude longer than the typically 5ms long half-

lire for neurotransmitters. In addition, while there are feedback mechanisms to control their activity, hormones also have the capability to act upon the neurons releasing them. They do this by acting on the G protein-coupled receptors of these neurons causing Ca+ to be released from intracellular store which primes more vesicles in the dendrites to release more of the neuropeptide creating a loop that does not require electrical activity at any point in the process (Ludwig & Leng, 2006).

The varied mechanisms by which they may act upon neural circuits seem to support the potential for these substances to have a role in modulating preferences and general motivation social cognition at the scale necessary for value-related cognition. The hormones may prime and/or modulate attentional, affective and reward networks to promote certain behaviors in situations or around people that represent appropriate contexts. The behaviors for which these hormones are responsible, such as trust, generosity and intimacy, are also associated with feelings. These feelings may be descriptions of the processes for which the prolonged effects of these hormones likely have a significant role. The duration of the hormones' effects makes sense considering the need for trusting and intimate behaviors to be maintained despite occasional instances in which the target of such behavior does not reciprocate them. As such, the feelings associated with these behaviors may be critical for tuning attentional, affective and reward systems to the contexts in which these behaviors are advantageous, rather than simply promoting certain behaviors indiscriminately.

1.5.2 Interaction with neurotransmitter systems. Both OXY and VAS have been shown to affect the dorsal raphe nucleus through their action on the extended amygdala (Mottolese, Redouté, Costes, Le Bars, and Sirigu, 2014; Rood & Beck, 2014). Mottolese and

colleagues performed a positron emission tomography study on binding affinity in dorsal raphe nucleus in humans receiving either intranasal OXY or a placebo. They showed effects on receptor binding in this area that also correlated with changes in the hippocampus, amygdala, insula, subgenual ACC and the OFC, a network in which serotonin is implicated in effects on mood and social behavior.

Both hormones are known to interact with dopamine in the nucleus accumbens in rats and voles (Burkett & Young, 2012;). Their interaction with dopamine has been shown to occur specifically in social situations, either in the establishment of pair bonds or the promotion of maternal/paternal nurturing and protective behaviors (Liu & Wang, 2003; Bosch & Neumann, 2008). Liu and Wang (2003) also found that blockade of either OXY or dopamine D2 receptors on the nucleus accumbens prevented female prairie voles from establishing a pair bond upon mating. Strong effects in the nucleus accumbens are less likely in humans given the distribution of receptor locations seen thus far. In addition the lateral septum, the reward processing area with the greatest density of receptors, is not part of the dopaminergic system. However, even lesser densities of receptors in reward areas may be behaviorally meaningful. For instance, profound effects were seen by altering the ventral pallidum of the promiscuous male montane vole to provide it with AVP1a receptors, which it lacks. This change alone was sufficient for its mating behaviors to resemble that of the monogamous prairie vole (Lim, et al., 2004).

Dopamine has a well-established role in learning the intrinsic worth of stimuli and goals (Montague & Berns, 2002). However, its critical and universal role in reinforcement learning would likely preclude it from having a relationship with preferences associated to specific

classes of behaviors or stimuli. Hormones, such as oxytocin and vasopressin, may be better suited to biasing the output of reward processing to reflect preferences based on context. Their ability to interact with dopaminergic and serotonergic systems may mean that these hormones, and any others that may operate similarly, are strong candidates contributing to the processing of specific types of contextual rather than intrinsic value. Possessing properties such as a long half-life and the ability to perpetuate their release may allow hormones to coordinate processing in affective and reward systems in a sustained rather than a transient manner during decision making. Such sustained effects are likely to be better for accommodating persistent social cues, such as the presence of offspring.

1.6 Oxytocin and Prosocial Behavior

In humans, administration of OXY has been shown to affect social perception and increase a variety of nurturing parental behaviors (Goodson & Thompson 2010; Gordon, Martin, Feldman, & Leckman, 2011). OXY may promote empathy, especially emotional rather than cognitive empathy (Hurlemann, et al., 2010), but generalization may be hampered by the influence of other phenomena such as mimicry and emotional contagion (Norman, 2012). It has also been seen to increase perceptions of harm for victims but not the desire to punish the offending individuals (Krueger, et al., 2013).

Its effect on trust is one of its most well-known and most controversial effects (Nave, Camerer, & McCullough, 2015). It has been seen to increase facial trustworthiness ratings (Theodoridou, Rowe, Penton-Voak, & Rogers, 2009), and it has demonstrated effects in several versions of the trust game. In the trust game, one player could keep a small amount of money or entrust it to the second player knowing that the amount of money would then be multiplied and

that the other player could choose to keep this larger amount rather than returning part of it. OXY was seen to increase the median amount entrusted to the second player by 25% (Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005). When the trust game is performed over multiple rounds, players receiving OXY did not decrease the amount of money they entrusted after the second player had refused to share multiple times, as players typically do (Baumgartner, et al., 2008), unless that other player was described as having an untrustworthy reputation (Mikolajczak, et al., 2010). However, several studies have failed to replicate these findings and this may indicate that the effects of OXY on trust are dependent on specific social contexts (Nave, et al., 2015).

There are also conflicting results regarding what contexts OXY increases trust for, particularly during cooperative activities. A series of experiments used the Implicit Associations Task and moral dilemmas to show that intranasal OXY promotes both in-group favoritism and out-group derogation when names of different racial groups were used (de Dreu, Greer, Van Kleef, Shalvi & Handgraaf, 2011). While this group has been the only one to observe a clear bias against out-group members, others have also demonstrated a relationship between OXY and an in-group bias. Recent research indicates that OXY increases likeability and arousal for symbols related to in-group membership (Ma, et al., 2014), and it increases the conformity of ratings of attractive faces with confederates arbitrarily assigned to one's team, while having no effect on out-group symbols or conformity with those assigned to an out-group team (Stallen, De Dreu, Shalvi, Smidts, & Sanfey, 2012). These results appear to reflect differences between Universalism and Benevolence values which are respectively defined as having concern for the welfare of out-group members or for in-group members. Promotion of an in-group bias would

suggest an influence to prioritize Benevolence over Universalism. Further indication of this may come from evidence showing that plasma OXY levels among family members tend to be inter-related and are associated with synchronization of affective behaviors and self-reported romantic and parental bonding (Feldman, Gordon, & Zagoory-Sharon, 2011). These results suggest that OXY strongly supports the maintenance and growth of familiar, in-group relationships.

1.7 Vasopressin, Behavior and Genetics

Research on the behavioral effects of VAS has been largely restricted to studies on animals and has focused on two contrasting lines of research: one linking VAS to caregiving and bonding, and the other linking it to aggression, especially between males (Heinrichs & Domes, 2008). However, it has not been seen to increase motivation to dominate, a trait seen to relate more to testosterone in animals (van Honk, Bos & Terburg, 2014). Levels of circulating cerebro-spinal fluid levels of VAS have been positively associated with life-history of aggressive behavior in human males with personality disorders (Coccaro, Kavoussi, Hauger, Cooper, and Ferris, 1998), but this has either not been shown or has not been investigated for healthy males. To date, positive effects of VAS on aggressive behavior have only been observed in one experiment and only within a condition in which the aggression could also be considered prosocial. Buffone and Poulin (2014) found specific VAS receptor polymorphisms to correlate with the assignment of hot sauce as an aversive stimulus the purpose of which was to hinder one individual during a competition when a competing third party was portrayed as financially distressed and the participant was manipulated to feel empathy toward the distressed competitor.

Furthermore, a few studies have observed prosocial effects for VAS. Knafo, et al. (2008) found genetic variations of the AVP1a receptor to positively correlate with monetary offers from

one player who was given money for the study, any amount of which could be kept or shared with an anonymous partner with no repercussions. In the same study, VAS increased ratings of Universalism and Benevolence related stimuli like those used in this dissertation (Knafo, et al., 2008). While this genetic study seems to indicate prosocial effects in line with both BHVT values, no study using nasal spray vasopressin has observed effects that align with a relationship to social phenomena related to Universalism.

An effect related to Benevolence, however, has seen some support. Due to the relationship to male aggression in animals, one study using a game paradigm hypothesized that players given VAS would act more competitively (Rilling, et al., 2012). In this game, known as the prisoner's dilemma game, two players choose independently to either cooperate or defect and the outcome for a given player is determined by what both have decided. If a player cooperates, he or she can expect either to earn $2 if the other player also cooperates or $0 if the other player defects. However, a player who defects could expect to earn either $3 if the other player cooperates or $1 if the other player defects. Thus, defecting is the most profitable strategy. Rather than act more competitively, VAS increased players' reciprocation toward those who previously displayed trust. If the player receiving VAS had been defecting, changing to a cooperative strategy to match another player who is signaling a play-style that can be exploited is strictly less profitable. Thus, VAS increased how much players valued maintaining building a relationship with a trustworthy individual, even an anonymous one, in comparison with earning more money. The case for a Benevolence related effect is bolstered by evidence of positive effects for VAS on bonding. In humans, both VAS receptor variations and higher blood plasma

levels of VAS have shown a positive relationship in paternal and marital interactions (Walum, et al., 2008, Gouin, et al., 2010).

1.8 Oxytocin, Vasopressin and Face Perception

The effects of OXY on social perception are generally aligned with other evidence for prosocial effects, while the results for VAS are not. OXY has been shown to increase judgments of facial trustworthiness (Theodoridou, et al., 2009) or, at least, the accuracy of these judgments (Lambert, Declerck, and Boone, 2014). One study showed that participants remember faces with either happy or angry expressions better than those with neutral expressions after receiving intranasal VAS (Guastella, Kenyon, Alvares, Carson, & Hickie, 2010). However, only memory for happy faces was enhanced by intranasal OXY in a related study (Guastella, Mitchell, & Mathews, 2008). Another group found that VAS increased agonistic facial expressions measured by electromyogram (EMG) in men's responses to unfamiliar male faces with neutral expressions, making the response similar to that evoked by angry faces in the control condition (Thompson, George, Walton, Orr, & Benson, 2006). They also observed increased autonomic (i.e. heart rate and skin conductance) responses toward threatening social stimuli and decreased friendliness/approachability ratings for men with happy, affiliative expressions. This seems to reveal increased vigilance against threats as a function of VAS in humans as well as mammals.

1.9 What do values offer neuroimaging?

Being expressions of universal, higher-order needs (Rokeach 1973, Schwartz1992), values are broader constructs than the more narrowly defined attitudes and goals. Values may be in the unique position to be descriptions of the cognitive, affective and behavioral products of biological processes that assess social context. Thus, values theory can offer social neuroscience

a mature vocabulary of concepts from well-defined theoretical frameworks that are consciously available to participants, and thus readily assessed in experimental settings, yet known to influence lower processes such as attention and emotion. Their trans-situational nature should allow neuroimagers to use these constructs to examine the common patterns of brain activity related to classes of stimuli that represent specific, universal social motivations and to understand what socio-affective and reward processes may support them.

1.9.1 A cognitive neuroscience theory of values. Brosch and Sanders (2013) proposed a tentative cognitive neuroscience model of values. They asserted that values may influence choices through two routes. The first is described as a direct route that utilizes the same neural circuitry that processes motivational rewards for all primary and secondary reinforcing stimuli (Montague, King-Casas & Cohen, 2006). They hypothesize that social values influence neural representations of reward value in the striatum and OFC, and may increase prioritization of information received in these areas from neural regions such as the TPJ and DMPFC that are involved in social cognition. Brosch and Sanders (2013) additionally hinted at a possible second, more indirect, route by which values inform self-conception by influencing beliefs and norms. In this way, individuals may not simply react to incentives and punishments currently present in the environment but may seek situations suited to express through action those values that are central to their self-conception, such as expressing prosocial values by volunteering (Hitlin, 2003).

1.10 Neuroimaging of The Reward Processing System

A general reward processing network has been observed to serve all manner of incentives thus far studied (Montague, King-Casas & Cohen, 2006). These brain areas, primarily the

orbitofrontal cortex (OFC) and ventral striatum, were first seen to support evaluation of choices concerning stimuli such as food (O'Doherty, Rolls, Francis, Bowtell, McGlore, 2001; Plassmann, O'Doherty & Rangel, 2007), viewing attractive faces (Smith, 2010, and secondary reinforcers such as money (Breiter, Aharon, Kahneman, Dale & Shizgal, 2001; Knutson, Adams, Fong & Hommer, 2001). The ventral striatum is the primary area for predicting the likelihood of a choice resulting in the receipt of reward (Ernst, et al., 2004; O'Doherty, et al., 2004). The OFC maintains complex representations of the rewarding properties of stimuli across multiple modalities (Sescousse, Caldú, Segura & Dreher, 2013), and is activated during the experience of pleasurable stimuli. It also contributes to calculating the value of choices related to goal-directed decisions (Hare, O'Doherty, Camerer, Schultz & Rangel, 2008), including choices internally generated with little external structure (Cunningham, Johnson & Waggoner, 2011). This link to high-order, internally driven decision making is crucial for supporting the highly self-relevant and goal-oriented nature of value-related choices. Additionally, the dorsal striatum has been found to encode subjective value to facilitate goal-oriented action selection (Delgado, 2007).

1.10.1 Research contrasting altruism and self-interest. More recently these reward system areas have been found to activate in response to the social information gained during the viewing of trustworthy faces, or cooperation with others (Fehr & Camerer, 2007). This has helped prompt a recent surge in neuroscience research on prosocial behavior. Much of this has been supported by the rise of experimental paradigms that have been inspired by game theory or donation tasks popular in behavioral economics (Camerer, Loewenstein, & Prelec, 2005). These tasks all have well-defined dominant strategies that yield the most gain for a participant. Deviating from such a strategy is considered irrational from a purely self-interested perspective

and different tasks operationalize deviation from the dominant strategy to reveal a preference for a specific social outcome over personal gain. For example, donation tasks may force participants to choose predetermined outcomes, some of which allot them money while others force them to donate part of that allotment to another person or a to a charity. Other donation paradigms do not force this choice, instead letting the participant decide whether to donate or keep an amount of money presented in a trial. In such a design the dominant rational strategy would be to always accept any amount presented rather than to donate it.

Brain activation representing reward, regardless of the reward class (e.g financial, hedonic or social) has been consistently seen within the ventromedial PFC (VMPFC), while activation representing social preferences has typically converged on a more specific region containing portions of the VMPFC and ventral anterior cingulate cortex (ACC). This area has been reported under various names across different studies. It has been referred to as the subgenual ACC during donation tasks conditions in which individuals were able to freely choose whether or not they wished to donate allotted money to charity (Moll, et al., 2006; Camerer, Knoepfle, O'Doherty & Rangel, 2010). Another study employed a game in which one player could keep a small amount of money or entrust it to the second player knowing that the amount of money would then be multiplied and that the other player could choose to keep this larger amount rather than return part of it. In this instance, people expressing unconditional trust by always entrusting or sharing engaged the septal area (Krueger, et al., 2007). A similar region was reported as the medial OFC when it was observed for the cooperative condition of a computerized game in which a player was instructed to help, rather than block, another player from forming a shape out of tokens (Decety, et al, 2004). The close proximity of these

activations in a variety of social tasks seems to indicate an area that is a strong candidate for having a primary role in prosocial value-based appraisals and may support the idea that the subgenual ACC and immediately adjacent areas are more selective to rewarding outcomes of a prosocial nature than other VMPFC areas.

