Implicit Motives

Chapter 10

Biopsychological and Neural Processes of Implicit Motivation

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Introduction

Virtually all mammalian and many nonmammalian species share fundamental evolutionarily preserved motivational systems that propel them toward the formation of attachments with their kin to ensure safety and protection (i.e., affiliation). In addition, they are also propelled by a need to move upward in the dominance hierarchy to obtain more resources and mating opportunities (i.e., power). As a result, animals and humans share similar biopsychological and neural systems that facilitate affiliation-motivated and power-motivated behavior (Schultheiss & Wirth, 2008). For example, the gonadal steroid hormone testosterone

promotes power-motivated and dominant behavior across species (Monaghan & Glickman, 1992). On the other hand, the peptide hormone oxytocin promotes affiliative and attachment behavior across species (Insel & Young, 2001). In comparison to power and affiliation motivation, relatively less is known about the hormonal and neural mechanisms involved in achievement motivation and whether the need for achievement is universal across species or a species-specific motive.

In the first part of this chapter, we will review the hormonal aspects of implicit motives and their role in immune system functioning and health. We will summarize and integrate the existing research on power motivation and the release of the hormones testosterone, epinephrine, norepinephrine, and cortisol within the framework of a psychoneuroendocrine model of power motivation; discuss its applicability to male and female power motivation; and examine its validity in the context of research on the effects of stressed power motivation on health. Next, we will review past and current research on the hormonal and health correlates of affiliation motivation with a particular focus on recent findings of the role of progesterone and cortisol in affiliation motivation, and discuss links between research on the neuroendocrine and health aspects of affiliation motivation and the literature implicating oxytocin in social bonding and stress buffering. Finally, we will also review evidence for a hormonal basis of achievement motivation, focusing on the role of arginine vasopressin in the cognitive and behavioral correlates of this motive.

In the second part of the chapter, we will describe a core motivational brain circuit consisting of the amygdala, striatum, and orbitofrontal cortex, which we hypothesize to be critically involved in implicit motivation. We will present fMRI research findings in which several of these structures have been found to be more activated in power-motivated and achievement-motivated individuals and less activated in affiliation-motivated individuals. In

closing, we will discuss parallels between the functional dissociation of the core motivational brain circuit and brain structures involved in conscious goal setting and action regulation on the one hand, and the lack of overlap between implicit motives and explicit goals and needs on the other.

Biopsychological Processes of Implicit Motivation

Power Motivation and Sympathetic Nervous System Activation

Power motivation has consistently been linked to activation of the sympathetic nervous system, a branch of the autonomic nervous system that becomes more active during times of stress (McClelland, 1982). Power-motivated individuals respond to experimental arousal of the power motive and social dominance challenges with increases in salivary and urinary metabolites of epinephrine and norepinephrine, two catecholamines that are released by the sympathetic nervous system in response to stressors (McClelland, Davidson, & Saron, 1985; McClelland, Floor, Davidson, & Saron, 1980; McClelland, Ross, & Patel, 1985; Steele, 1973, reported in McClelland, 1987). In addition, they also respond with increases in blood pressure (Fontana, Rosenberg, Marcus, & Kerns, 1987) and muscle tone (Fodor, 1985).

For example, Steele (1973) compared participants whose power motive had been aroused through the presentation of inspirational speeches with participants in achievement-arousal and control conditions. Steele found that power-arousal participants had significantly higher postarousal power motive scores than control and achievement-arousal participants. Furthermore, postarousal power motive scores were positively correlated with increases in epinephrine ($r = .71$) and norepinephrine ($r = .66$) in power-arousal participants. By contrast, changes in sympathetic catecholamines after the experimental manipulation were not significantly associated with power motive scores in control and achievement-arousal participants. These results suggest that

experimental arousal of the power motive is uniquely associated with an enhanced response in the sympathetic nervous system as reflected by increases in epinephrine and norepinephrine.

McClelland and colleagues (1980, 1985) have found further support for an association between power motivation and greater sympathetic nervous system activation. McClelland and colleagues (1980) found that power-motivated college males who experienced frequent power challenges in their daily lives and were unable to spontaneously express power-related impulses showed above average epinephrine excretion rates in urine. In a later study, McClelland, Ross, and Patel (1985) collected saliva samples in college students immediately after an important midterm exam, 105 minutes later, and several days after the exam to obtain a baseline measure. The power stress of the exam was associated with an increase in norepinephrine, and this increase was greater for students whose power motive was stronger than their affiliation motive in comparison to students whose affiliation motive was stronger than their power motive. These findings provide additional support for the theory that power motivation, in combination with power-arousing situations and cues, predicts sympathetic nervous system activation and catecholamine release.

Power Motivation and Testosterone

Power motivation has also been linked with the gonadal steroid testosterone (Dabbs, Hopper, & Jurkovic, 1990; Schultheiss, Campbell, & McClelland, 1999; Schultheiss, Dargel, & Rohde, 2003; Schultheiss & Rohde, 2002; Schultheiss, Wirth, et al., 2005). In both humans and animals, high testosterone levels have been associated with dominance, social success, enhanced libido, assertiveness, and violent behavior (Albert, Jonik, & Walsh, 1992; Carter, 1992; Mazur & Booth, 1998; Monaghan & Glickman, 1992). In many primates, dominant males show transient testosterone increases in response to dominance challenges (Bernstein, Gordon, & Rose, 1983;

Mazur, 1985; Sapolsky, 1987). Human males respond with testosterone increases to victory and testosterone decreases to defeat in social dominance contests, including tennis matches, chess tournaments, and even games of chance against another person (reviewed in Mazur & Booth, 1998).

The relationship between dominance and testosterone is less consistent for women whose testosterone levels are about one-fourth to one-sixth of those found in men (Dabbs, 1990; Mazur & Booth, 1998). However, research suggests that testosterone is also crucial for female dominance. For example, elevated testosterone levels in women lead to increased attention and heightened physiological responses to angry faces (van Honk et al., 1999, 2001). Furthermore, women with high testosterone levels occupy higher occupational positions compared to women with low testosterone levels (Dabbs, Alford, & Fielden, 1998; Purifoy & Koopmans, 1979). In addition, high testosterone levels have also been associated with high rank in the prison hierarchy and a history of unprovoked aggression among female prisoners (Dabbs & Hargrove, 1997; Dabbs, Ruback, Frady, Hopper, & Sgoutas, 1988).