Most reward processing studies that investigate socially relevant outcomes contrast these with selfish outcomes. Using financially incentivized, self-interested outcomes as a contrast condition within a competitive task makes it difficult to interpret what brain activity might be related to behavior in what is perceived as a competitive task and what activity might be related to self-interested motives. Areas such as the MPFC and dorsolateral PFC (DLPFC), which are involved in mentalizing and strategic planning respectively (Bhatt, Lohrenz, Camerer & Montague, 2010; Coricelli, Nagel & Gazzaniga, 2009), and the reward-value processing OFC must be activated during these tasks regardless of whether or not a person's intentions are self-interested. However, the possibility remains that those motivated by self-interest may be more likely to engage in strategic thinking, thus activating the DLPFC in tasks that do not explicitly involve strategy.

1.11 Neural Correlates of Trustworthy and Dominant Faces

Trust in relationships is advantageous for survival. Avoiding those not worthy of trust and recognizing those whom one may trust to be cooperative are both crucial for human survival. Recent evidence seems to indicate that trustworthy faces and untrustworthy faces may differ in regard to the brain areas they engage. Trustworthiness judgments are highly correlated with attractiveness judgments (Oosterhof & Todorov, 2008), which demonstrates that trustworthy faces are stimuli with high reward value. This has been shown in a recent meta-analysis which

revealed that both trustworthy and attractive faces elicited the ventral striatum, OFC, and the pregenual ACC/VMPFC (Mende-Siedlecki, Said & Todorov, 2013). Trustworthiness has been shown to be negatively correlated with activity in the amygdala (Adolphs, Tranel, Damasio, 1998; Engell, Haxby, Todorov, 2007; Todorov and Engell, 2008; Winston, Strange, O'Doherty, Dolan, 2002), an area theorized to determine the valence of faces (Engell, et al., 2007). The pregenual ACC has a top-down influence over the amygdala for suppressing negative responses (Etkin, Egner, and Kalisch, 2011). The action of OXY on the pregenual ACC may be a potential mechanism enabling the behavioral effects of OXY on trustworthiness judgments via diminished negative responses.

Todorov and Engell (2008) describe attributing trustworthiness to faces as more clearly related to the perceived valence of the face than attributions of dominant facial features. Indeed, no relationship has been seen between amygdala activation and viewing dominant faces. This may be representative of the finding by Chiao et al., (2008) that participants did not judge faces with dominant expressions as being related to any one emotional dimension. This study also examined the brain activity related to viewing different facial expressions and found dominant expressions to elicit superior temporal gyrus (STG), fusiform gyrus and insula activity. The STG and fusiform gyrus observations are typical in fMRI studies presenting face stimuli. However, given that the STG was activated only for faces with dominant and submissive expressions may indicate that the STG processes information pertaining to social standing. Interestingly, in the two fMRI studies on the effects of vasopressin on facial processing, both using a negative emotional face matching task, changes in amygdalar activity were not observed in either (Zink, et al., 2011). In one of these studies, less fear-related decreases in subgenual ACC activity were

observed in the vasopressin condition when faces were compared to shapes. Another fMRI study found that connectivity representing top-down suppression of the amygdala by the MPFC was diminished when participants were given nasal spray vasopressin while looking at line drawings depicting a threatening scene between two people (Brunnlieb, Münte, Tempelmann & Heldmann, 2013). This result and the absence of observed changes in amygdalar activity may implicate vasopressin as enhancing vigilance toward threats without a typically associated enhanced fear response. However, the evidence for how vasopressin affects behavioral responses associated with viewing dominant faces has not been tested. Also, unknown is how the circuitry associated with behavioral effects in humans, namely the amygdala/subgenual ACC connections and the fear producing amygdala/brainstem connections, might be involved given that modulation of amygdalar activity is not typically observed in neuroimaging studies.

1.12 Values and Self-Processing Networks

Some values researchers have asserted that values are central to a person's self-concept (Hitlin, 2003). Results from the few relevant fMRI studies seem to corroborate this. One fMRI study compared appraisals of abstract value-based actions to rewarding leisure activities and found greater BOLD intensity in the MPFC and dorsal striatum for the former and greater mOFC intensity for the latter (Brosch, Coppin, Schwartz, & Sander, 2011b). The abstract value-based actions used in this study were adapted from items on a BHVT values assessment. While this study did not look at individual BHVT values, it did demonstrate brain activity in the MPFC that the authors attributed to self-relevance processing. In another study, the same group found that individuals who highly prioritized self-interested BHVT values gave less money allotted to them during a charity donation paradigm (Brosch, et al., 2011b). fMRI results from this study also

showed that activity in the ventral striatum and right amygdala increased as a function of self-reported prioritization of self-interested values. Personality traits describe stable dispositions rather than enduring goals but are similar to values in regard to their stability, abstract nature and perceived self-relevance. One fMRI study found activity in the VMPFC extending from the rostral PFC to the rostral anterior cingulate gyrus (rACC) to be selective for emotional importance, rather than descriptiveness ratings of traits ascribed to the self (D'Argembeau, et al., 2012). The subject response required for this task was similar to assessments of value importance in many surveys.

1.13 Oxytocin, Vasopressin and the Salience Network

The pregenual and subgenual sections of the rACC are heavily influenced, respectively, by activity of oxytocin and vasopressin neurons in the amygdala (Zink &Meyer-Lindenberg, 2011). Given the amygdala's crucial role in emotion, the contribution of the rACC in self-processing and the role both have as members of the salience network that helps identify goal-related stimuli for conscious processing (Seeley, 2007), there is potential for OXY and VAS to affect conscious representations of goal-relevant, emotionally salient stimuli. Additionally, the insula is a critical hub in the salience network and drives the production of conscious feeling states, including moral sentiments and intuitions (Allman, et al., 2005; Craig, 2009). AVP1a receptors are found in von Economo neurons in the anterior insula and rACC and OXY has been seen to influence functional connectivity between this area and the rACC and amygdala (Pincus, et al., 2010; Riem, et al., 2011; Rilling, et al., 2012). This physiological evidence and the context-sensitivity of the effects of OXY and VAS may suggest that the effects of these

hormones on social behavior largely results from an influence on the salience of social information.

1.14 Summary and Task Synopsis

The influence of OXY and VAS on the serotonergic system, dopaminergic reward system and the affective, salience and self-processing systems that promote the conscious expression of emotion show that these hormones may contribute to many processes expected to play a role in producing values-related thoughts, feeling and behaviors. The range of stimuli for which OXY and VAS have exhibited effects including faces, monetary exchanges and even familiar brands would seem to indicate that these hormones affect behavior regardless of how abstract the stimuli or context is. The specificity of the social preferences that OXY and VAS promote and especially the contexts that they promote them in seems to put them in a unique position as potential biological substrates for the concepts developed by values theorists. However, it is not known how well these preferences will map onto specific values within established values models or what insights neuroimaging experimental designs informed by such models may provide regarding the neural underpinnings of social behavior. Furthermore, it remains unclear how reliable the effects of OXY on the perception of trust are and what the potential neural correlates supporting these effects my be. It is also unknown whether OXY or VAS influences the processing of social hierarchy cues, such as dominance, in humans and what neural regions may support this.

This study explored these topics using two tasks performed while undergoing fMRI scanning on each of three separate days in which OXY, VAS or a placebo nasal spray was received and self-administered in a pseudo-randomized, double-blinded procedure. The facial

judgment task required participants to view photos of faces and rate each on how trustworthy they appear in one block of trials and rate how dominant they appear in another block. The second task used single-sentence descriptions of common activities that are presented in blocks of trials corresponding to one of four core values proposed by the BHVT. This activities task was structured identically to the facial judgment task with blocks of trials featuring one of two ratings, either how worthwhile the activities were perceived to be or how likely one was to participate in them.

1.15 Hypotheses

1.15.1 The effects of hormones on activity ratings. I expect the effects of treatment with OXY on behavioral ratings to align with the recent studies showing the hormone to preferentially enhance concern for in-group rather than out-group individuals. Specifically, OXY is expected to increase preference ratings for the novel activity stimuli related to Benevolence when compared to the placebo condition, but cause no change in ratings pertaining to Universalism or the self-interested values Power and Achievement. Note that while some theorize that OXY contributes to derogation of out-group members (de Dreu, 2012), that has not been observed in other studies and I do not expect that result.

Expectations are more tentative for VAS because it has been the subject of fewer studies and because of the difficulty in interpreting the seemingly paradoxical promotion of both prosocial and aggressive behaviors. Its propensity to increase vigilance against threats (Thompson, et al., 2006), and its historic association with aggression in animals, both of which may be due to the functional relationship with testosterone (van Honk, et al., 2014), may suggest a relationship with the Power value, yet no laboratory study has demonstrated VAS to increase

competitive behavior. More evidence exists to support a positive effect for VAS on ratings for prosocial activities. Given the strongest associations between VAS and human social behavior have been observed for positive parental and marital behaviors and reciprocity, I also expect it to increase ratings for Benevolence rather than Universalism activities. I am only hypothesizing positive relationships between the hormones and activity ratings as there is little evidence to suggest that either hormone will have negative effects on behaviors associated with any core value.

1.15.2 BOLD response with respect to the activity response variables. The two response variables may differ with regard to the mental processes recruited for each type of evaluation. Judgments of participation likelihood are expected to be a more pure preference evaluation. Thus, the expected activation in the frontal lobe is expected to be mainly confined to the OFC and pregenual ACC (Harbaugh, Mayr, Burghart, 2007; Hare, Camerer, Knoepfle, O'Doherty, Rangel, 2010; Moll, et al., 2006; Smith, et al., 2010). However, judgments of worthiness probe the degree of personal identification with the intentions expressed by activities. This is expected to elicit MPFC activity that is nearby but more dorsally located than activity elicited by the participation likelihood ratings (D'Argembeau, et. al., 2007; D'Argembeau, et. al., 2012; Johnson, et al., 2006).

1.15.3 Neural correlates of activity ratings by value type. Universalism and Benevolence are concerned with the degree of attention devoted to the well-being of others (Schwartz, 1992). I expect this empathic concern to be supported by greater TPJ activation for endorsements of prosocial activities, but not self-interested activities, for both worthiness and participation likelihood ratings. The MPFC is involved in both self-relevance processing and the

ability to take the perspective of others. Thus, greater activity may be observed in this region for higher worthiness responses. I hypothesize that stimuli related to self-interested values are more purely supported by reward processing and will thus elicit activity of a comparatively greater magnitude in the OFC for highly rated self-interested activities than for highly rated prosocial activities, but only for ratings of participation likelihood. The participation likelihood response better captures hedonic preferences that self-interest values represent conceptually and the OFC is thought to represent in the brain. Additionally, the strategic thinking that the self-interested values emphasize may be reflected in DLPFC activity, which is related to planning and has been observed in response to success in competitive tasks.

1.15.4 Effects of hormones on neural correlates of activity ratings for specific values. The worthiness response is intended to better capture the personal relevance of each activity than the participation likelihood response. Given the relationship between values and self-concept, modulation of value-related brain activity by hormones may be more likely to occur in areas that process self-relevance. The MPFC is involved in both self-relevance processing and the ability to take the perspective of others. This functional convergence seems to suggest that this area is likely to be affected by OXY or VAS if either hormone is observed to affect worthiness responses for prosocial activities.

1.15.5 Neural correlates of facial judgments. Activity in the amygdala, nucleus accumbens and OFC extending into the pregenual anterior cingulate cortex is expected to be positively related to judgments of facial trustworthiness. Activity in the superior temporal gyrus and insula are expected to be positively related to judgments of facial dominance. I expect

activity in the OFC to positively track with ratings of both participation likelihood for the activities and facial trustworthiness judgments.

1.15.6 Effects of hormones on facial judgments and related neural activity. A positive relationship is expected between treatment with OT, trustworthiness ratings, and activation in each of the brain areas expected to correlate with ratings of trustworthiness. Treatment with VAS is expected to positively relate to dominance ratings and insula activation.

CHAPTER 2

METHODS

2.1 Recruitment

Twenty male participants were recruited from the University of Dallas student population using flyers and the university's sona systems online recruitment software package. Females were excluded to avoid the potentially confounding interaction between hormone administration and menstrual cycle and to avoid any complications that could occur should a female be unaware of pregnancy. Those interested in participating first completed online medical history questionnaires to screen for cardiovascular and renal diseases and mental disorders, including major depression. Participants were also excluded for recreational drug use including smoking tobacco. Basic demographics questions regarding age and ethnicity were recorded for those determined as eligible for the study.

2.2 Design of Activity Appraisal Task

The stimuli consisted of single sentence descriptions of activities designed to reflect specific value concepts modeled by the BHVT. Behavioral responses were captured via two ratings recorded during two separate presentations (i.e. trials) of each stimulus: "how worthwhile do you believe this activity is?" and "how likely are you to participate in this activity?" The worthiness rating solicited the personal importance of the concepts presented in the activity. Participants were instructed to consider an activity's worthiness based on whether the activity implies an intention that they feel is worthwhile regardless of the participant's capability or willingness to perform it. A person's willingness to perform the activity, as captured by the

participation likelihood rating, was assessed as a proxy of the hedonic value anticipated for each activity, regardless of whether the person considers himself or herself to have the talent or skills necessary to perform the activity. Additionally, participants were instructed not to consider their current schedule, commitments, or stage of life as barriers for rating whether they were willing to participate. Each rating was recorded via mouse using a user-generated visual analog scale package in e-prime downloaded from http://pfcgroot.nl/e-prime.html. This package generates a cursor that allows only horizontal movement within the bounds of the graphical representation of a scale that is created by the user. In this case, participants could select any point along a range of not worthwhile/not likely to highly worthwhile/highly likely by clicking the left mouse button. Ratings were recorded as integers ranging from one to 100. This slider measurement was intended to control for the brain activity that may have been elicited by use of other devices, such as buttons, that might require participants to think about which finger corresponds to a given response.

2.2.1 Design of activity stimuli. Activity stimuli have been used previously in values research (Bardi, and Schwartz, 2003; Knafo et al., 2008). However, for viability in fMRI research, more specific context is necessary than has been provided by stimuli used in prior studies to constrain what participants may imagine during scanning and decrease variability in the BOLD signal that is unrelated to the factors of interest. Stimuli corresponding to the value of Universalism were inspired by listings on volunteer opportunity websites and the stimuli representing the other three values were created following this format. All stimuli were developed to concisely convey the activity to be performed (e.g. helping build a home) and the personal goal, individual(s) or type of cause benefitted by performing the activity (e.g. providing

shelter for the needy). Where applicable, some detail is provided on the setting where the activity is to be performed; however, in some cases it was only specified that the activity would take place locally. The relevant concerns for each value are captured by the stimuli (see Figure 2 for examples). The Universalism stimuli described activities that help unfamiliar others, often those disadvantaged in some way, regardless of class or group affiliation. Benevolence activities primary consisted of social favors to friends, neighbors, and non-immediate relatives. Achievement activities described the pursuit of personal skills or vocational expertise as a means of gaining responsibility and success. Power activities demonstrated a desire for prestige, control, money, and position without regard for the pursuit of personal merit that defines Achievement. Rather, the gains sought by those who value Power are often obtained at the expense of others. Stimuli development was aided by preliminary data gained by creating a Qualtrics survey that was presented to users of Amazon's Mechanical Turk labor outsourcing service. The survey had participants match many different potential activity stimuli with one of ten representative items from the PVQ, one for each value. This has allowed me to calibrate development of the stimuli toward themes that meet both the theoretical definitions of each value and what a consensus of the target young adult demographic perceived to represent each value.

Self-Transcendence Values		Self-Enhancement Values	
Universalism	Benevolence	Achievement	Power
Volunteer to travel with and help an organization that builds homes for needy families in developing countries.	Volunteer a few hours every week talking and reading to a terminally ill neighbor at a local hospital.	Spend a few hours doing practice problems for a graduate or professional school admissions exam.	Insist that rookies carry sports equipment for you and the other experienced players on your team.

Figure 2. Examples of activity stimuli representing BHVT concepts. Activities for the higher order categories of self-transcendence and self-enhancement are further divided into the four values Universalism, Benevolence, Achievement, and Power.

2.2.2 Stimuli inclusion preliminary studies. Preliminary testing was conducted for each activity stimulus to determine its viability. Samples of male students were recruited using either the sona-systems online recruiting system at the University of Texas at Dallas or by recruiting male, U.S. citizens via Amazon's Mechanical Turk labor outsourcing service. These participants were assessed for values priorities using the PVQ before rating the stimuli for worthiness and participation likelihood using the same six-point scale that was used during the experiment. Based on the results, stimuli were deemed worthy of inclusion into the experiment based on three criteria. First, the responses for the worthiness and/or participation likelihood ratings for each stimulus had to correlate with the composite rating for a BHVT value at least at a $P < .1$ significance level. Second, the stimulus description was required to conceptually align with the correlated value theoretically. A behavior may be impacted by more than one value (Bardi & Schwartz, 2003). Thus, a third criterion specified that each included stimulus have a higher correlation with the conceptually congruent target value than any of the other 3 BHVT values included in the study. Less than five stimuli were included for which a higher correlation was found for a value not included in the study. Thus, this last criterion was to prevent including stimuli that were not primarily influenced by the single intended value. Thirty-six stimuli were created per value for a total of 144 (see section 2.6 for how final activity stimuli were vetted). The activities may be further collapsed into seventy-two stimuli for each of the categories of self-transcendence and self-enhancement to allow for additional, higher-order comparisons.

2.3 Facial Judgment Task Stimuli

One hundred and forty-four face images were gathered from black and white photos taken of young adults. Additional images from the Karolinska Directed Emotional Faces database were also used after being converted to black and white (Lundqvist, Flykt, & Ohman, 1998). All individuals photographed were of Caucasian ethnicity but split evenly across male and female sexes. All photos featured forward facing individuals photographed from the neck up while they displayed a neutral facial expression.

2.4 Preliminary Baseline Assessment and Screening

Following the medical screening, eligible participants were also screened for those who are outliers on the Portrait Values Questionnaire (PVQ), a forty-item measure of value priorities based on the BHVT. The PVQ assesses a person's prioritization of each value via a composite score derived from responses on each item associated with that value. Those with very high priorities will be excluded to control for potential ceiling effects for participants who self-report as being so prosocial that their preferences have no room to be further increased by hormone treatment. Additionally, the oxytocin receptor allele rs53576A is associated both with a resistance to the effects of oxytocin and with lower prosocial behavior (Bakermans-Kranenburg, & van IJzendoorn, 2008; Marsh, et al., 2012; Rodrigues, Saslow, Garcia, John & Keltner, 2009). Excluding those who are assessed as being particularly low in prioritization of prosocial values may have helped prevent those with this problematic genotype from participating in the study.

2.5 Experimental Protocols Prior to fMRI Scanning

On the day of each experimental session, participants were brought into a computer lab where they were first screened for any changes in condition for which the exclusion criteria might apply. If they remained eligible, they proceeded to complete the consent form and receive

instructions before receiving the nasal spray. Participants were given one nasal atomizer for self-administration of a hormone or the placebo as chosen at random in a procedure double-blinded to both recipient and the experimenter.

Cerebrospinal fluid concentrations of VAS have been shown to increase 10 minutes after intranasal dosing, peak at 80 minutes, and remain above baseline up to, and likely beyond, 120 minutes, which is the latest time point measured in humans (Born et al., 2002). Due to the similarity of VAS and OXY molecules, researchers using either of these hormones have referred to this result to plan the scheduling of experimental tasks to best measure the effects of hormones on behavior and brain activity. However, more recently, some discrepancies have emerged between different methods of measuring the time-course of OXY absorption. Striepens et al., (2013) showed that cerebrospinal fluid concentrations of OXY do not increase until approximately 75 minutes after administration. To accommodate this period of peak efficacy, I began the first experimental task approximately forty-five minutes after hormone delivery. During the intervening wait time between dosage and tasks in the first session, participants received task instructions and were show examples of trials from both the face judgment and activity judgment tasks on a computer outside of the scanner.

2.6 Task Trial Structure for fMRI Scanning

Both the facial judgment task and activity evaluation task were presented in blocks designed to be as similar in structure as possible.

2.6.1 Activity task structure. The task was presented in eight blocks with each trial consisting of two phases: the presentation of one stimulus followed by a stimulus rating period. In each block, participants responded to only one of the two dependent variable ratings

respective to each task (see Figure 3). Each activity description viewed during a single experimental session was presented twice to obtain a response for it on both dependent variables. The block presentation order was pseudo-randomized to prevent both presentations of any specific activity stimulus from occurring near in time.

A prompt was included at the beginning of each block to make the participant aware of which rating response was required for that block of trials. These prompts consisted of a single

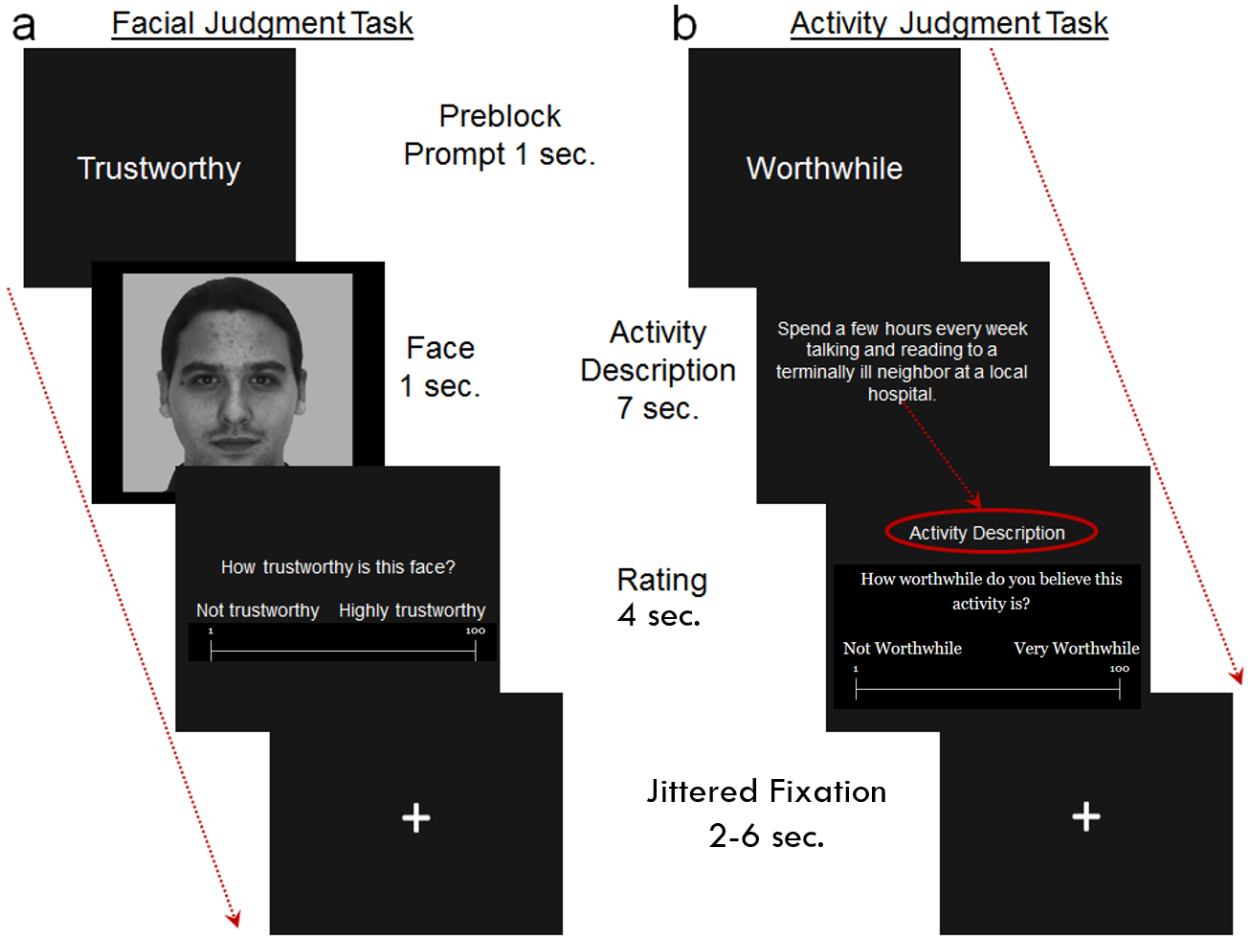


Figure 3. Design of facial and activity judgment tasks. In both tasks a preblock prompt preceded trial presentation for each block. Each trial began with display of the stimulus, proceed to the response phase, and ended with a jittered fixation cross. Not shown is a fixation cross that appeared between each block for 12 seconds. (a) Block sequence for the facial judgment task. (b) Block sequence for the activity judgment task. Note that in this task the activity description remained onscreen during the response phase.

word, “worthwhile” or “participate,” which appeared onscreen for one second. The activity stimulus was displayed for seven seconds to allow adequate time to read and consider the stimulus and the subsequent response phase lasted for two seconds. A fixation cross appeared between the trials of each task for a 2-6 second period. This variable period was included to provide the participant time to prepare for the next trial and for the removal of the periodic effects of the hemodynamic response from the data during analysis (Huettel, Song & McCarthy, 2009, p. 318-319). A 10-14 second period displaying a fixation cross separated each block to allow the hemodynamic response to return to its baseline.

2.6.2 Facial judgment task structure. The block sequence for facial judgments was identical to that of the activity task. The only difference in time structure between the two tasks was the length of the stimulus presentation phase. Faces were displayed for one second. A pre-block was also included for this task and consisted of the words “trustworthy” and “dominant.”

2.7 Hormone Dosage and Formulation

Born et al. (2002) studied the concentration of intranasal administration of VAS in cerebrospinal fluid using a spinal tap. They found that this method of delivery significantly increased concentrations of VAS after a short build up time at both the investigated doses of 80 and 40 IU. While there have been fMRI studies showing significant results on behavior and changes in BOLD signal using 20 IU of VAS (Rilling, et al., 2012; Feng, et al., 2015; Brunnlieb, et al., 2013), I used the more common doses of 40 IU for VAS and 24 IU for OXY. Formulations of each of the three solutions were made to ensure equivalency of all perceivable properties (e.g. solution taste, smell, etc.) and of the amount inhaled for all treatment conditions.

2.8 Double Blinding Procedures

A staff member at the pharmacy was instructed to assign each participant to a pseudo-randomized order of the oxytocin, vasopressin and placebo treatment and maintain records regarding which session each participant received the given treatments. Each nasal spray atomizer was labeled with the participant number and a letter (A, B and C) designating the treatment condition. Each atomizer was picked up by a research assistant on the day in which it was to be administered to a participant. This assistant recorded the letter assigned to the treatment condition on the nasal spray label and then covered this with a new label. This was done to prevent me from having the opportunity to generate hypotheses regarding the meaning of conditions A, B or C that might influence the way I gave task instructions. The data pertaining to the effects of the hormones were not analyzed or interpreted until all subjects had been run.

2.9 Medical Safety measures

Vital readings for blood pressure and pulse were recorded at three time points: prior to receiving the hormones, immediately prior to entering the scanner, and after exiting the scanner. Additionally, participants wore an MRI-safe pulse oximeter on their finger to monitor changes in heart rate during scanning. All experimental procedures occurred in a hospital setting with physicians available in case of an adverse reaction to the hormones nasal sprays. No participant reported or appeared to experience adverse drug effects.

2.10 MRI Acquisition

Scanning was performed in a 3.0 tesla Phillips Achieva scanner using a 32-channel phased array head coil. Structural images consisting of 160 sagittal slices were acquired using

T1-weighted MPRAGE sequence with the following parameters: repetition time = 8.2 ms, echo time = 3.8 ms, flip angle = 12°, field of view = 256 x 204 x 160 and voxel size = 1 x 1 x 1mm. Slice thickness was 4mm with no gap. T2*-weighted echo planar images (EPI) sensitive to BOLD contrasts were acquired with a single-shot gradient echo- EPI sequence optimized to allow for full ventral coverage including the orbitofrontal cortex (OFC); repetition time = 2s, echo time = 25 ms, flip angle = 60°, field of view = 220 x 220 x 150 and voxel size = 3.4 x 3.4 x 4 mm. Thirty-eight, 4mm axial slices were obtained in an interleaved manner with no gap, providing whole-brain coverage. Five dummy volumes were acquired prior to running any sequence to allow scanner signal to reach equilibrium.

2.11 Image Preprocessing

All image preprocessing steps were performed using SPM12 (Wellcome Department of Imaging Neuroscience, London, UK). The point of origin of the raw structural image for each scanning session was set to the anterior commissure. The point of origin for one functional scan from each run was set to the anterior commissure and this change was applied to all other functional scans for that run. All images were oriented to conform to standard viewing convention. Functional images were realigned to the first volume via a six parameter, rigid body transformation. They were corrected for spikes in signal using ArtRepair, a quality control toolbox for SPM (http://cibsr.stanford.edu). I applied toolbox functions that use realigned images and the six rigid-body realignment parameters to replace outlier volumes containing scanner signal spikes or spikes from motion in excess of 3mm with the linear interpolation of values from the two nearest non-outlier volumes. Images were then resliced to the first volume using a fourth-degree spline interpolation, slice-time corrected, coregistered to the T1 image, normalized

into standard MNI space (Montreal Neurological Institute), and resampled to a final 3 x 3 x 3 mm voxel size. Spatial smoothing was performed using an 8 mm full-width at half-maximum (FWHM) Gaussian kernel.