Subjectively, high testosterone levels are associated with feelings of vigor and activation (Dabbs, Strong, & Milun, 1997; Sherwin, 1988). Research also suggests that testosterone has significant antidepressant effects for men with very low or absent endogenous testosterone production (Rabkin, Wagner, & Rabkin, 1996). However, at above-average doses, testosterone can lead to addiction (Pope & Katz, 1994). Consistent with testosterone's addictive properties, animal studies provide evidence for a reinforcing role of testosterone. Systemically or locally administered testosterone increases dopamine transmission in the nucleus accumbens (Packard, Schroeder, & Alexander, 1998), a core structure in the brain's incentive motivation system (Cardinal, Parkinson, Hall, & Everitt, 2002). Administration of testosterone has also been shown to reinforce behavior in conditioned-place-preference paradigms (Alexander, Packard, & Hines,

1994; Wood, Johnson, Chu, Schad, & Self, 2004). Furthermore, testosterone-induced conditioned place preference can be abolished by the concomitant administration of dopamine antagonists (Packard et al., 1998; Schroeder & Packard, 2000). Accumbens-mediated reinforcing effects of testosterone are particularly pronounced after testosterone has been metabolized to 3α-androstanediol (Frye, Rhodes, Rosellini, & Svare, 2002).

Research in our laboratory has found a slight positive association between basal testosterone levels and implicit power motivation (Schultheiss et al., 1999, 2003, 2005; Schultheiss & Rohde, 2002), particularly in males. In a study using an experimental motive arousal design, Schultheiss, Wirth, and Stanton (2004) found that a movie depicting the aggressive pursuit of dominance (i.e., *The Godfather II*) elicited increases in power motivation in both men and women. In addition, testosterone levels increased in men with high basal testosterone levels. However, no testosterone changes occurred in women regardless of their basal testosterone levels. For participants in the power-arousal group, testosterone changes correlated substantially with changes in power motive scores among men, but not women. While these findings may suggest that power motivation and arousal of the power motive are not specifically associated with testosterone in women, it is also conceivable that the relatively higher measurement error for the comparatively low testosterone levels in women and the smaller magnitude of situation-induced testosterone changes in women may mask a more substantial positive association between testosterone and power motivation in women.

Research conducted in our laboratory also suggests that both the anticipation of success and actual success outcomes during social dominance contests lead to transient testosterone increases in power-motivated men (Schultheiss et al., 1999, 2005; Schultheiss & Rohde, 2002). During the social dominance contests, same-sex pairs competed on several rounds of an implicit learning task that required them to learn a complex visuomotor pattern in a paper-and-pencil task

(Schultheiss & Rohde, 2002) or on a computer screen (Schultheiss et al., 2005). The outcome of the contests was experimentally manipulated: one participant in each pair was randomly assigned to be the winner and the other to be the loser. Participants' motivational dispositions and personality were assessed with the Picture Story Exercise (PSE) and self-report questionnaires prior to the contest. Salivary testosterone levels and self-reported affect were assessed before and after the contest. Instrumental learning was assessed by learning gains on the implicit learning task after the contest. Notably, participants had no conscious intention to acquire the visuomotor sequence featured on the implicit learning task, nor did they become aware of the fact that they had learned anything in the first place. Thus, learning was implicit in the sense that it happened automatically and was not mediated by declarative processes (e.g., through explicit memory and self-instruction).

Across three studies conducted with male college students in the United States and Germany, Schultheiss and colleagues (Schultheiss et al., 1999, 2005; Schultheiss & Rohde, 2002) consistently found that power motivation predicted testosterone increases among winners and testosterone decreases among losers. By contrast, social dominance contests led to transient testosterone increases regardless of contest outcome in women (Schultheiss et al., 2005; Study 2). This testosterone increase was particularly strong in power-motivated losers immediately after the contest whereas power-motivated winners showed only a very slight and nonsignificant testosterone increase at this time.

In contrast to the gender differences seen in hormonal responses to experimentally manipulated social victory and defeat, power motivation predicted contest-outcome effects on instrumental learning in the same manner and magnitude in men and women. In both men and women, power motivation predicted enhanced instrumental learning (i.e., sequence execution accuracy) among winners and impaired instrumental learning among losers (Schultheiss et al.,

2005). These results replicate findings from an earlier study obtained by Schultheiss and Rohde (2002) in a German sample of male college students. Together these studies provide strong evidence for a moderating role of implicit power motivation on instrumental learning of behavior that has impact on others (i.e., beating one's opponent on a contest) and the inhibition of behavior that leads to the frustration of the need for impact (i.e., being beaten by one's opponent on a contest).

Consistent with the reinforcing effects of testosterone observed in the animal literature, Schultheiss and colleagues (Schultheiss & Rohde, 2002; Schultheiss et al., 2005) also found that men's testosterone changes after a social dominance contest were associated with instrumental learning and statistically mediated the effect of power motivation on instrumental learning. In their study, Schultheiss and Rohde (2002) found that among male power-motivated winners, testosterone increases transmitted the boosting effect of power motivation on instrumental learning. In addition, Schultheiss et al. (2005) found that testosterone decreases mediated the negative effect of power motivation on instrumental learning in male power-motivated losers.

However, Schultheiss and colleagues (2005) did not find any evidence for a reinforcing effect of testosterone on instrumental learning in women. In fact, higher postcontest testosterone levels showed a negative association with speed of visuomotor pattern execution on the implicit learning task, which is inconsistent with a role of testosterone in reinforcement. The lack of evidence for a reinforcing effect of testosterone on instrumental learning in women does not rule out priming effects of testosterone on power-motivated behaviors. Animal studies show that testosterone lowers the threshold for aggressive behavior in males and females (Albert et al., 1992), and research conducted in our laboratory suggests that a priming role of testosterone on female assertiveness also exists in humans (Schultheiss et al., 2005). Consistent with the hypothesis that testosterone primes self-assertion in women, Schultheiss (2007) reports that in the

Schultheiss et al. (2005) study, female losers with the strongest postcontest testosterone increases also showed the greatest power imagery increases in response to a postcontest PSE picture suggesting aggression (e.g., a woman with an angry face and bared teeth), but not to nonaggressive PSE pictures. Thus, while elevated testosterone levels after a social defeat do not seem to reinforce instrumental learning in women, they are associated with what seems to be a compensatory need to assert oneself in a forceful manner.

Stressed Power Motivation and Cortisol

While T appears to scale the reward value of social dominance contest outcomes in men and may subserve a general power-motivation-enhancing function in women, recent evidence points to a role of cortisol in stressed power motivation in both men and women. Cortisol is released by the adrenal gland during uncontrollable stress and induces the body to shunt available energy into coping with the stressor. While cortisol is not consistently related to declarative measures of negative affect and stress (Dickerson & Kemeny, 2004), it increases reliably during social stressors such as the Trier Social Stress Test (TSST; Kirschbaum, Pirke, & Hellhammer, 1993) and is chronically elevated in depressed individuals (Rothschild, 2003). Wirth, Welsh, and Schultheiss (2006) analyzed saliva samples for cortisol levels collected during social dominance contests in a male German sample and a mixed-sex U.S. sample. In both samples, power motivation predicted changes in salivary cortisol levels after winning or losing a dominance contest. Power motivation was associated with increased cortisol levels after a defeat and decreased cortisol levels after a victory. These findings suggest that losing a social dominance contest is particularly stressful for high-power individuals whereas winning a social dominance contest reduces stress levels.