2.12 Behavioral Statistics

The results for mean ratings in each condition were assessed with analyses of variance (ANOVA) using r software. I performed a one-way, repeated measures ANOVA for each of the trustworthiness and dominance responses of the facial judgment task by the three treatment conditions, OT, VAS and the placebo. In the event of a revealed main effect of treatment, Bonferroni corrected pairwise t-tests were run to better determine the relationship between the means of specific treatment conditions. For the activity appraisal task, I ran a 3 x 4 ANOVA for each of the worthwhile and participation likelihood judgments to compare the influence the three treatments had on the ratings of each BHVT value: Universalism, Benevolence, Achievement and Power. Each 3 x 4 ANOVA yielding a significant main effect of treatment or a treatment by value interaction was followed up by one-way ANOVAs to find which values were affected by the treatment. Bonferroni corrected pairwise t-tests were then run for those values conditions to better understand which treatments impacted the mean ratings. I additionally performed a Bonferroni corrected pairwise t-test between the two face judgments and another on the two activities judgments for information indicating that participants were considering each set of judgments separately and not simply responding to all faces or all activities similarly regardless of instructions. A separate 2 x 3 x 2 ANOVA was run on the responses for the two response types and the three treatment conditions with respect to the two higher-order values dimensions of self-transcendence and self-enhancement.

2.13 fMRI Image Analysis

All comparisons of BOLD responses related to the facial judgment and core values tasks were performed in random-effects, epoch-related analyses performed in two stages. First, I estimated general linear models for each participant for each session. Contrasts of the various factors were created in a voxel-wise manner using a general linear model that convolves task designs with the canonical hemodynamic response function in SPM12. Although these estimates were analyzed in an epoch-related manner, durations and onsets for each stimulus were entered individually, trial-by-trial, to allow for each participant's ratings on the visual analog scale to be entered as first-order, subject-level parametric modulators. Covariates entered at this level were age, years of education. A temporal high-pass filter of 128 s was included to remove low-frequency signal drifts and a first-order autocorrelation model was used to account for serial autocorrelations.

At the second level, separate models were created for the facial judgments and judgments of core values tasks to assess how brain activity related to each were affected by OXY and VAS . Contrast maps from each model was then entered into SPM12's flexible factorial design. Here, three factors were specified: subject, session, and all conditions related to treatment, rating type, and BHVT value, which were collapsed into a third factor to allow more freedom in contrasting different combinations of interest. In each model, the experimental condition factor was entered as a non-independent measurement to correct for the fact that – due to repetition – the error term of this factor is not spherical, which is an assumption made in SPM models. Flexible factorial models were also run for contrast maps corresponding to only the parametric modulator

regressors for the purpose of isolating what brain regions might track, respectively, any linear or quadratic trends related to ratings. Whole brain inferences for both task were made by comparing specific contrast maps created at this level at a voxel-wise threshold of $P < .001$, uncorrected and cluster corrected at $P < .05$ family-wise error rate (FWE). All image results were visualized using the xjView toolbox (http://www.alivelearn.net/xjview).

2.13.1 Region of interest analyses of mean BOLD percent signal change. To better determine and visualize the relative influence of the three treatment conditions on BOLD activity, I assessed the mean percent signal change in several *a priori* regions of interest (ROI) either previously related to hormone function or to relevant studies of social cognition for which hormones have not yet demonstrated effects. The following ROIs were anatomically defined using the Automatic Anatomical Labelling Atlas (aal) in the WFU PickAtlas software for analysis of the activities task (Maldjian, Laurienti, Kraft, Burdette, 2003): the amygdala, insula, inferior OFC, medial OFC, superior OFC, superior MPFC, middle temporal pole, and superior temporal pole. Individual ROIs were used for the left and right hemisphere of each region. The aal ROI for the ACC was also used but was extended to include the pregenual and subgenual areas. Other ROIs included the bilateral nucleus accumbens (Nielsen & Hansen, 2002), and a twelve-millimeter radius spheroid ROI of the left and right TPJ regions that I created manually using the marsbar toolbox for spm with the center coordinates obtained from the TPJ locates found in a relevant meta-analysis of moral, theory of mind and empathy processes (Brett, Anton, Valabregue, & Poline, 2002; Bzdok, et al., 2012). Many of the same ROIs were applied to the facial judgment data, except for the TPJ and the superior MPFC. Instead, aal definitions for the FFA and the superior temporal cortex were included for each hemisphere. BOLD PSC values

were obtained using marsbar and analyzed using r software to perform a series of ANOVAs and Bonferroni corrected pairwise t-tests. The comparisons made were identical to those in the whole-brain analyses for each task. This analysis was included for the additional purpose of capturing effects in smaller regions such as the amygdala and nucleus accumbens in which potentially meaningful clusters of BOLD might be too small to survive the strict cluster correction threshold.

CHAPTER 3

RESULTS

3.1 Behavioral Results for Activities and Facial Judgment Task Responses

Responses from both the activities and facial judgment task were analyzed via separate repeated measures ANOVAs.

3.1.1 Activities task results. Responses on the activities task differed between the two types of ratings, $F(1, 19) = 23.55$, $p = .001$, $\eta_G^2 = .026$, with the mean worthwhile ratings ($M = 62.79$, $SD = 17.38$) being greater than the mean participation ratings ($M = 58.33$, $SD = 17.52$). I then entered the willingness to participate and worthiness ratings into separate ANOVAs to explore the potential effects of the treatment conditions on each response and to determine if potential values by treatment interactions warranted further ANOVAs at the core value level to better understand how the treatments may affect ratings pertaining to specific values. No effect of treatment or value by treatment interaction was shown for participation responses. No effect of treatment was seen for worthwhile responses, however, a value by treatment interaction was observed warranting further ANOVAs on worthiness responses for each core value, $F(6, 114) = 2.22$, $p = .046$, $\eta_G^2 = 0.014$. The subsequent one-way ANOVAs run on worthwhile ratings for each core value revealed an effect of treatment for only the Universalism value [$F(2, 38) = 4.53$, $p = .017$, $\eta_G^2 = 0.043$] with VAS increasing worthwhile responses ($M = 68.00$, $SD = 13.46$) over ratings in the placebo condition ($M = 61.55$, $SD = 14.15$), $p = .013$ (Figure 4).

3.1.2 Facial judgment task results. In the face task, participants rated faces as generally more dominant ($M = 51.97$, $SD = 6.63$) than trustworthy ($M = 47.18$, $SD = 7.71$) but this difference was not significant, $F(1, 19) = 3.67$, $p = .071$. However, this ANOVA did reveal a

rating type by treatment interaction, $F(2, 38) = 3.72, p = .033, \eta_G^2 = .020$. Separate ANOVAs were then run on mean ratings of trustworthiness and dominance and found that OXT increased ratings of dominance ($M = 53.78, SD = 6.71$) over placebo ($M = 50.39, SD = 5.16$), $p = .031$.

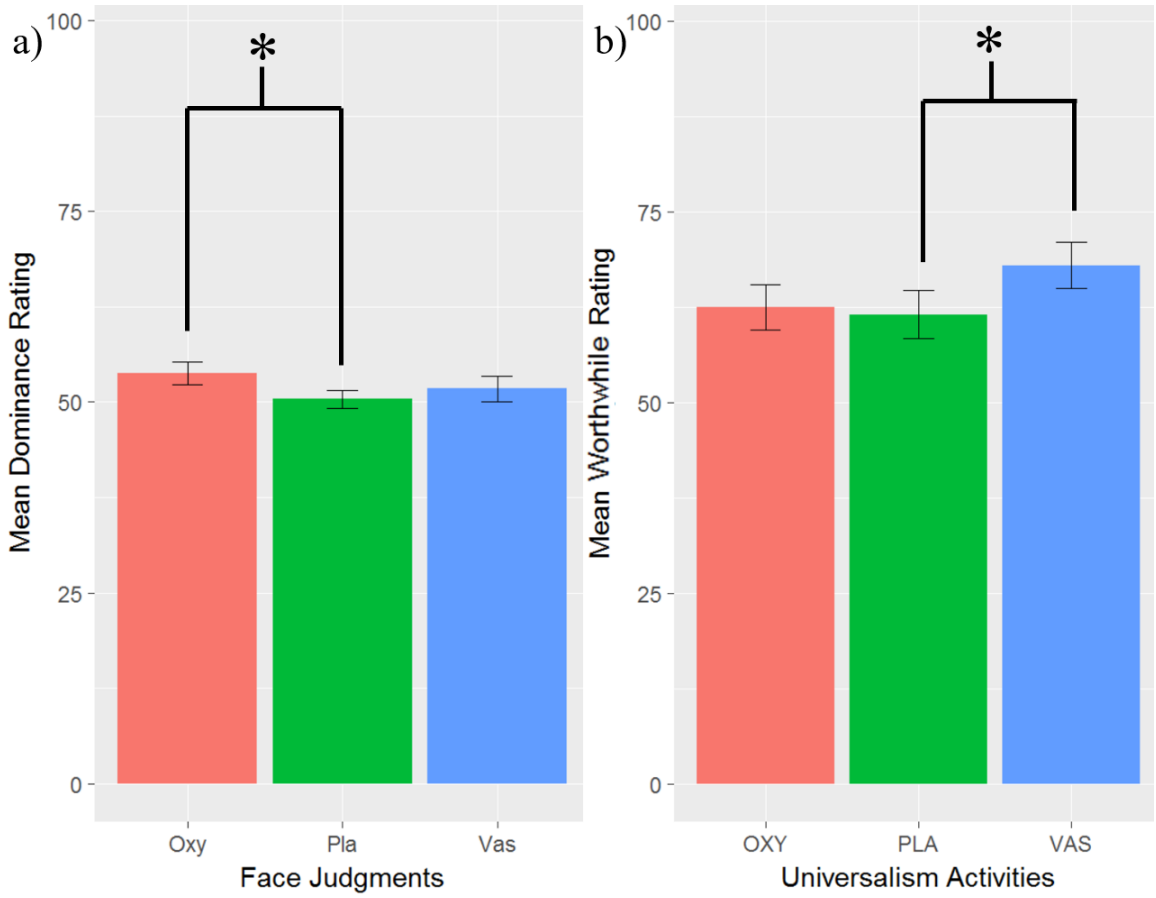


Figure 4. Significant effects of treatment conditions in separate ANOVAs on mean responses for a) perceptions of dominance in faces and b) willingness to participate in Universalism activities. Error bars: SEM. OXY = oxytocin, PLA = placebo, VAS = vasopressin. * < .05.

3.2 Whole-Brain BOLD Analyses of Stimulus Factors for the Activities Task

Whole-brain analyses revealed significant clusters of activation at the chosen statistical thresholds of $P = .001$ for the voxel level and $P = .05$ FWE cluster correction. Several contrasts were performed on trials acquired only during the placebo condition to examine potential relationships between brain regions and the two ratings in the activities task as well as the

different core values proposed by the BHVT. First, comparisons of BOLD related to the two task response rating types, "participation" and "worthwhile" revealed a single cluster of activation for participation trials over worthwhile trials. This cluster was located at the right middle temporal gyrus (BA 22/39) at the TPJ.

No contrast between specific BHVT core values survived cluster correction when only trials featuring worthwhile ratings were included. Thus, all reported results from placebo condition comparisons in Table 1 feature activation from trials rated for willingness to participate. When the core values were collapsed to make the higher-order comparison of prosocial minus self-interested activities, a cluster was revealed in the bilateral MPFC (BA 10) that included the ACC on the right and stretched more dorsally on the left (BA 9). No significant results were seen in the reverse contrast.

Interestingly, each contrast of specific BHVT values that yielded a significant result involved the Achievement value being subtracted from one of the other three values. In each of these, the left TPJ was prominent, particularly the angular gyrus, and often extended to the posterior superior and/or middle temporal gyri. Only in the Universalism minus Achievement contrast did this cluster fall short by one or two voxels of the strict cluster correction. Beyond the left TPJ cluster, each of these contrasts revealed a second cluster specific to whichever core value was being compared to Achievement. When Universalism was compared to Achievement, the anterior portions of inferior, middle and superior temporal gyri (BA 21/38) were observed. For Benevolence, the same MPFC cluster seen for the prosocial minus self-interested contrast was seen, this time enlarged with bilateral inclusion of the ACC and dorsal MPFC. Furthermore, contrasting it against all other core values revealed this MPFC activity to be selective for

benevolence. Lastly, the left pars triangularis and opercularis of the inferior frontal cortex (BA 44/45) was shown when contrasting Power against Achievement.

Table 1. Whole-Brain Contrasts of Placebo Conditions Showing Meaningful Differences in Activities Task Factors.

Hemi	**Regions (Brodmann Areas)**	**T-stat**	**X**	**Y**	**Z**
Participation Trials > Worthwhile Trials					
R	Middle Temporal Gyrus (BA 39)	4.71	48	-61	18
R	Middle Temporal Gyrus (BA 22)	3.75	54	-49	10
Participation Trials: Prosocial > Self-Interested					
L R	Medial PFC (BA 10)	4.16 3.52	-12 9	56 50	18 18
Participation Trials: Power > Achievement					
L	IFG Triangularis/Opercularis	4.28	-45	17	18
L	IFG Triangularis	3.57	-48	23	30
L	Angular Gyrus (BA 39)	4.21	-39	-58	22
Participation Trials: Universalism > Achievement					
L	Inferior Temporal Gyrus (BA 21)	4.75	-45	2	-38
L	Middle Temporal Gyrus (BA 21)	3.71	-51	2	-22
L	Middle Temporal Gyrus (BA 22)	3.99	-36	-58	18
L	Angular Gyrus (BA 39)*	3.55	-39	-58	30
Participation Trials: Benevolence > Achievement					
L R	Medial PFC (BA 10)	4.67 3.95	-12 9	53 50	22 18
L	Medial PFC (BA 9)	3.97	-6	53	34
L	Angular Gyrus (BA 39)	3.93	-36	-59	23
Participation Trials: Benevolence > All Others					
L	Dorsomedial Prefrontal Cortex (9/10)	4.55	-12	50	18
R	Anterior Cingulate Gyrus (32)	3.55	9	50	18

Note: The names of the included contrasts are in italics. All areas reported, unless otherwise noted, were thresholded at $p<.001$, uncorrected, at the voxel level and $p<.05$ FWE cluster correction.

* Areas reported that fall 1-2 voxels below FWE cluster threshold.

3.3 Whole-Brain BOLD Comparisons of Treatment Effects for the Activities Task

In general, when compared with the placebo condition, oxytocin and vasopressin were seen to influence BOLD signal more widely across cortical networks than has been previously reported in the literature (Zink & Meyer-Lindenberg, 2012). In every core values-related

contrast producing a significant result, their influence was revealed as clusters representing only either enhanced or diminished BOLD signal, depending on the given contrast. These clusters were typically observed in functional networks of cortical and subcortical regions related to motor intention, and some unusually large clusters were seen in cortical networks related to social cognition.

When examining all prosocial trials rated for willingness to participate, two clusters of brain regions had increased BOLD signal for placebo rather than VAS conditions (see Table 2). One cluster consisted of bilateral cerebellar areas and the right fusiform face area, while the other cluster included the bilateral MCC (BA 24/31), supplemental motor area (BA 6), precentral and postcentral lobules and extended to the left parietal operculum, posterior insula and supramarginal gyrus. Two clusters of brain regions also had increased BOLD signal for placebo rather than OXY conditions during prosocial trials rated on participation. One was comprised of bilateral supplemental motor area, paracentral lobule and across the marginal sulcus into the midcingulate cortex. A second cluster in the left hemisphere extended from the posterior insula and parietal operculum laterally to the anterior temporal lobe and ran back to the posterior superior temporal gyrus. In contrast to the results for prosocial trials, OXY increased BOLD compared to the placebo condition in two clusters during trials featuring self-interested activities rated on participation. One cluster consisted of the left postcentral lobule, parietal operculum and the supramarginal gyrus up to the superior temporal sulcus, while the other cluster included the bilateral PCC, precuneus and the left lingual gyrus (BA 19/30).

Table 2. Whole-Brain Comparisons of Treatment Effects Related to Higher-Order BHVT Axes.

Hemi	Regions (Brodmann Areas)	T-stat	X	Y	Z
Prosocial Activities Rated on Participation: Placebo > Vasopressin					
L	Midcingulate Gyrus (BA 24)	4.63	-6	-19	46
L	Parietal Operculum (BA 13)	4.39	-24	-25	50
L	Precentral Gyrus (BA 4)	4.33	-36	-28	62
L	Insula/Parietal Operculum	4.23	-36	-31	22
L	Postcentral Gyrus (BA 3/4)	4.21	-33	-28	50
L	SupraMarginal Gyrus (BA 40)	3.49	-48	-31	26
L/R	Cerebellum Vermis	4.26	0	-58	-22
R	Cerebellum	4.24	12	-55	-10
R	Fusiform Gyrus BA (36)	3.74	24	-37	-18
Prosocial Activities Rated on Participation: Placebo > Oxytocin					
R	Posterior Insula	4.95	45	-4	-2
R	Superior Temporal Gyrus (BA 22)	3.75	60	-10	2
R	Superior Temporal Gyrus (BA 42)	3.63	66	-31	6
R	Midcingulate Cortex (BA 31)	3.43	3	-13	50
L	Paracentral Lobule (Marginal Sulcus)	3.91	-9	-34	50
L	Supplemental Motor Area (BA 31)	3.50	-3	-22	50
Self-Interested Activities Rated on Participation: Placebo > Oxytocin					
L	SupraMarginal Gyrus (BA 40)	4.32	-48	-28	22
L	Parietal Operculum (BA 13)	4.14	-36	-37	18
L	Postcentral Gyrus (BA 2)	4.11	-39	-28	46
L	Postcentral Gyrus (BA 3)	3.97	-45	-22	50
L/R	Posterior Cingulate (BA 23/31)	3.98	0	-49	26
L/R	Precuneus (BA 30)	3.79	0	-52	14
L	Lingual Gyrus	3.63	-6	-52	2
R	Calcarine Sulcus	3.55	12	-61	14

Note: The names of the included contrasts are in italics. All areas reported, unless otherwise noted, were thresholded at $p<.001$, uncorrected, at the voxel level and $p<.05$ FWE cluster correction.

My further examination of the effects of the hormones on individual BHVT values revealed that their influence on BOLD during trials of only the two prosocial values involved vastly larger networks of regions than in contrasts involving the two self-interested values. No hormone affected BOLD during trials rated on worthiness but each hormone affected a different self-interested value during trials rated for willingness to participate. Oxytocin increased BOLD

signal during Achievement trials in two clusters. It increased precentral and postcentral lobule activity in a left hemisphere cluster and the other cluster had increased activity in the bilateral MCC that extended in the left hemisphere from the PCC across the calcarine sulcus to the lingual and angular gyri. Conversely, VAS was observed to decrease activity in the right caudate nucleus and inferior frontal cortex for Power activities.

An effect on BOLD activation was seen in the corresponding condition in which VAS increased behavioral ratings for Universalism activities during trials rated on worthiness. In this condition, compared to placebo, VAS decreased activity in a left hemisphere cluster including the MCC, the precentral and postcentral lobules (BA 3/4) and in two other clusters of subcortical regions including the left ventral posterior thalamic nucleus, medial and lateral globus pallidus, the right pulvinar thalamic nucleus and bilateral activation of the ventral lateral thalamus and caudate nuclei. While, the effect by VAS to increase perception of how worthwhile Universalism activities were, as captured by task responses, may be related to decreased BOLD activity in these areas, no regional BOLD differences were seen when the task responses were entered as a parametric modulator and the VAS versus placebo, or the reverse contrast, comparison was made on that regressor alone.

For Benevolence trials when compared to placebo, OXY and VAS had opposing effects on BOLD and differed by which rating was performed during the trials they affected (Table 3). OXY increased BOLD during participation ratings of Benevolence activities and VAS decreased BOLD during ratings of the worthiness of Benevolence activities. Both contrasts elicited a similar, widespread network of regions implicated in socio-moral cognition (Bzdok, et al., 2012). This network was comprised of clusters covering much of the rostral to caudal extent

Table 3. Whole-Brain Comparisons of Treatment Effects on Benevolence Activities.

Hemi	Regions (Brodmann Areas)	T-stat	X	Y	Z
Worthwhile Trials: Oxytocin > Placebo					
R	Parietal Operculum	5.56	-39	-37	22
L		4.35	42	-34	22
L	Anterior Insula	4.13	-27	20	-2
R		4.72	36	11	-6
R	Putamen	4.81	27	17	6
L		3.98	-33	-10	-2
R	Middle Temporal Gyrus (22/39)	3.92	54	-52	6
R	Globus Pallidus	3.68	21	-13	-2
L	Posterior Insula	4.17	-39	-25	-6
L	Hippocampus	3.89	-36	-7	-18
L	IFG Triangularis/Opercularis (45)	3.89	-42	20	14
L	Caudate	3.83	-18	17	6
L	Supramarginal Gyrus (BA 40)	3.79	-54	-46	26
L	Superior Temporal Gyrus (BA 41)	3.72	-45	-34	2
Participation Trials: Placebo > Vasopressin					
R	Cerebellum	4.58	9	-58	-22
R	Anterior Insula	4.50	39	8	-14
L		4.13	36	11	-6
R	Posterior Insula	4.32	39	-16	14
L		4.26	-36	-10	-6
R	Parietal Operculum	4.14	48	-13	10
L		3.77	-48	-4	14
R	Superior Temporal Gyrus	4.04	57	-46	14
R	Postcentral Gyrus (BA 4)	3.71	60	-4	26
R	Middle Temporal Gyrus (BA 39)	3.70	42	-64	18
R	SupraMarginal Gyrus (BA 40)	3.62	63	-37	30
R	IFG Triangularis (BA 45)	4.10	48	29	6
R	Inferior OFC (BA 47)	3.98	36	32	-6
L	Precentral/Postcentral (BA 3/4)	4.20	-39	-28	62

Note: The names of the included contrasts are in italics. All areas reported, unless otherwise noted, were thresholded at $p<.001$, uncorrected, at the voxel level and $p<.05$ FWE cluster correction.

of the brain (Figure 5). The primary difference between these patterns of activation was that OXY produced a bilateral increase of BOLD in basal ganglia nuclei while VAS increased signal

in the left precentral and postcentral lobules and bilaterally in the cerebellum. Additionally, more frontal lobe coverage was observed in the placebo minus VAS contrast, but BOLD

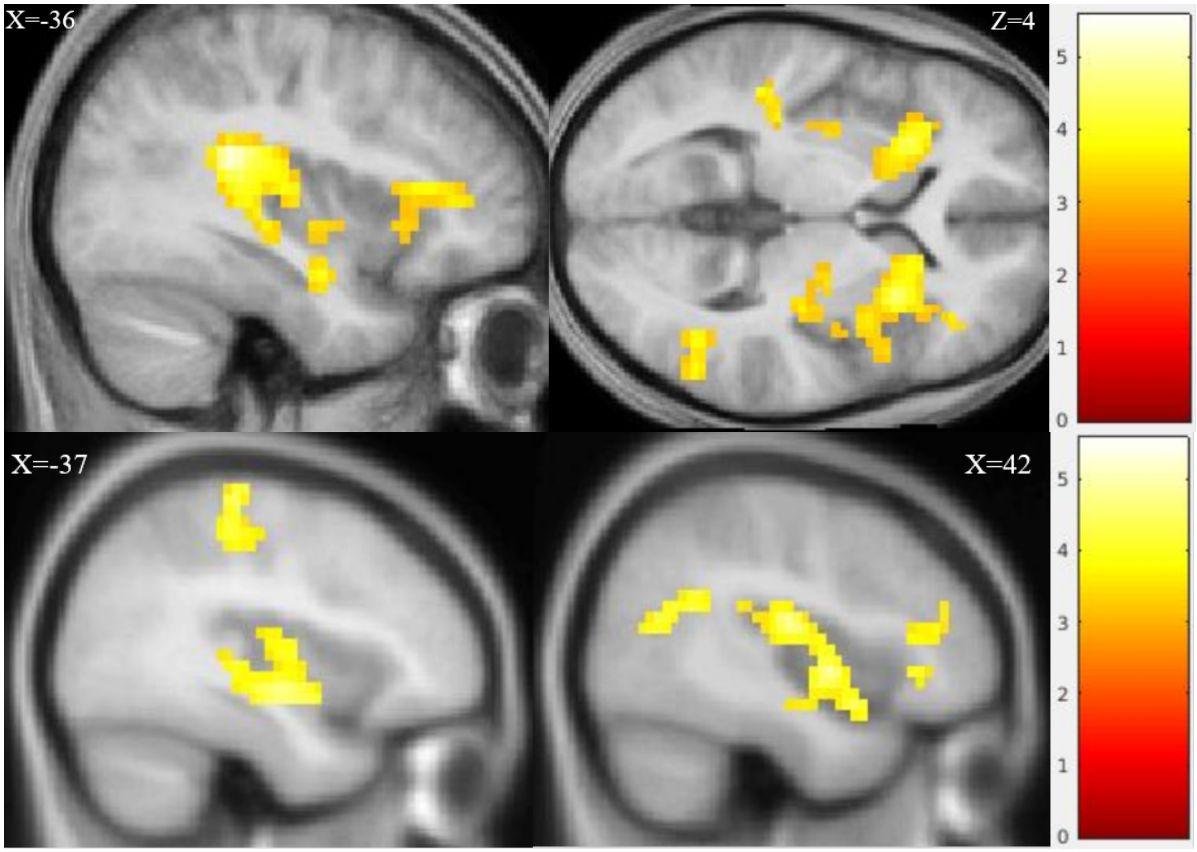


Figure 5. For Benevolence activities, similar BOLD patterns were observed for contrasts of a) OXY > placebo conditions during ratings of activity worthiness and b) placebo > VAS conditions during ratings of participation willingness. Whole-brain BOLD analysis with voxel thresholds of $P < .001$ uncorrected and family-wise error rate cluster correction of $P < .05$. BOLD activation is in MNI space and viewed overlying a mean T1 image of all participants.

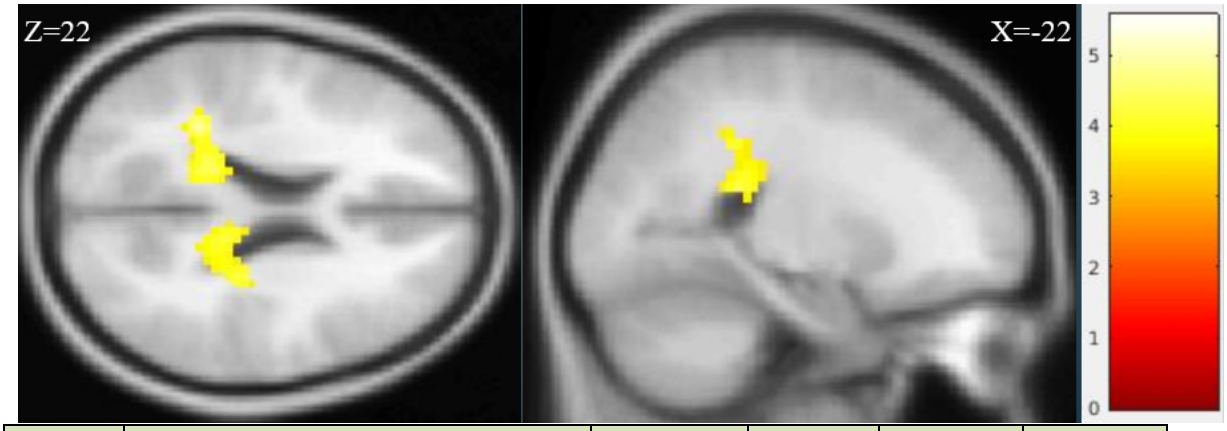
activation did not extend into TPJ areas of the left hemisphere. Although opposite effects were not seen for contrasts between OXY and VAS within trials of one type of response, they were seen when the two ratings were collapsed. When comparing all Benevolence trials OXY enhanced BOLD in the left insula and Brodmann's areas 44 and 45 with a peak in the inferior frontal gyrus (-33, 29, 10, $T = 4.63$, $P < .001$, uncorrected), though it should be noted that this cluster was two voxels shy of the FWE cluster correction ($P < .05$).

3.4 Regional BOLD Variations as a Function of Activities Task Responses

Finally, contrasts were made investigating brain regions in which BOLD may be parametrically modulated by the rating response regressor. When examining only data from the placebo conditions, no contrasts of this type revealed regional differences between the two rating types or the various core values. When the other treatment conditions were included, increased BOLD signal was seen for placebo compared to the oxytocin condition as a function of worthiness ratings of Universalism stimuli. This contrast produced clusters of activation similar to the large networks seen for Benevolence as produced by OXY over placebo during trials rated on worthiness and by placebo over VAS during trials rated on participation willingness. This contrast differed in that no subcortical regions were seen but the extent of the decrease by OXY on BOLD in the cortex was the greatest of all reported contrasts. Relative to BOLD contrasts for Benevolence, this contrast included additional coverage of the bilateral cerebellum and fusiform gyrus, the left middle temporal gyrus and the left middle occipital gyrus.