In several studies, stressed power motivation has been associated with impaired immune system functioning and health (Jemmott, 1987; McClelland, 1989). During academic examinations, high-power students compared to low-power students show elevated and prolonged sympathetic stress activation and decreased levels of salivary immunoglobulin A (s-IgA), a measure of B-cell immune function (Jemmott et al., 1983; McClelland et al.,1985). Similarly, McClelland, Alexander, & Marks (1982) found that male prisoners with high levels of power motivation and self-reported stress showed the highest levels of illness and the lowest concentrations of s-IgA compared to high-power, low-stress, and low-power groups.

Stressed power motivation is also associated with decreased natural killer cell activity (Jemmott et al., 1990). As a consequence of depressed immune system functioning, individuals high in power motivation and power stress are more likely than low-power individuals to report more frequent and severe illnesses (McClelland & Jemmott, 1980; McClelland et al., 1980, 1982, 1985). Although the specific mechanism underlying the relationship between stressed power motivation and impaired immune function is unclear, McClelland and colleagues (1980, 1985) suggest that the immunosuppressive effects of chronic sympathetic activity may make individuals characterized by this syndrome more susceptible to illness. Additionally, Wirth and colleagues (2006) propose that another mechanism underlying this relationship may be greater or chronically elevated cortisol levels. It is important to note that high levels of power motivation in combination with low power stress and success in power-related efforts have been found to predict low levels of physical symptoms and overall good health (McClelland, 1989), which suggests that power motivation is not associated with a general vulnerability for impaired immune function or illness.

Psychoneuroendocrine Model of Power Motivation

The observed changes in sympathetic catecholamines, testosterone, and cortisol in response to arousal of the power motive and outcomes during social dominance contests represent the operation of a functionally integrated neuroendocrine mechanism that subserves dominance motivation in males (Sapolsky, 1987; Schultheiss, 2007; see Fig. 1). Sympathetic catecholamines cause general changes in physiology that prepare the body for physical activity in response to stress (i.e., fight-or-flight response). They have fast, stimulating effects on testosterone release from the gonads, and they are typically released in situations in which the individual can actively cope with the stressor, such as beating an opponent in a social dominance contest (Sapolsky, 1987). Testosterone further aids active coping by increasing energy supply to the muscles (Tsai & Sapolsky, 1996) and lowering the threshold for aggressive behavior through its actions on the brain (Albert et al., 1992).

By contrast, cortisol is released by the adrenal gland during situations in which the individual is exposed to an uncontrollable stressor (e.g., social defeat, being subjected to another's dominance; Sapolsky, 2002). Cortisol inhibits testosterone release from the gonads (Sapolsky, 1987), thereby lowering the individual's inclination to engage in further, potentially costly and fruitless dominance battles. According to Sapolsky's (1987) balance model of testosterone release, testosterone increases in male power-motivated winners of a social dominance contest represent the net effect of relatively greater sympathetic catecholamine release throughout a surmountable challenge, whereas testosterone decreases in male power-motivated losers represent the net effect of relatively greater cortisol release during and after a confrontation that overtaxes the individual's capabilities and ends in a defeat.

Although testosterone is known to be positively associated with violence, aggression, and dominance in females (Dabbs, Ruback, Frady, Hopper, & Sgoutas, 1988; van Honk et al., 2001), the mechanisms underlying this relationship and the precise role of the contest-induced

testosterone increases observed in power-motivated women are still not well characterized. In addition, it remains to be determined whether contest-induced testosterone increases lead to long-term increases in power motivation and, conversely, whether contest-induced testosterone decreases lead to long-term reductions in power motivation, as predicted by models of reciprocal effects of dominance behavior and testosterone (Mazur, 1985; Oyegbile & Marler, 2005).

Estradiol and Female Power Motivation

Recent research suggests that estradiol plays an important role in women's need for dominance (Stanton & Schultheiss, 2007). Behaviorally, estradiol has been linked to increases in women's efforts to impress and attract a mate (Grammer, Renninger, & Fischer, 2004; Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007) in addition to sexual activity (Adams, Gold, & Burt, 1978; Udry & Morris, 1968). Research on female rats indicates that estradiol enhances dopamine release and sensorimotor functioning in the striatum (Hu & Becker, 2003). In addition, there is also evidence that estradiol plays a role in reward and reinforcement mediated by the mesolimbic dopamine system (Bless, McGinnis, Mitchell, Hartwell, & Mitchell, 1997; Russo et al., 2003).

Stanton and Schultheiss (2007) found that estradiol in women may serve a similar role in power motivation as testosterone in men. During social dominance contests, estradiol changes in women varied as a function of power motivation and contest outcomes. Estradiol levels increased in power-motivated winners—an effect that was still evident 24 hours after the contest—whereas they decreased in power-motivated losers. Although the mechanism through which these rapid and sustained estradiol changes come about still needs to be clarified, these findings mirror the T changes seen in power-motivated men as a result of social dominance contest outcomes.

Biopsychological Correlates of Implicit Affiliation Motivation

Whereas power motivation is strongly associated with sympathetic nervous system activation, which prepares the body for action, affiliation motivation is correlated with indices of parasympathetic nervous system activity, which returns the body to a state of rest and recovery (Jemmott, 1987; McClelland, 1989). Individuals high in affiliation at age 30 have lower blood pressure at age 50 compared to low-affiliation individuals (McClelland, 1979). They also show better immune system function (e.g., increases in s-IgA) during stressful situations, such as academic examinations (Jemmott et al., 1983; McClelland et al., 1985). In the absence of stressors, high-affiliation individuals show greater natural killer cell activity than individuals low in affiliation motivation (Jemmott et al., 1990), and they also respond with greater s-IgA increases to positive affiliation arousal through films (McClelland & Kirshnit, 1988). Experimental arousal of affiliation motivation also leads to increases in dopamine concentration levels in saliva and plasma (McClelland, Patel, Stier, & Brown, 1987). As a result of its association with parasympathetic nervous system activity and immune system function, affiliation motivation may have protective and beneficial effects on health (Jemmott, 1987; McClelland, 1989; McClelland & Jemmott, 1980), particularly if it is coupled with low levels of stress or activity inhibition, indicating left-hemispheric engagement during stress (Schultheiss, Riebel, & Jones, 2009; Wittling, 1995).

Research also indicates links between implicit affiliation motivation and the steroid hormone progesterone. Women using oral contraceptives, which contain progesterone, have higher levels of affiliation motivation than men or normally cycling women (Schultheiss, Dargel, & Rohde, 2003). In addition, higher levels of affiliation motivation are preceded by greater increases of progesterone in the course of women's menstrual cycles (Schultheiss et al., 2003). Furthermore, Schultheiss and colleagues (2004) found that experimental arousal of affiliation

motivation, but not power motivation, led to increases in progesterone levels in both women and men (Fig. 2; for related findings linking social bonding to progesterone release, see also Brown et al., 2009). Schultheiss et al. (2004) speculated that the observed changes in progesterone may reflect the ovarian action of oxytocin, a hormone implicated in attachment and affiliative behavior in both animals and humans (Insel & Young, 2001; Uvnäs-Moberg, 1998).