3.4 Whole-Brain BOLD Comparisons for the Facial Judgment Task

Compared to the amount of whole-brain contrasts yielding significant differences in BOLD magnitude in the activities task, surprisingly only one contrast from the facial judgment data produced BOLD activation that survived the statistical thresholds. Specifically, one activation cluster was observed as a function of increasing dominance ratings in the OXY condition compared to the placebo condition (Figure 6). This cluster included the bilateral MCC and extended into the inferior parietal lobe on the left and the PCC on the right.



Hemi	Region	T-stat	X	Y	Z
L	Inferior Parietal Lobule	4.46	-33	-43	26
L	Midcingulate Gyrus	4.04	-15	-34	26
R		3.91	9	-17	30

Figure 6. Regions of increased BOLD for oxytocin compared to placebo as a function of dominance ratings of facial stimuli. Whole-brain BOLD analysis with voxel thresholds of $P < .001$ uncorrected and family-wise error rate cluster correction of $P < .05$. BOLD activation is in MNI space and viewed overlying a mean T1 image of all participants.

3.5 Percent Signal Change in Regions of Interest for the Activities Task

To effectively examine the relationship between the effects of the three treatment conditions on BOLD activity, PSC was acquired for twenty *a priori* regions of interest (see section 2.13.1) and a series of ANOVAs was performed in like manner to those conducted for the behavioral responses. An overall task by treatment by value ANOVA for activities task revealed differences between ratings of participation or worthiness, with all other factors collapsed, in two ROIs: the right TPJ [$F(1, 19) = 8.11, p = .010, \eta_G^2 = .007$], and left VMPFC, $F(1, 19) = 4.60, p = .045, \eta_G^2 = .009$. BOLD signal was higher in the right TPJ during participation trials ($M = 0.16, SD = 0.31$) than during worthiness trials ($M = 0.11, SD = 0.31$), $p = 0.009$. Results were similar in the left VMPFC with participation trials eliciting higher BOLD signal ($M = 0.10, SD = 0.37$) than worthiness trials ($M = 0.03, SD = 0.37$), $p = 0.008$. An effect of treatment, with all other factors collapsed, was observed in another two ROIs: the nucleus

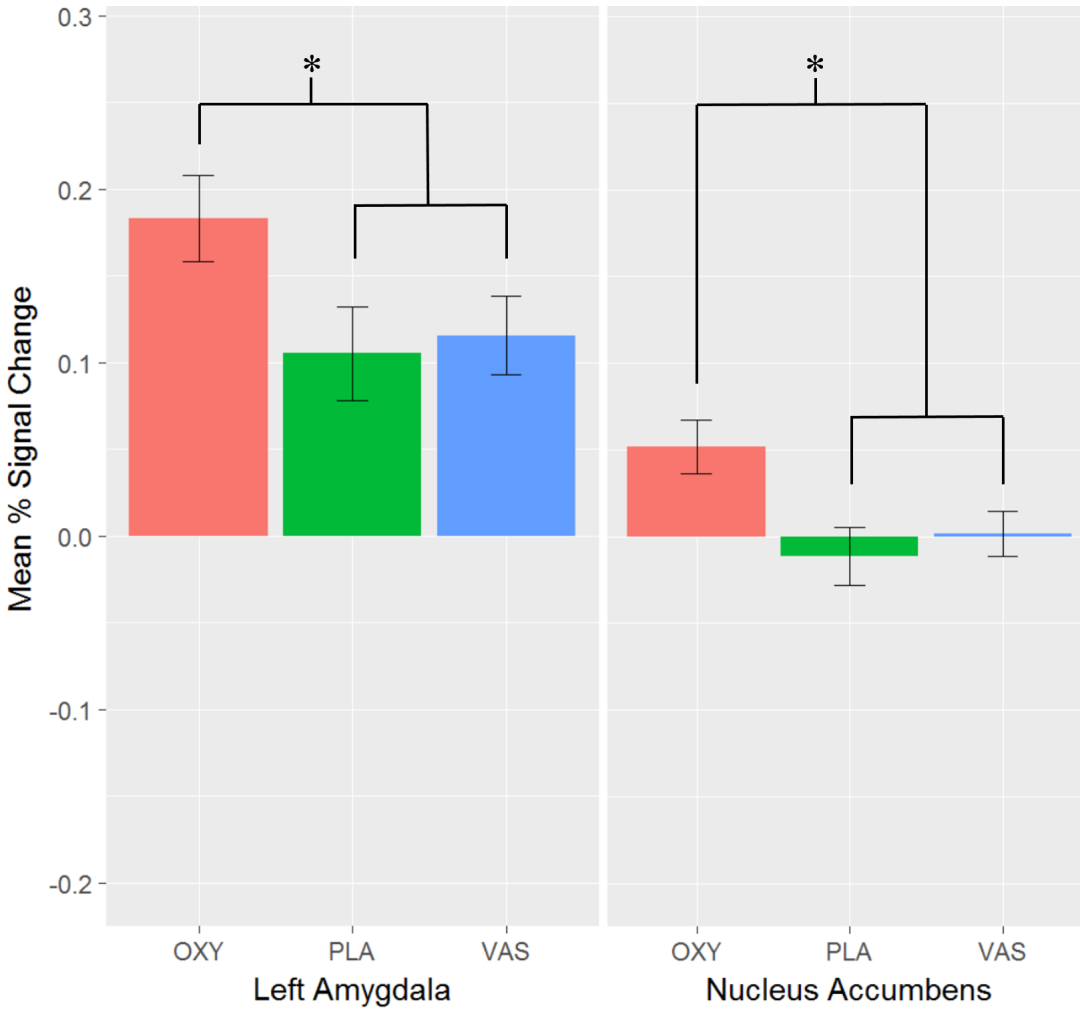


Figure 7. Activities task ANOVA results on BOLD mean percent signal change in selected brain regions for treatment conditions when collapsing across all other factors. Error bars: SEM. OXY = oxytocin, PLA = placebo, VAS = vasopressin.

accumbens [$F(2, 38) = 4.17, p = .023, \eta_G^2 = .020$], and the left amygdala, [$F(2, 38) = 3.86, p = .030, \eta_G^2 = .012$]. In the nucleus accumbens, BOLD signal was higher with OXY ($M = 0.05$, $SD = 0.20$) than VAS ($M = 0.00$, $SD = 0.17$), $p = 0.014$, increased BOLD over placebo ($M = -0.01$, $SD = 0.21$), $p = 0.004$. Likewise, OXY increased BOLD signal ($M = 0.18$, $SD = 0.32$) over placebo in the left amygdala ($M = 0.11$, $SD = 0.34$), $p = .018$, and over VAS ($M = 0.11$, $SD = 0.29$), $p = .026$ (Figure 7).

To further explore regions influenced by the treatment conditions or demonstrate interactions between certain treatments and values, ANOVAs were performed, respectively, for the participation trials and worthiness trials for each ROI. For participation trials, the nucleus accumbens was the only ROI showing an effect of treatment across all values, $F(2, 38) = 4.32$, $p = .020$, $\eta_G^2 = .023$. Here, OXY increased BOLD signal ($M = 0.05$, $SD = 0.17$) over placebo ($M = -0.02$, $SD = 0.21$), $p = 0.039$. The following ROIs had at least statistically trending treatment by value interactions during participation meriting one-way ANOVAs at the core value level to better understand how the treatments might be influencing different values: the right TPJ [$F(1.29, 24.28) = 4.56$, $p < .001$, $\eta_G^2 = .042$], the left TPJ [$F(1.24, 23.56) = 4.25$, $p < .001$, $\eta_G^2 = .045$], the right insula [$F(2, 38) = 4.52$, $p < .001$, $\eta_G^2 = .051$], the left insula [$F(2, 38) = 3.03$, $p = .009$, $\eta_G^2 = .033$], the right pole of the superior temporal cortex [$F(2, 38) = 2.99$, $p = .009$, $\eta_G^2 = 0.050$], the left pole of the superior temporal cortex [$F(2, 38) = 2.43$, $p = 030$, $\eta_G^2 = .030$], and a trend was observed in the left pole of the middle temporal cortex, $F(2, 38) = 2.09$, $p = .059$, $\eta_G^2 = .029$. Mauchly's test for sphericity determined that assumptions of sphericity for treatment were violated for the right TPJ ($W = 0.138$, $p = ,034$, $\varepsilon = .639$) and the left TPJ ($W = 0.085$, $p = ,004$, $\varepsilon = .620$). The degrees of freedom for that test were corrected using Greenhouse-Geisser estimates of sphericity.

Analysis of PSC within these regions for Universalism revealed only a trending effect of overall treatment within the right insula, $F(2, 38) = 3.14$, $p = .054$, $\eta_G^2 = .073$. An effect of treatment was seen for Benevolence along with significant differences between specific treatment conditions for several brain regions, $F(2, 38) = 5.10$, $p = .011$, $\eta_G^2 = .089$ (Table 4). In the right TPJ, VAS decreased BOLD signal compared to placebo, $p = .019$. In the insula, VAS

also decreased BOLD signal compared to placebo in the right hemisphere [$F(2, 38) = 4.75, p = .014, \eta_G^2 = .073$], and had a similar effect on PSC compared to placebo in the left hemisphere, $F(2, 38) = 3.76, p = .032, \eta_G^2 = .063$.

Table 4. Pairwise T-tests of BOLD Percent Signal Change for the Activities Task.

Task Response	Core Value	Region	Treatment = Mean (SD)	Treatment = Mean (SD)	*P*-value
Participation	------	Nucleus Accumbens	Oxytocin 0.05 (0.17)	Placebo -0.02 (0.21)	*P* = .039
Participation	Benevolence	Right TPJ	Placebo 0.25 (0.36)	Vasopressin 0.02 (0.24)	*P* = .019
Participation	Benevolence	Right Insula	Placebo 0.33 (0.35)	Vasopressin 0.11 (0.24)	*P* = .016
Participation	Benevolence	Left Insula	Placebo 0.31 (0.25)	Vasopressin 0.15 (0.22)	*P* = .030
Participation	Achievement	Left TPJ	Oxytocin 0.25 (0.26)	Placebo 0.02 (0.29)	*P* = .015
Participation	Achievement	Left MTP	Oxytocin 0.26 (0.23)	Placebo 0.06 (0.28)	*P* = .046
Participation	Achievement	Right STP	Oxytocin 0.20 (0.23)	Placebo 0.01 (0.33)	*P* = .026
Participation	Achievement	Left STP	Oxytocin 0.30 (0.29)	Placebo 0.07 (0.35)	*P* = .013
Worthwhile	------	Right Insula	Oxytocin 0.26 (0.29)	Vasopressin 0.19 (0.23)	*P* = .037
Worthwhile	------	Left Insula	Oxytocin 0.27 (0.24)	Vasopressin 0.21 (0.19)	*P* = .039
Worthwhile	Power	Left Amygdala	Oxytocin 0.24 (0.32)	Vasopressin 0.08 (0.15)	*P* = 0.26

Note: All results provided survived Bonferroni correction.

Effects of treatment on PSC of BOLD activity were seen for the following brain regions when participants considered participating in Achievement activities: the right TPJ [$F(2,38) = 4.58, p = .017, \eta_G^2 = .057$], the left TPJ [$F(2, 38) = 7.29, p = .002, \eta_G^2 = .104$], the left pole of the middle temporal cortex [$F(2, 38) = 5.51, p = .008, \eta_G^2 = .110$], the right pole of the superior temporal cortex [$F(2, 38) = 3.28, p = .048, \eta_G^2 = .077$], and the left pole of the superior temporal

cortex, $F(2, 38) = 5.08, p = .011, \eta_G^2 = .082$. OXY increased BOLD signal in the right TPJ compared to placebo, however this difference only trended toward significance. A similar increase for OXY over placebo was seen in the left TPJ. Greater BOLD signal was elicited by OXY in the pole of the left middle temporal cortex than did placebo. Compared to placebo, VAS also increased BOLD signal in this region. OXY also affected the pole of the superior temporal cortex by increasing BOLD signal over placebo in the right hemisphere, and increased BOLD signal over placebo in the left hemisphere. No effects of treatment were observed in BOLD PSC for the power value.

When participants considered how worthwhile activities were, BOLD PSC was affected by the treatment conditions in the following ROIs: the right insula [$F(2, 38) = 4.36, p = .020, \eta_G^2 = .013$], the left insula [$F(2, 38) = 3.78, p = .032, \eta_G^2 = .016$], and the left amygdala, $F(2, 38) = 3.65, p = .036, \eta_G^2 = .009$. In the right insula, OXY increased BOLD signal over VAS. In the left insula, OXY increased BOLD signal over VAS. In the left insula, no contrast between treatment conditions survived Bonferroni correction during the pairwise t-tests. Subsequent PSC analyses in these regions for each value revealed only a trending effect of overall treatment within the right insula, $F(2, 38) = 3.08, p = .058, \eta_G^2 = .054$. The significant effect of treatment was found for Power in the left amygdala, $F(2, 38) = 4.23, p = .022, \eta_G^2 = .063$, with OXY increasing BOLD over VAS.

3.6 Percent Signal Change in Regions of Interest for the Facial Judgment Task

ANOVAs were also performed on BOLD activity PSC for the set of twenty *a priori* regions of interest relevant to the facial judgment task (see section 2.13.1). An overall task x treatment ANOVA did not show PSC differences in any ROI for the task factor between

trustworthiness and dominance judgments, however, it did reveal treatment effects in three ROIs: the right superior temporal cortex [$F(2,38) = 3.40, p = .044, \eta_G^2 = .029$], the left VMPFC [$F(2,38) = 4.59, p = .016, \eta_G^2 = .041$], and the right VMPFC [$F(2,38) = 5.33, p = .009, \eta_G^2 = .056$. Of these, the only specific contrast of treatment conditions that survived Bonferroni correction in pairwise t-tests was an effect of OXY to decrease BOLD ($M = -0.11, SD = 0.21$) compared to placebo ($M = 0.02, SD = 0.29$) for the right VMPFC, $p = .018$.

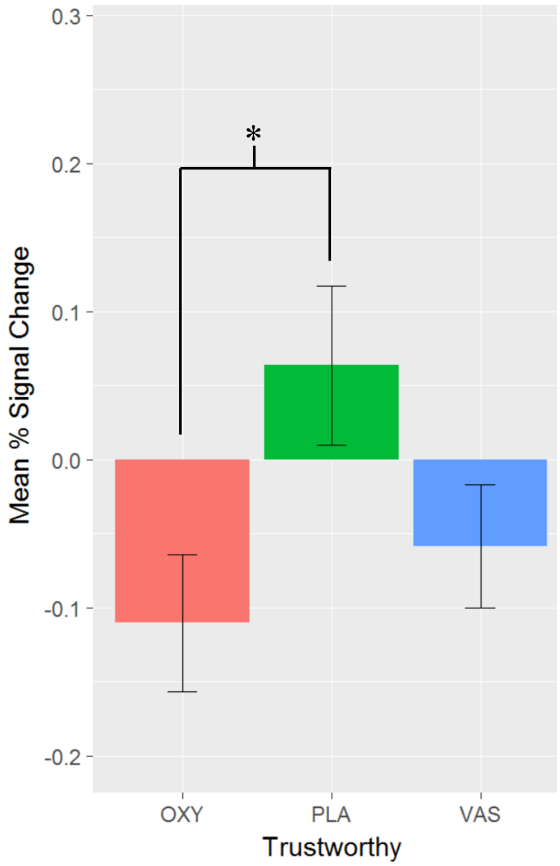


Figure 8. Mean BOLD percent signal change observed in the ventromedial PFC when participants rated faces on perceived trustworthiness. Error bars: SEM. OXY = oxytocin, PLA = placebo, VAS = vasopressin.

Separate ANOVAs were then performed, respectively, for the trustworthiness trials and dominance trials for each ROI. No effects of treatment were seen for dominance, but despite not

indicating a meaningful task by treatment interaction in the higher-order ANOVA, effects of treatment were again seen during trustworthiness judgments in the left [$F(2, 38) = 4.12$, $p = .024$, $\eta_G^2 = .071$] and right VMPFC, $F(2, 38) = 5.72$, $p = .007$, $\eta_G^2 = .110$. Here again, as shown in Figure 8, the only significant contrast was right VMPFC decrease in BOLD for OXY ($M = -0.11$, $SD = 0.21$) compared to placebo ($M = 0.06$, $SD = 0.24$), $p = .03$.

CHAPTER 4

DISCUSSION

4.1 Effects of OXY and VAS on Behavior and BOLD Signal for Facial Judgments

This study aimed to provide new insight into the contribution of OXY and VAS on social cognition in two contexts: a task judging faces based on how dominant and how trustworthy they appear and a task for rating how worthwhile and how likely one would be to participate in activities based on the BHVT. The results for the facial judgment task ran counter to my hypotheses and to the broader literature as well for the trustworthiness responses. VAS affected neither the judgments of trustworthiness nor of dominance despite its previously being shown to increase perception of how threatening faces appear, a feature correlated with facial dominance. OXY, however, did increase the perception of dominance but had no effect on trustworthiness which it was expected to increase based on previous research.

It is unclear why OXY would increase the perception of dominance. One explanation could be that dominance ratings increase as the salience of features indicative of position within a social hierarchy are enhanced. Alternatively, variation in OXY may help establish social hierarchies by prompting those with higher basal OXY to more often perceive others as relatively higher in social status than the perceiver, thereby reducing intra-group conflict by ensuring that some proportion within a group are comfortable with a subordinate status. Elevated baseline OXY has been observed in dominant Rhesus monkeys (Michopoulos, Checchi, Sharpe, and Wilson, 2011), which may be contrary to this idea; however, variation in the effects of these hormones across species is not uncommon (Goodson & Thompson, 2010).

The clusters of BOLD signal that tracked increasing dominance ratings during the OXY condition do not provide much insight into what mental processes OXY may be influencing. The right posterior MCC is not strongly implicated in the dominance or social hierarchy literature, and all other activation occurs bilaterally within large masses of white matter making it difficult to speculate on what mental processes may be implied by this result.

Effects of OXY on trust have been particularly difficult to replicate and have been subject to critical review by Nave, et al. (2015). However, as more is learned about the contextual sensitivity of OXY, it seems likely that more social information is required to observe an effect (Bartz, et al., 2011). Declerck, Boone, and Kiyonari (2010) found that without supplying additional social information about other players, OXY decreased cooperation during an interactive game, while it increased cooperation when additional social context was provided. It is reasonable that an effect on trust in the present task may require additional information regarding familiarity or in-group status of the trustee for the faces presented to yield an effect. OXY was observed to decrease BOLD percent signal change (PSC) in the ROI analysis for the right VMPFC during the trustworthiness condition. This may suggest a negative impact on how trustworthy or, potentially, how attractive, participants perceived them to be, but did not elicit a strong enough reaction to be detected in behavioral testing or whole-brain analysis.

4.2 Neural Correlates of BHVT Core Values

This study offers early evidence that the BHVT model of core values may be useful beyond its well-established role in characterizing core values and associated behaviors at a descriptive level. The data presented here suggests that the mental processes that selected BHVT categories represent are related to different biological substrates. Strong evidence for this theory

came more from the combination of behavioral, fMRI and neuropharmacological methods than the simple comparisons of the neural correlates for the placebo conditions of each value. Strong support for this model would have been expected to show more shared brain networks for the two prosocial values and the two self-interested values and less shared between these higher order classifications.

Instead, no regions were observed to be particularly related to the self-interested values and the MPFC activity that was seen for the two prosocial values was driven by its strong association with Benevolence while presenting no relationship with Universalism. Contrasting placebo condition data corresponding to different core values did elevate BOLD in brain regions particular to several values, but these distinctions were only seen when a value was contrasted against Achievement. These results may have been largely due to a lack of distinct mental processes pertaining to Achievement but could potentially indicate a deemphasis of social mental processes when considering participation in certain contexts.

Regardless, these comparisons may be informative as to the mental processes supporting the different values. Achievement was singularly characterized by lesser activation of the angular gyrus in comparison with each of the other values, likely suggesting decreased demand for taking the perspective of others. Achievement is most defined by one's personal goals as they pertain to societal expectations of success (Schwartz, 1992). The other three values entail more consideration of others on an individual level. Power attends to others' perspectives and goals to gain position or leadership in order to maintain social position. Thus, engaging with the perspective of others is necessary to express this value despite doing so with a self-interested

focus. Activities related to the two prosocial values directly address the feelings and concerns of others.

In addition to the angular gyrus, the inferior frontal gyrus was elicited for Power activities. This region is critical for understanding and simulating others' actions and goals while also contributing to emotion recognition and regulation. The inferior frontal gyrus is implicated in socio-affective processes (Shamay-Tsoory, Aharon-Peretz, Perry, 2009; van der Meer, Groenewold, Nolen, Pijnenborg, and Aleman, 2011; Vogeley, et al., 2001). Studies have shown that those high in the trait Machiavellianism activate this region while using strategies that take advantage of others (Bereczkei, Deak, Papp, Perlaki, and Orsi, 2013). While those findings are conceptually relevant to Power, the number of affective and executive functions associated with the inferior frontal gyrus makes interpreting its role difficult as an isolated region.

For Benevolence, the focus on the well-being of close others and the maintenance of relationships corresponds well with the observation of activity in MPFC which is associated with representations of close others and social norms (Fiddick, Spampinato, and Grafman, 2005; Mitchell, Macrae, and Banaji, 2006; Ochsner, et al., 2005). Universalism also focuses on the well-being of others but activities related to it require an understanding of what factors may promote or undermine well-being on a broader level. The activation observed in the left anterior temporal lobe suggests that these activities elicit greater abstraction in processing the implied social concepts (Noppeney & Price, 2004; Pobric, Ralph, and Jeffries, 2009; Skipper, Ross, and Olson, 2011; Zahn, et al., 2007).

The temporal pole also has a role in processing familiarity. It should be noted that Universalism would not be expected to have elicited BOLD in this region due to an of high familiarity with these activities as they are not as commonly encountered as Benevolence activities. Should be due to abstraction of social concepts that help generate a reason to participate in the activity, which may be similar to the function of the MPFC to potentially provide norms relevant for evaluating participation in Benevolence activities.

Only two previous fMRI studies have used the BHVT to investigate neural correlates of social phenomena and neither did so at the individual core values level (Brosch, Coppin, Scherer, Schwartz, and Sander, 2011a; Brosch, et al., 2011a). Together, these studies showed that the stimuli inspired by the BHVT could reveal differences in brain patterns related to pleasant activities and conceptually meaningful activities related to core values and that how one prioritizes core values can modulate behavior and neural activity related to generosity. My results more explicitly show that contrasting higher-order BHVT categories elicits different patterns of brain activity and are the first results showing differences in neural activity related to individual core values. While the only difference between two values within the same higher-order category (i.e. self-interest) was observed between Power and Achievement, this study does present several comparisons showing evidence of neural correlates that may be critical for mental processes related to specific values. This early evidence suggests that the BHVT has value in providing social neuroimagers with theoretical constructs of social phenomena that are relevant for eliciting both brain activity and complex behaviors and attitudes.

4.3 Effects of OXY and VAS on Core Values Related Behavior and BOLD Signal

OXY and VAS were seen to have an influence on wider brain networks and a greater number of contrasts in the activities task than the facial judgements task. OXY and VAS were hypothesized to influence behavior and brain activity associated with a positive effect for Benevolent activities. Neither OXY nor VAS influenced behavioral responses related to Benevolence, but each modulated brain activity in response to these activities during different rating conditions: worthwhile for OXY and participation for VAS. The wide-spread cortical network modulated was highly similar but OXY uniformly enhanced BOLD while VAS uniformly attenuated it.

It is noteworthy that the ACC/MPFC, which was observed when comparing Benevolence to all other BHVT values, was not part of the networks affected by the hormones here. The lack of MPFC changes by the hormones helps narrow down the social processes potentially influenced, making unlikely the processes of social norm compliance (Fiddick, et al., 2005), mentalizing *per se* (Molenberghs, Johnson, Henry, Mattingley, 2016), self-representation (D'Argembeau, et. al., 2007; Johnson, et al., 2006;), personal importance, and attribution of persistent rather than situational personal traits (D'Argembeau, et. al., 2012). Processes more likely to be influenced here, though themselves often involving the MPFC, are empathy, bottom-up attention and determination of social salience both of which are strongly associated with the insula and areas within the temporo-parietal junction and IFG (Bzdok, et al., 2012; Decety & Lamm, 2007; Downar, Crawley, Mikulis, and Davis, 2002; Eckert, et al., 2009; Hillis, 2014; Kahnt & Tobler, 2013; Sevinc, Gurvit, and Spreng, 2017). First, the majority of regions observed in this large network are associated with either cognitive or emotional empathy and

both OXY and VAS have been seen to improve empathy. If this were the case here it would provide some support for the hypothesis that Benevolence rather than Universalism is related to the functions of these neuropeptides as potential biological substrates supporting kinship and in-group social bias. However, without a behavioral effect, this study can only suggest that some effect seems to exist, by at least one hormone, without respect to the direction of the effect.

This elicited network is also part of the salience network potentially lending support to the theory that OXY, and/or perhaps VAS by extension, influence the salience of stimuli in social contexts relevant to its function (Averbeck, 2010; Bartz,et al., 2011; Burkett & Young, 2010). This theory may best account for downstream effects that allow for widespread cortical effects to areas in which no OXY receptors have been found, while also allowing adaptive flexibility across different contexts and modalities in which a relevant cue might be presented. Bartz, et al. suggested that this theory of social salience may not be entirely independent of prosocial theories of OXY function in that "activating affiliative goals should increase people's attention to and processing of socially relevant information." A modification of this idea may be the best interpretation of the data here, that the salience of social cues implied by Benevolent activities gain attentional advantage which elicits affiliative goals and/or enhances empathic processes.

Additionally, activation in the left anterior insula/IFG just below the cluster correction threshold was observed when comparing the influence of OXY over VAS on all Benevolence trials. This suggests a role for OXY in emotion generation and/or regulation and a de-emphasis of these processes for VAS. Both regions contribute to emotion recognition and generation (Carr, Iacoboni, Dubeau, Mazziotta, and Lenzi, 2003; Wicker, et al., 2003), and emotion

regulation (Buhle, et al., 2014; Diekhof, Geier, Falkai, and Gruber, 2011; Kohn, et al., 2014), and the insula is critical for emotional awareness (Craig, 2009; Gu, Hof, Friston, and Fan, 2013; Singer, Critchley, and Preuschoff, 2009). Both have been seen to produce Broca's aphasia when damaged and the IFG is associated with semantic elaboration (Kaneda, Shigemune, & Tsukiura, 2017). A key consideration here is that the single sentence descriptions of activities featured in this task likely required further elaboration by the participants. Engaging in semantic elaboration of the socio-emotional contexts may aid in identifying relevant emotions and other internal states and integrating these with contextual features implied by these for the purpose of evaluation or regulating the emotional response to the stimuli. Whatever the affective processes influenced by the hormones are, to my knowledge this is the first dissociation for OXY and VAS regarding effects on these regions.

VAS decreased activity in several areas during Universalism trials rated on worthiness, the same condition for which it increased ratings when compared to placebo. These areas, the precentral and postcentral gyri, the caudate and the middle cingulate cortex are typically associated with initiating or simulating motor action. Middle cingulate cortex activation has been linked to the perception of effort costs (Burke, Brünger, Kahnt, Park, and Tobler, 2013; Prevost, Pessiglione, Météreau, Cléry-Melin, and Dreher, 2010), while the caudate contributes to motivated action (Delgado, Locke, Stenger, and Fiez, 2003; Delgado, Stenger, and Fiez, 2004). A decrease in these decision-making and motor areas may indicate a decreased need for action simulation and motivation due to the selective discounting of effort costs entailed in egalitarian social activities. However, interpretation of these action-oriented areas is somewhat confused by their being elicited during worthiness trials rather than during the participation trials for which

one would more reasonably be required to weigh costs and simulate potential engagement. Thus, while an influence of brain activity would appear to support the behavioral findings, it is unclear how the mental processes related to these areas might connect with the stimuli or BHVT concepts related to Universalism.

A particularly unexpected finding was the influence by OXY on Achievement activities rated for participation likelihood. OXY increased BOLD primarily in the PCC and inferior parietal regions extending to the left TPJ and lingual gyrus with additional activation in the precentral and postcentral lobules. The majority of these regions are involved in several social processes that involve the intentions (den Ouden, Frith, Frith, and Blakemore, 2005), Theory of Mind and perspective taking (Arora, Schurz, and Perner, 2017; Molenberghs, et al., 2016), and judgments of other individuals or the self (Denny, Kober, Wager, and Ochsner, 2012). This left TPJ activation included the angular gyrus which was least active during Achievement activities rated on participation compared to all other values. It is likely that participants spent less time during Achievement trials switching to others' perspectives than when considering activities related to other values. Seeing it enhanced here is of interest as the lingual gyrus, PCC/precuneus, and TPJ have all been linked to Theory of Mind processes, particularly attributing intentions to others (Brunet et al., 2000; Juan et al., 2013). Thus, OXY may enhance the degree to which the goals and concerns of others are accounted for even when considering activities for which doing so is ancillary to the implied goal.

4.4 Effects of OXY and VAS on BOLD Percent Signal Change for Core Values

I analyzed the BOLD PSC for different sets of ROIs relevant to each task primarily for two purposes. First, examining the mean PSC better enabled me to assess effects in important

smaller regions such as the amygdala and nucleus accumbens than the whole-brain comparisons in which it was appropriate to employ a high cluster-size threshold to reduce the chance of reporting false positives that could result due to the large number of comparisons explored in the study. Secondly, this could better assess and visualize the relationships between the effects of the three treatment conditions in these ROIs than could pairwise comparisons.