Following up on this research, Wirth and Schultheiss (2006) found a connection between implicit affiliation motivation and progesterone. Using film segments containing approach- or avoidance-oriented affiliation themes, they found that progesterone covaried positively with affiliation motivation, and baseline affiliation motivation predicted progesterone increases during avoidance-oriented affiliation arousal. Based on these findings, Wirth and Schultheiss (2006) suggested that progesterone may exert anxiolytic effects in the brain and may therefore help down-regulate "fight-or-flight" stress responses and promote "tend-and-befriend" affiliative behavior (Taylor et al., 2000). This interpretation is consistent with high-affiliation individuals' better stress resistance (McClelland, 1989) and with the observation that affiliative behavior increases during threat (Gump & Kulik, 1997; Schachter, 1959). Thus, Wirth and Schultheiss (2006) argue for a bidirectional relationship between affiliation motivation and progesterone, in which a strong affiliation motive leads to increased progesterone release, particularly during stress, and high levels of progesterone in turn facilitate affiliation motivation.

Biopsychological Correlates of Implicit Achievement Motivation

The biopsychological systems involved in achievement motivation have received considerably less attention despite the fact that intriguing clues to the existence of such a foundation emerged from the beginning of achievement motivation research. For example, Mücher and Heckhausen (1962) found that higher levels of achievement motivation correlated

strongly (r = .65) with leg muscle tone during rest. In addition, Mueller and colleagues (Mueller & Beimann, 1969; Mueller, Kasl, Brooks, & Cobb, 1970) reported that men with high levels of uric acid, a risk factor for gout, have higher levels of hope for success, the approach component of the achievement motive, and lower levels of fear of failure, the avoidance component of the achievement motive, compared to men with normal uric acid levels. Finally, Bäumler (1975; cf. Schultheiss & Brunstein, 2005) showed that administration of a drug that increases dopaminergic transmission leads to increases in hope for success, whereas administration of a drug that decreases dopaminergic transmission leads to decreases in both hope for success and fear of failure. These findings suggest that achievement motivation is mediated in part by a neurotransmitter system whose role in various types of incentive seeking (e.g., food, sex, affiliation) has been thoroughly studied in primates and other mammals (see Panksepp, 1998). Unfortunately, the suggestive links of achievement motivation to muscle tone, uric acid concentration, and dopamine levels in the brain have not been further investigated.

The relationship between achievement motivation and urine excretion has been explored somewhat more systematically. After observing in two previous studies that high achievement motivation was associated with low-volume urine samples collected from research participants (McClelland et al., 1980, 1985; reported in McClelland, 1995), McClelland (1995) experimentally tested the notion that high levels of achievement motivation lead to low urine excretion. McClelland (1995) found that participants' baseline achievement motive scores predicted low urine sample volume after achievement arousal, but not in a neutral control condition. Moreover, in the arousal condition, achievement motivation predicted better recall for achievement-related material on a memory test, and better recall was negatively correlated with urine sample volume. McClelland (1995) attributed these effects to the release of the peptide hormone arginine vasopressin, which promotes water retention in the body and episodic memory

processes in the brain (cf. Beckwith, Petros, Bergloff, & Staebler, 1987; Stricker & Verbalis, 2002). However, arginine vasopressin levels in individuals varying in achievement motivation have not yet been directly measured or manipulated, and thus the link between achievement motivation and arginine vasopressin remains to be determined.

To summarize, a large body of evidence indicates that implicit motives are closely linked to hormone release and related physiological processes. The evidence is particularly compelling for the power motive, which has been linked to stress responses, immune system function impairment, and testosterone release; moderately substantial for the affiliation motive, which is involved in enhanced immune system functioning and progesterone release; and suggestive for the achievement motive, which may be functionally related to the body's fluid retention processes and central dopamine release. The regulation of these endocrine, immunological, and physiological processes by the hypothalamus and other regions of the "emotional brain" (LeDoux, 1996) is well known. Therefore, we will next turn to the evidence linking implicit motives to brain regions critically involved in motivational processes.

Neural Processes of Implicit Motivation

Core Motivational Brain Circuit

Evidence from affective neuroscience reveals a network of core motivational brain structures dedicated to the analysis of a stimulus for emotional content and the preparation of motivated action toward or away from the stimulus (for reviews, see Cardinal, Parkinson, Hall, & Everitt, 2002; LeDoux, 1996, 2002; Panksepp, 1998; Rolls, 1999; Schultheiss & Wirth, 2008). The core motivational brain circuit (Fig. 3) includes the amygdala, striatum, and orbitofrontal cortex (OFC) in addition to structures with direct connections to and from these regions (e.g., hypothalamus, insula). These core motivational structures receive highly processed and

integrated information through association cortices and send their output to the motor cortex for the regulation of behavior and to the hypothalamus for the regulation of autonomic responses, including the release of hormones.

A growing body of evidence indicates that activity in the core motivational brain circuit occurs largely outside of conscious awareness and guides implicit motivational responses to incentives whereas other brain areas (e.g., dorsolateral prefrontal cortex, cortical areas involved in language) are dedicated to the explicit regulation of goal-directed behavior (see Berridge, 1996; LeDoux, 1996, 2002; Rolls, 1999). LeDoux (2002) has therefore suggested that the implicit motive construct proposed by McClelland and colleagues is closely tied to activity in the core motivational brain circuit. To test this hypothesis, our laboratory conducted an fMRI study to investigate how individual differences in implicit motivation influence brain activation in the core motivational brain circuit in response to social dominance cues (Hall, Wirth, Waugh, Stanton, & Schultheiss, 2007; Schultheiss et al., 2008). We focused our region of interest analyses on the amygdala, striatum,and orbitofrontal cortex.

Amygdala

The amygdala is an almond-shaped structure located deep within the medial temporal lobes of the brain in higher vertebrates. It is considered part of the limbic system and plays a primary role in the generation of emotional reactions and the memory of emotional cues. The amygdala can be considered a motivational “homing-in” device that allows individuals to adjust their physiological states and overt behavior in response to cues that predict the occurrence of unconditioned rewards and punishers (Schultheiss & Wirth, 2008). Such cues are learned through Pavlovian conditioning, a process that enables an organism to make emotional and motivational responses to previously neutral stimuli that have become associated with rewards and punishers.

The amygdala consists of two important structures, the central nucleus and basolateral nucleus, which allow it to mediate the organism's emotional and motivational responses to motivationally charged stimuli. The central nucleus influences *emotional reactions* mediated by the hypothalamus and brainstem. It sends impulses to the hypothalamus, which activates the sympathetic nervous system (e.g., skin conductance, heart rate, blood pressure, pupil dilation) and the release of stress hormones, such as cortisol. The central nucleus also connects to the brainstem, which is involved in autonomic reflexes and the release of neurotransmitters, such as norepinephrine, through which it increases arousal and vigilance. By contrast, the basolateral nucleus of the amygdala connects to the ventral striatum to influence *motivated behavior*. Animals with central nucleus lesions are still able to show motivated behavior but fail to exhibit emotional reactions to the stimulus. On the other hand, animals with basolateral nucleus lesions show impairments on motivational action, but their emotional reactions to the stimulus remain intact (Killcross, Robbins, & Everitt, 1997).

Early research on rhesus monkeys provided insights into the function of the amygdala. As early as 1888, researchers found that rhesus monkeys with lesions in the temporal cortex, including the amygdala, had considerable social and emotional deficits (Brown and Schafer, 1888). Klüver and Bucy (1939) later showed that lesions in the anterior temporal lobe produced behavioral abnormalities characterized by overreaction to objects, hypoemotionality, loss of fear, hypersexuality, and hyperorality, a condition that was later named Klüver-Bucy syndrome. Klüver and Bucy (1939, p. 984) described what they observed in one monkey: "The […] monkey shows a strong tendency to approach animate and inanimate objects without hesitation. This tendency appears even in the presence of objects which previously called forth avoidance reactions, extreme excitement and other forms of emotional response." Thus, amygdala damage leads to an inability to assess the motivational value of an object from a distance ("psychic

blindness" or, perhaps more aptly, emotional blindness). As a result, the monkey must get in direct contact with the object in order to assess its hedonic significance.

Recent research using functional magnetic resonance imaging (fMRI) has provided explanations concerning the function of the amygdala in humans. The amygdala appears to play a critical role in the recognition and processing of facial expressions of emotion (FEEs), particularly those involving negative emotions such as fear, anger, and sadness (Adolphs, 2002). In an early fMRI study, Whalen and colleagues (1998) found that the amygdala was activated in response to fearful faces even in the absence of explicit knowledge that the stimuli were presented. However, in animals and humans, the amygdala is also involved in motivated responses to stimuli predicting reward (Baxter & Murray, 2002).

Striatum

The striatum plays a critical role in the acquisition, execution, and invigoration of behavior that is instrumental for incentive attainment (e.g., Rolls, 1999; Schultz, Tremblay, & Hollerman, 2000). The striatum is divided into two sections: the dorsal part consisting of the caudate nucleus and putamen, and the ventral part consisting of the nucleus accumbens. While most research has focused on the role of the ventral striatum in motivation, studies conducted on both primates and humans suggest that the motivational functions of the striatum also extend to its dorsal part, particularly the caudate nucleus (Apicella, Ljungberg, Scarnati, & Schultz, 1991).

The dorsal striatum is critically involved in the acquisition of complex stimulus–response sequences, as evidenced by its involvement in implicit visuomotor learning in humans (Seger, 2006). It also supports the execution of instrumental behavior in response to incentive cues. For example, the desire to punish a cheater on an economic exchange game and the actual severity of the punishment applied are associated with neural activation in the right anterior caudate (de

Quervain et al., 2004). These results suggest that the caudate is involved in the anticipated reward value of aggressive acts.

Furthermore, research indicates that the functions of the dorsal striatum are not limited to antagonistic forms of motivation. For example, the presentation of food stimuli to food-deprived participants was associated with increased activation in the caudate nucleus (Volkow et al., 2002). In addition, right anterior caudate activation can be observed in individuals in the early stages of romantic love when they see pictures of their loved one (Aron et al., 2005). Thus, the dorsal striatum seems to mediate the acquisition and execution of both appetitive and aversive forms of instrumental behavior.

On the other hand, the ventral portion of the striatum, the nucleus accumbens, is particularly involved in tagging unpredicted reward cues and invigorating instrumental behavior in response to these cues. This effect is mediated by dopamine release in the nucleus accumbens, which modulates the effects of input from the amygdala and OFC on motor output such that higher dopamine levels augment the likelihood that the incentive cue will be acted upon (Schultz, 1998). Conceptually, one can think of the nucleus accumbens as contributing a "Go and get it!" impulse to the motivational process that invigorates behavior in response to incentive cues (Berridge, 1996; Ikemoto & Panksepp, 1999).

While lesioning the nucleus accumbens or blocking dopamine transmission in the nucleus accumbens abolishes vigorous approach behavior to reward, the following processes remain intact: the capacity for motor behavior, affective responding to the reward mediated by the OFC, and conditioned emotional reactions to reward cues mediated by the amygdala (Berridge, 1996; Everitt, 1990; Ikemoto & Panksepp, 1999). These findings suggest that the greater availability of dopamine in the nucleus accumbens can be equated specifically with a stronger "magnetic pull" of incentives on instrumental behavior (Schultheiss & Wirth, 2008).

Orbitofrontal Cortex

The orbitofrontal cortex (OFC) is the ventral part of the prefrontal cortex that rests directly above the orbits of the eyes and receives projections from the amygdala and mesolimbic dopamine system. It also receives highly processed olfactory, visual, auditory, and somatosensory information from the mediodorsal thalamus. Because of its role in emotion and reward, the OFC is often considered part of the limbic system. A considerable research literature indicates that the OFC is involved in sensory integration, the representation of the affective value of reinforcers, as well as decision making and expectation (Kringelbach, 2005). The OFC is also thought to play a specific role in regulating planning behavior associated with sensitivity to reward and punishment (Bechara, Damasio, Damasio, & Anderson, 1994). The proposed functions of the OFC are supported by corroborating evidence from research in rodents, nonhuman primates, human studies of healthy individuals, and neuropsychology studies of individuals with damage to the OFC.

Research indicates that the reward value, the expected reward value, and even the subjective pleasantness of a broad array of primary and conditioned reinforcers (e.g., food, monetary gains and losses, FEEs) are represented in the OFC (Kringelbach, 2005; Rolls, 1999, 2000). Furthermore, research indicates that different types of reinforcers are represented by anatomically distinct areas of the OFC (reviewed in Rolls, 2000, 2004). A large meta-analysis of existing fMRI studies demonstrated that activity in medial parts of the OFC is related to the monitoring, learning, and memory of the reward value of reinforcers, whereas activity in lateral parts of the OFC is related to the evaluation of punishers, which may lead to a change in ongoing behavior (Kringelbach & Rolls, 2004).

For example, O'Doherty and colleagues (2001) found that monetary punishment was associated with activation of the lateral OFC while monetary reward was associated with activation of the medial OFC. In addition, the presentation of happy faces is associated with medial OFC activation (Monk et al., 2003). On the other hand, the presentation of angry faces is associated with lateral OFC activation (Blair, Morris, Frith, Perrett, & Dolan, 1999). These findings support the assertion that the medial OFC represents the reward value of reinforcers whereas activity in the lateral OFC is related to the evaluation of punishers that require a change in ongoing behavior (Kringelbach & Rolls, 2004).

A second important feature of the OFC is that it responds to reward based on the motivational needs of the organism. For example, monkeys show strong activation in the OFC to food when hungry, but they show little OFC activation when fed to satiety. The decrease in OFC activation is directly proportional to the animals' decreasing willingness to have another bite (Rolls, Sienkiewicz, & Yaxley, 1989). In addition, the OFC is also one of the most potent sites of brain self-stimulation, which suggests that activation of the OFC is pleasurable (Rolls, 1999). However, the likelihood of OFC self-stimulation depends on the motivational state of the organism. Hungry animals show vigorous self-stimulation of OFC sites related to food reward whereas satiated animals do not (Mora, Avrith, Phillips, & Rolls, 1979).