This analysis was informative toward this second aim in that it did not reveal any comparisons for which the two hormones demonstrated strong opposing effects. Specifically, there were no instances of significant comparisons between OXY and VAS in which BOLD PSC was positive for one hormone and negative for the other. Rather, the relationships between the changes in signal for the treatment conditions in the various regions were characterized by either stepwise differences, with each moving in the same positive or negative direction, or both hormones affecting signal in one direction and the placebo in the other, or one hormone simply enhancing positive PSC more than the other hormone and significantly more than placebo.

Beyond the change in BOLD seen in the left anterior insula and IFG when contrasting OXY with VAS for Benevolence activities at the whole-brain level, the only results from this study suggesting areas in which these hormones might have opposing effects were for OXY increasing PSC more than VAS in the nucleus accumbens and left amygdala globally across all activity task factors as well as in the bilateral insula for worthwhile ratings generally and in the left amygdala for Power. The nucleus accumbens and OFC/VMPFC are key components of the reward system and were expected to be elicited more for participation rather than worthiness ratings due to greater consideration of motivation for personal engagement during these trials (Harbaugh, et al., 2007; Hare, et al., 2010; Smith, et al., 2010). An increase in PSC for the

VMPFC was a main effect of the task when comparing participation and worthiness ratings, but no main effect of treatment was seen. Instead, the effect of OXY treatment on the nucleus accumbens (which was stronger during participation trials but only against the placebo) and the left amygdala seems to support a role for OXY in enhancing motivational salience rather than reward processing (Zink, Pagnoni, Martin, Dhamala, and Berns, 2003; Zink, Pagnoni, Martin-Skurski, Chappelow, and Berns 2004).

4.5 Consideration of the Differential Effects of OXY and VAS for Both Tasks

Although BOLD patterns between the facial judgment and activity evaluation tasks were not statistically compared, it was clear that the hormones influenced BOLD in a greater number of activities task contrasts and often that influence resulted in a wider network of affected regions. Given the high biological significance of faces compared with the greater demand from the activities task for imagining additional social context, this result is surprising. However, it has been previously observed that OXY is most impactful on the behavior of those who show the least ability social ability or for whom social stimuli are less salient, as faces are for those with autism (Bartz, et al., 2010; Declerck, Boone, and Kiyonari, 2014; Guastella, 2010; Lambert, et al., 2014). The activities task likely requires deeper processing of the provided information to derive a social meaning and it may be that the greater demand for elaborating on the social contexts implied in that task provided more opportunity for the hormones to influence brain activity than did the facial judgments which are naturally highly salient for neurotypical participants and less likely to elicit contextual elaboration. This may be especially likely for OXY considering that it enhanced BOLD PSC relative to the other two treatments in two regions

related to motivational salience, the nucleus accumbens and left amygdala, selectively for stimuli in the activities task but not during the face task.

4.6 Limitations and Future Directions

As previously mentioned, I presented the photos with no additional context or social characteristics that might have helped participants relate to them. The facial stimuli were made to be as uniform as possible and this homogenized photo set of Caucasian individuals may not have represented a group of people that the ethnically diverse participants in this study (only 40% were non-Hispanic and non-Middle Eastern Caucasians) found readily relatable. Even providing simple, nominal descriptors to groups of participants or person-related stimuli has been seen to trigger an effect by OXY that may not have otherwise occurred.

An outstanding issue for investigating the neural correlates of core values is the difficulty in devising an appropriate control task. Unfortunately, all activities related to long-term goals or concerns that would be suitable for contrasting with activities related to the four BHVT studied here would also be subject to having that goal or concern subsumed by some other core value. Conversely, activities that do not reflect long-term goals or concerns (e.g. descriptions of chores or errands) are almost certainly unsuitable by definition as control stimuli for the task as I have designed it.

One issue regarding use of these hormones to examine BOLD signal is their effects on vasculature. Vasopressin is known to constrict blood vessels while oxytocin has been shown to dilate them (Koshimizu, et al., 2012; Thibonnier, et al., 1999). Furthermore, Galbusera, et al., (2017) showed that intranasal OXY increases, and VAS decreases, cerebral blood flow in a network of reward and social processing areas in the rat using high-field fMRI techniques.

However, this cannot account for the selective effects of the hormones in these networks during conditions hypothesized to be relevant to their action. Nor can it account for the treatment affect seen for OXY selectively in the left amygdala and nucleus accumbens. Rather, the results here reinforce those from Galbusera, et al. by demonstrating in humans the opposing actions of OXY and VAS upon networks of social processing areas during relevant task conditions.

Hormones may strongly contribute, as the results here seem to indicate, to specific aspects of social behavior and the changes in neural activity associated with them. Most studies operate on the premise that potential changes by a hormone on some social behavior will happen in the same direction in the majority of people. However, the influence of hormones on mental activity and behavior is not only sensitive to environmental context but also to individual differences (Bartz, et al., 2011). Though it has not been reported here, efforts could and should be made to find associations between how one prioritizes core values and how this relates to the effects of the hormones. It remains to be seen whether the transient effects of intranasal administration have difficulty overcoming well-learned preferences. Hormones may, for example, promote behaviors related to strong social preferences, effectively enhancing a person's dominant response in that context. However, they may instead moderate behavior by promoting concern in certain social contexts only for those who are relatively less sensitive to those contexts while dampening concern in those overly sensitive to those contexts.

Finally, nasal spray administration of these hormones has been shown to increase their concentration in cerebrospinal fluid (Born, et al., 2002; Striepens, et al., 2013), but the mechanism by which they affect the brain via this method is unknown. Thus, this research is limited by uncertainty regarding what proportion of a puff of nasal spray enters the brain and

what the most effective dose might be for a given hormone. Furthermore, the nature of a potential dose-response curve is not known. Some researchers have proposed an inverted U-shaped curve for OXY in which moderate levels of the hormone promote the social behaviors associated with it but too high or low a level could decrease it (Bieslky & Young, 2004; Rilling, et al., 2014). This idea largely stems from evidence of diverging effects of OXY on behaviors and brain responses in each sex (Dumais & Veenema, 2015), along with evidence of higher baseline cerebro-spinal fluid concentrations of OXY in women compared with men (Altemus, et al., 1999). While no such sex differences have been observed in cerebro-spinal fluid concentrations of AVP (Coccaro, et al., 1998; Sørensen, Gjerris, and Hammer, 1985), the overall sex differences revealed in previous studies caution against generalizing to women the results from the all-male sample in the current study. While the mechanism by which intranasal administration enters the brain remains unclear, further research into sex and individual differences will help build consensus regarding how and in what manner these hormones affect the mental and neural processes of individuals.

CHAPTER 5

CONCLUSION

This study provided insights into the effects of OXY and VAS on social behavior by investigating their influence on two tasks with an identical structure, but presenting very different stimuli. No study has previously examined the neural correlates of rating the perceived trustworthiness or dominance of faces. Nor have any prior studies operationalized concepts from values theory to provide meaningful social context for investigating the effects of OXY and VAS on behavior and the associated brain responses.

Contrasting different conditions related to the BHVT values within the placebo sessions revealed early support for the hypothesized relationships between the values being reflected in patterns of brain activation. Contrasting across the prosocial versus self-interested axis revealed bilateral MPFC activity. While this activation was selective for Benevolence when contrasted with all other values, it was not significant when contrasting with Universalism alone. This differentiation across the higher-order axis but not within the prosocial values agrees with the relationships between these values proposed by the BHVT. However, the predicted relationships between the self-interested values did not hold. The TPJ was less active for Achievement in each contrast with the other values, including Power, indicating that the patterns of brain activation for these two values are as distinct from one another as they are from the prosocial values. Overall, exploration of the other values proposed by this theory appears promising for relating categories of social motivations with mental processes revealed by neuroimaging.

Each task revealed a novel behavioral finding pertaining to the function of a hormone. No behavioral result was observed for VAS on the facial judgments task and OXY did not

produce an increased perception of trustworthiness for faces as I had expected. OXY was seen to increase the perception of dominance for faces, which was not expected and has only limited support in the animal literature. This behavioral result was supported by BOLD activity that decreased as dominance ratings increased for the MCC and bilaterally in the white matter posterior to the lateral ventricles and inferior to the parietal lobe, regions near areas crucial for social cognition but not close enough for confident interpretation.

It is noteworthy that the pattern of BOLD signal was more impacted by the hormones while participants read and considered the descriptions of the highly contextualized social activities than when they evaluated the face stimuli. Faces are the more concrete and, likely, more salient class of stimuli while the activities task gave participants more opportunity to imagine and elaborate on additional social contexts. The finding that OXY increased BOLD PSC in the nucleus accumbens and left amygdala relative to the other treatments, specifically during the activities task and not the face task, may help interpret this observation. If these regions were elicited to increase the salience of social information, then it may support the idea that this is a primary function of OXY and that the effects of exogenous administration of the hormone are more pronounced when there is more social information to process or when doing so is more challenging.

Defining the activity stimuli according to BHVT categories allowed me to observe an effect of VAS for a class of prosocial behavior and a dissociation between the influence of OXY and VAS in brain activity. VAS increased ratings of how worthwhile Universalism activities were compared to placebo, demonstrating that it may, contrary to my tentative hypothesis, selectively promote egalitarian, rather than parochial, social actions. This result corresponded to

decreases in BOLD for regions that have been associated with processing effort. Thus, VAS may de-emphasize considerations of practical concerns that could hinder assent to egalitarian prosocial behavior.

A distinct dissociation was observed between the effects of the two hormones on BOLD patterns when viewing Benevolent activities. Both hormones influenced a wide-spread network of regions previously associated with socio-moral processes and primarily observed here in the lateral cortical areas extending from the posterior IFG, through the insula into areas of the TPJ. This network was enhanced bilaterally by OXY compared to placebo when activities were rated for how worthwhile they seemed, although to a larger degree in the left hemisphere. VAS, however, attenuated BOLD in this network in the right hemisphere and left insula. OXY and VAS were expected to both enhance Benevolence ratings and influence BOLD signal. Given the absence of a behavioral influence on Benevolence ratings for either hormone, confident interpretation is difficult here. However, the established influence on socio-cognitive processes by OXY and theories linking it to increasing salience of social information make it likely that OXY is promoting such processes for Benevolence activities while VAS is not. Furthermore, when contrasting across all Benevolent activities, OXY enhanced BOLD in the left anterior insula and posterior inferior frontal gyrus which may be indicative of OXY increasing elaboration on the semantic or emotional meaning implied by these activities. Thus, incorporating the BHVT model allowed this study to produce the novel finding that VAS promotes egalitarian prosocial behavior and also reinforced prior findings showing that OXY enhances mental processes associated with parochial prosocial behavior not egalitarian behavior. More broadly, this study provides evidence suggesting that concepts defined by the BHVT,

which have previously been shown to be meaningful for an array of social behaviors, are relevant for investigating the neural mechanisms of social behaviors across multiple biological levels.

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BIOGRAPHICAL SKETCH

Mr. Teed received a Bachelor of Science degree in psychology from The University of South Carolina. There he studied in several neuroimaging laboratories gaining experience working on functional magnetic resonance imaging projects. Also during this time, he began working with young men who have intellectual handicaps, neurological disorders or autism. These experiences honed his long interest in the individual differences in human preferences during decision making toward a new focus on the neurological basis of social preferences and the mechanisms responsible for social dysfunction. He continued to be employed as a social worker for this population for two years before returning to school to pursue a PhD. In the Cognition and Neuroscience doctoral program at The University of Texas at Dallas, he studied neuroimaging and neuropharmacological methods and social psychology culminating in the doctoral project detailed in this document. Mr. Teed intends to continue using these methods as he pursues a career in basic and translational social neuroimaging research.

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Education

Doctorate: Cognition and Neuroscience **(Defending) June 5, 2017**
The University of Texas at Dallas Advisor: Daniel Krawczyk

Masters: Cognition and Neuroscience **2012**
The University of Texas at Dallas, 2012

Bachelor of Science: Experimental Psychology (Magna cum Laude) **2007**
The University of South Carolina, Columbia Advisor: Christopher Rorden

Grants & Awards

2014-2015 *Investigating Human Values through Hormones and Neuroimaging*. Prothro Clark Fund; Dallas Foundation: $30,000. Role: Co-Investigator (PI: Daniel Krawczyk)

2015-2016 *Genes, Hormones and Brain Activity: Learning the Biological Foundations of Positive and Negative Social Motivation*. Linda and Joel Robuck Distinguished New Scientist Award: $25,000. Role: Principal Investigator (Co-PI: Daniel Krawczyk)

2016 Society for Social Neuroscience Annual Meeting NSF Travel Award (ID: 1543122).

Manuscripts in Prep

Krawczyk, D.C., **Teed, A.** Multiple systems in decision making: Evidence from neuroscience and behavior.

Conference Presentations

Teed, A., Mark, D.B., Rakic, J., Krawczyk, D.K. *Evaluating Activities According to Values Theory: An fMRI Study of Social Values* (November, 2016). Society for Social Neuroscience Annual Meeting. San Diego, California.

Teed, A., Mark, D.B., Rakic, J., Krawczyk, D.K. *The neural correlates of social values: An application of the Basic Human Values Theory in Social Neuroscience* (May, 2016). 38th International Symposium of the Groupe de recherche sur le système nerveux central. Montreal, Canada.

Fang, L., **Teed, A.**, Shinkareva, S. *Neural Representation of Social and Nonsocial Stimuli: A Meta-Analysis* (April, 2010). Undergraduate Research Day. Columbia, South Carolina.

Invited Talks

Genes, Hormones and Brain Activity: Learning the Biological Foundations of Positive and Negative Social Motivation (October, 2015). Friends of BrainHealth Annual Lecture Series Invited Speaker. The Dallas Country Club, Dallas, TX.

Investigating Human Values via Hormones and Brain Imaging (September, 2013). Friends of BrainHealth Annual Lecture Series Invited Speaker. The Dallas Country Club, Dallas, TX.

Distinguishing Conceptual Motivations for Vegetarianism: A Pilot Study of Values in Routine Consumer Choice" (May, 2013). Psychological Sciences and Cognitive Science Brown Bag Series. University of Texas at Dallas.

Positions

Teaching Assistant, the University of Texas at Dallas, 2010-2017: 1 semester of Integrative Neuroscience, 1 semester of Research Design and Analysis, 2 semesters of Cognitive Psychology, 2 semesters of Social Psychology, 2 semesters of Abnormal Psychology, and 6 semesters of Experimental Projects in Psychology.

Honors & Service

Conference Travel Award, University of Texas at Dallas
Phi Beta Kappa, University of South Carolina, Columbia chapter
President's List, University of South Carolina
Dean's List, University of South Carolina
President's Volunteer Service Award – bronze level