Additional Motivational Brain Regions

While the amygdala, striatum, and OFC constitute what we have termed the core motivational brain circuit, other brain areas are also important in motivational processes. For example, the hypothalamus has bidirectional projections to the core motivational brain circuit and contributes, for instance, information about the organism's current need state. It is also important in regulating the body's autonomic and endocrine responses to incentives (Panksepp, 1998; Rolls,

1999). Some researchers have argued for motivational functions of association cortex structures, which feed information about incentives and contexts to the core motivational brain circuit (cf. Fig. 3). More specifically, Damasio (1994) has proposed that the insula and related associative cortices provide somatosensory information (i.e., "gut" feelings) about the affective qualities of incentives and thus inform individuals' motivated cognitions, decision making, and actions.

Core Motivational Brain Circuit: Evidence from Neuroimaging Research

Research conducted in our laboratory provides the first evidence that individual differences in implicit motivation predict activation in the motivational brain circuit we have just described (Hall et al., 2007; Schultheiss et al., 2008). Using an fMRI design, 24 participants viewed blocks of social cues signaling high dominance (i.e., angry faces) alternating with blocks of neutral faces during an oddball-task condition (surprised faces were also shown as low-dominance cues but will not be discussed here; see Schultheiss et al., 2008, for further details). Twelve individuals high in power motivation and twelve individuals low in power motivation were selected to participate based on their power motivation scores assessed with a Picture Story Exercise (PSE; McClelland et al., 1989) during a screening session. For the presentation of the following findings, we also coded PSEs for affiliation and achievement motivation. While in the scanner, participants viewed blocks of color pictures of individuals with either an angry or neutral facial expression followed by a white fixation cross. During the oddball task, participants were instructed to indicate with a button press whether an "X" appeared on the screen instead of the fixation cross.

Our results[1] show that while implicit power motivation and implicit achievement motivation are associated with greater activation in the core motivational brain circuit (amygdala, insula, caudate, nucleus accumbens, OFC), implicit affiliation motivation is associated with

activation only in the amygdala and deactivation in the insula, caudate, nucleus accumbens, and OFC. Scatterplots of the correlations between participants' motive z-scores and brain activation changes in response to angry versus neutral faces, along with the peak voxel coordinates, are shown in Figure 4.

As predicted, individual differences in implicit power motivation moderated brain activation in the core motivational brain circuit in response to FEEs signaling another person's anger. This pattern of activation is consistent with previous research in our laboratory indicating that angry faces are motivationally significant for power-motivated individuals (Schultheiss & Hale, 2007; Schultheiss, Pang, Torges, Wirth, & Treynor, 2005). Schultheiss and Hale (2007) have argued that angry facial expressions signal a challenge to the perceiver. For power-motivated perceivers, they represent a negative incentive and prompt behavior aimed at reasserting one's own claim to dominance. Thus, it is not surprising that power-motivated individuals show activation in areas of the brain associated with the preparation and invigoration of motivated action.

Significantly less research has been conducted on achievement motivation and FEEs as motivational incentives. Similar to power motivation, achievement motivation was also associated with greater activation in the core motivational brain circuit in response to angry versus neutral facial expressions in our study. Because the independent mastery of challenging tasks is at the core of achievement motivation and failure to deal with challenges autonomously is associated with parents' negative emotions in the socialization history of achievement-motivated individuals (e.g., Rosen & D'Andrade, 1959), we speculate that angry faces serve as a conditioned cue to which achievement-motivated individuals respond with active avoidance. That is, they have learned to escape others' anger by engaging in behavior aimed at mastering a

challenge, resulting in approach-related behavior and activation in the core motivational brain circuit.

Angry facial expressions also have aversive properties for affiliation-motivated individuals, although for a different reason: They represent a threat to the affiliation-motivated individual's need to have secure and harmonious relationships with others. As several authors have pointed out (e.g., Boyatzis, 1973; Schultheiss & Hale, 2007; see also chapter 3), the affiliation motive is characterized by a strong fear of rejection component, which makes affiliation-motivated individuals particularly sensitive for social signals that suggest rejection. The anger face is, of course, a cardinal signal of rejection, and it is therefore not surprising that high-affiliation individuals show brain activation patterns in response to this stimulus that differ markedly from those of low-affiliation individuals. It is interesting to note, though, that while they show signs of heightened emotional sensitivity to this FEE (increased amygdala response), the behavior-generating structures of the motivational brain (caudate, accumbens) show reduced activation. This perhaps suggests that affiliation-motivated individuals react with passive avoidance to emotionally highly aversive nonverbal signals of rejection. Alternatively, affiliation-motivated individuals may be responding to angry facial expressions with increases in progesterone and oxytocin, which may have deactivating effects on brain regions involved in core motivational processes. Clearly, further research is needed to resolve this issue.

In conclusion, our findings provide support for the original idea proposed by McClelland and colleagues (1989) that implicit motives are mediated predominantly by subcortical brain structures subserving motivation. They also support LeDoux's (2002) argument for a nonconscious motivational system that drives behavior in response to incentives and operates independently from a cortical system involved in the explicit regulation of behavior.

Conclusions and Future Directions

To summarize, research on the behavioral endocrinology of motives indicates that power motivation is strongly associated with sympathetic nervous system activation whereas affiliation motivation is associated with indices of parasympathetic nervous system activity. Power motivation is associated with higher basal testosterone levels and testosterone changes during social dominance contests as a function of victory or defeat in men. Recent research suggests that estradiol in women may serve a similar role in power motivation as testosterone in men. Power motivation predicts enhanced instrumental learning in both men and women. Furthermore, stressed power motivation has been associated with cortisol increases and impaired immune system functioning. By contrast, affiliation motivation is associated with resistance to illness and better immune system functioning, which may be linked to progesterone levels. The hormonal correlates of achievement motivation have not been systematically explored so far, although tantalizing clues exist that this may present a rewarding field for future research.

Affective neuroscience research suggests that the implicit motive construct may be closely tied to activity in motivational brain structures, including the amygdala, insula, caudate, nucleus accumbens, and OFC. Neuroimaging evidence from our laboratory reveals that power-motivated and achievement-motivated individuals show increased activation in the core motivational brain circuit in response to social cues signaling dominance whereas affiliation-motivated individuals show deactivation in all of these regions with the exception of the amygdala. Thus, the biopsychological roots of implicit motives have been well documented in research examining the associations between implicit motives, hormones, and immune system functioning. In addition, these connections are starting to be confirmed and further explored with fMRI research investigating the neural substrates of implicit motives.

A systematic exploration of the brain areas and functions involved in implicit and explicit forms of motivation represents a highly overdue and in all likelihood very fruitful next step for motivation research. Studies already indicate that implicit and explicit systems involved in emotional processing and motivated action compete with and suppress each other (e.g., Ochsner, Bunge, Griss, & Gabrieli, 2002; Lieberman et al., 2007; Poldrack et al., 2001). And several theorists of the biopsychology of motivation recognize the necessity to distinguish between brain systems dedicated to conscious, goal-directed forms of action and nonconscious, automatic forms of striving for incentives (e.g., Berridge & Robinson, 2003; LeDoux, 2002; Rolls, 1999). We believe that bringing implicit motive research into the affective neuroscience arena might be mutually beneficial to both fields. Work on implicit motives, particularly on how they contrast and interact with explicit motives and goals, can inform neuroscience research on the motivational and volitional wellsprings of action. Findings from cognitive and affective neuroscience can help motivation researchers better understand how and why implicit and explicit levels of motivation can exist independently and often be in conflict with each other.

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Author Notes

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Notes

[1] In contrast to the results reported in Schultheiss et al. (2008), who employed relatively rigorous significance thresholding for the presentation of their results, we used more lenient criteria for small-volume regions of interest like the nucleus accumbens and the amygdala ($p < .05$, uncorrected), for the findings we present here.

Figure Captions

Figure 1. Biobehavioral model of endocrine responses to victory and defeat during a dominance contest in individuals high in n Power. High n Power winners respond with greater sympathetic activation (catecholamine release) than cortisol release, which stimulates the release of gonadal steroids (testosterone in men, estradiol in women) that facilitate dominant behavior and are involved in brain reinforcement processes. In high-n Power losers, the cortisol response outweighs sympathetic activation, resulting in a net inhibition of gonadal steroid release and therefore transiently less competitiveness and behavioral reinforcement. Based on Schultheiss (2007) and Stanton and Schultheiss (2007).

Figure 2. Effects of motivational arousal through 30-min movie excerpts on post-movie salivary progesterone levels, residualized for pre-movie progesterone. Participants who had watched an affiliation-arousing movie ("Bridges of Madison County") had higher post-movie progesterone than participants who had watched a neutral movie (Amazon documentary) or a power-arousing movie ("The Godfather II"). Adapted with permission from Schultheiss, O. C., Wirth, M. M., & Stanton, S. J. (2004). Effects of affiliation and power motivation arousal on salivary progesterone and testosterone. *Hormones and Behavior, 46(5),* 592-599.

Figure 3. Sagittal cut of the brain at the midline, with approximate locations of key structures of the motivational brain. Closed circles represent structures fully or partly visible in a sagittal cut; dashed circles represent structures that are hidden from view in a sagittal cut. The amygdala is hidden inside the frontal pole of the temporal lobe; the striatum lies at the front of the subcortical forebrain, with its tail extending to more posterior regions. Modified from Schultheiss, O. C., & Wirth, M. M. (2008). Biopsychological aspects of motivation. In J.

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Figure 4. Effects of implicit motives (z scores) on brain activation changes (peak voxels) in response to angry versus neutral faces in the insula, amygdala, caudate, nucleus accumbens, and orbitofrontal cortex. Results represent peak activation voxels from significant region-of-interest analyses. Correlation coefficients ≥ .39 are significant at $p < .05$, correlation coefficients ≥ .50 are significant at $p < .01$. The numbers given below each correlation coefficient represent x, y, and z coordinates in the brain space of the Montreal Neurological Institute. Based in part on Hall et al. (in preparation) and Schultheiss et al. (2008).

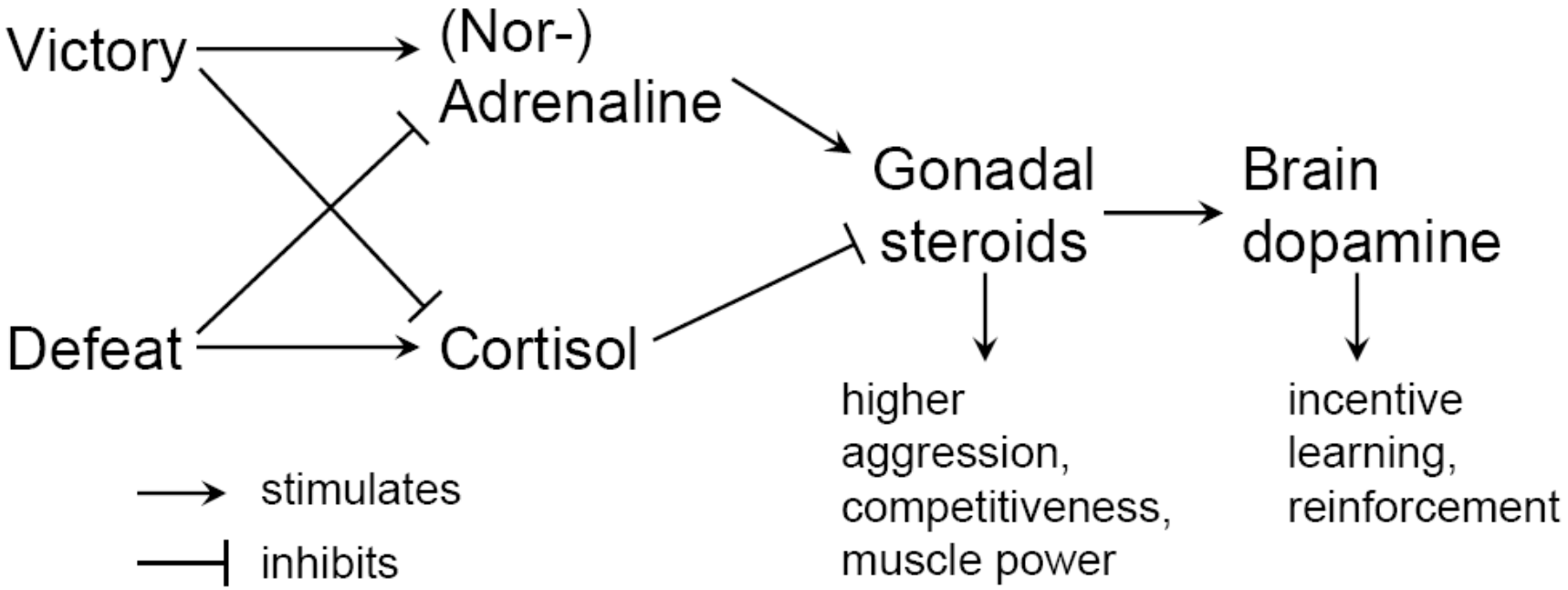
Victory
(Nor-)
Adrenaline
Defeat
Cortisol
Gonadal
steroids
Brain
dopamine
higher
aggression,
competitiveness,
muscle power
incentive
learning,
reinforcement
stimulates
inhibits

Figure 1

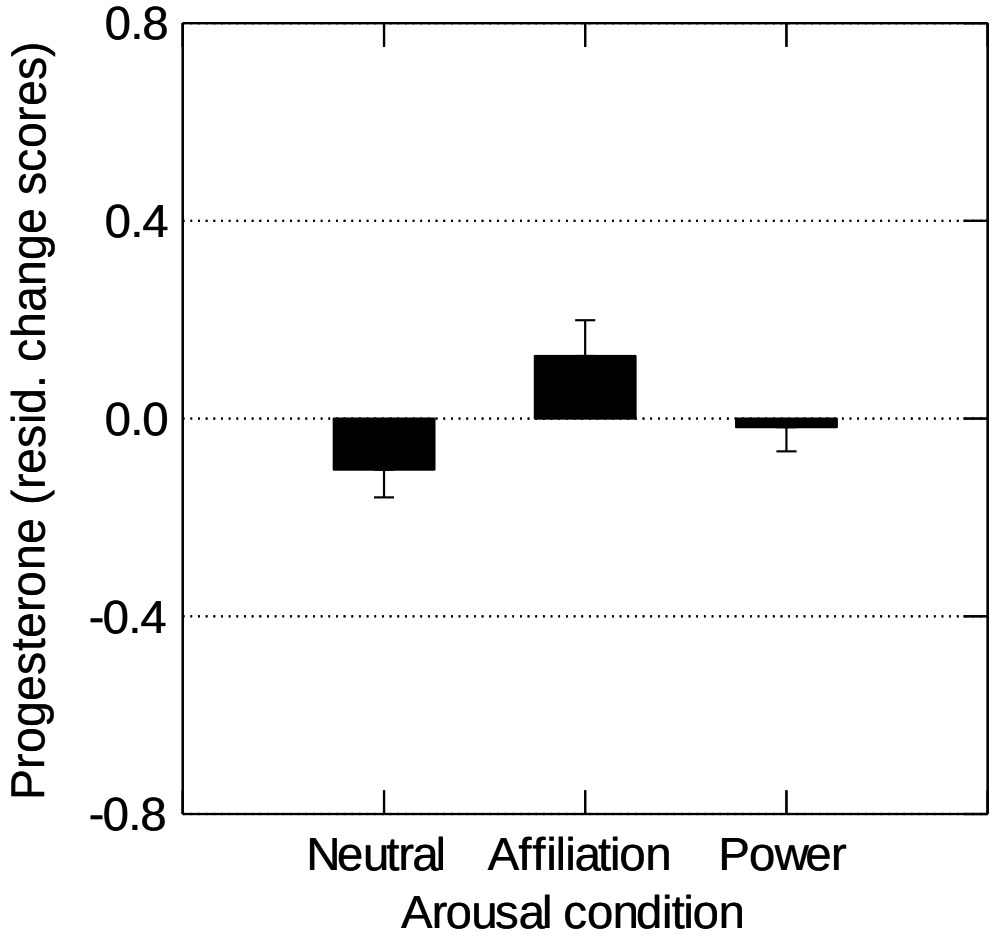
0.8
0.4
0.0
-0.4
-0.8
Progesterone (resid. change scores)
Neutral
Affiliation
Power
Arousal condition

Figure 2

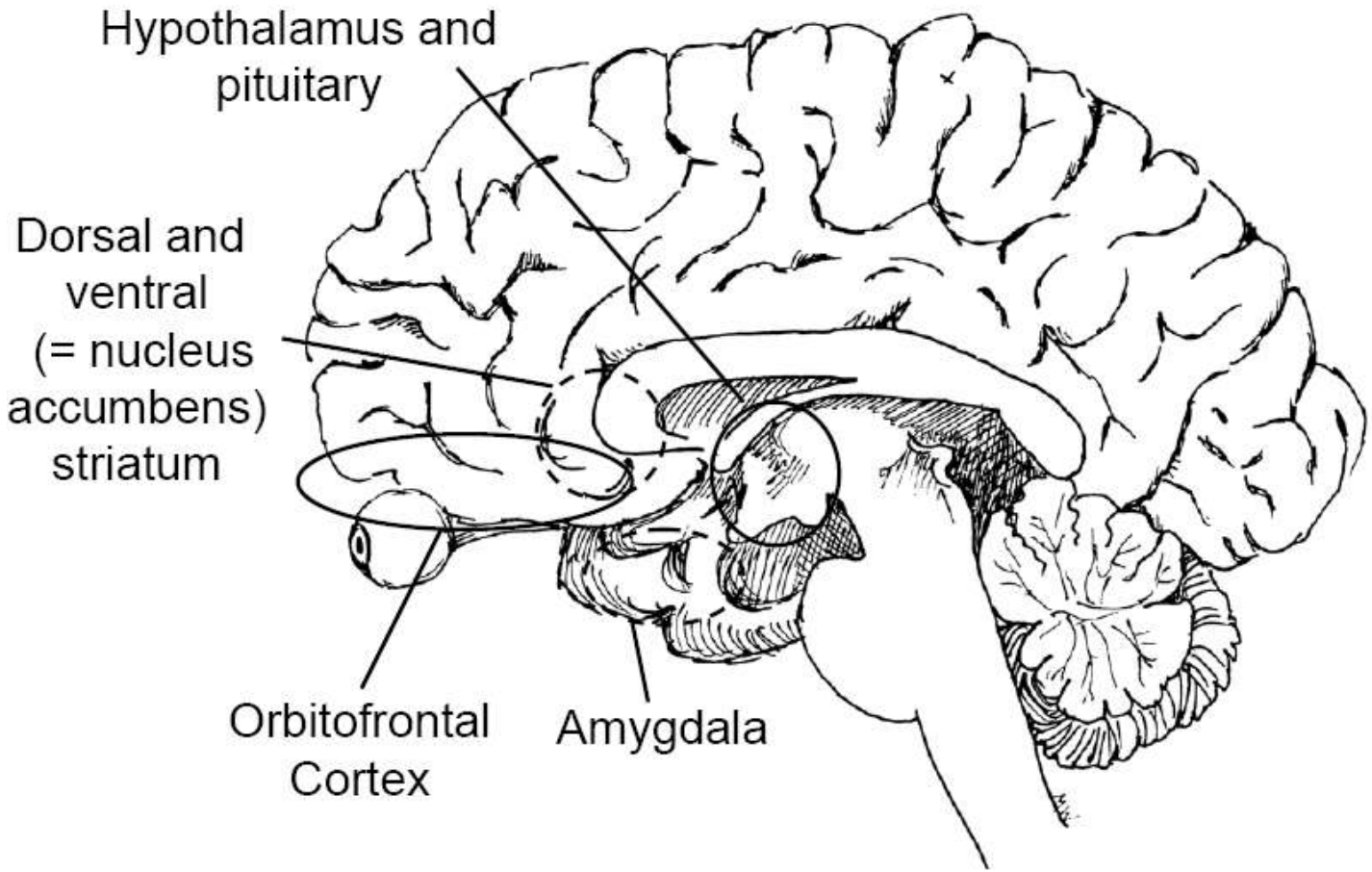
Hypothalamus and pituitary
Dorsal and ventral (= nucleus accumbens) striatum
Orbitofrontal Cortex
Amygdala

Figure 3

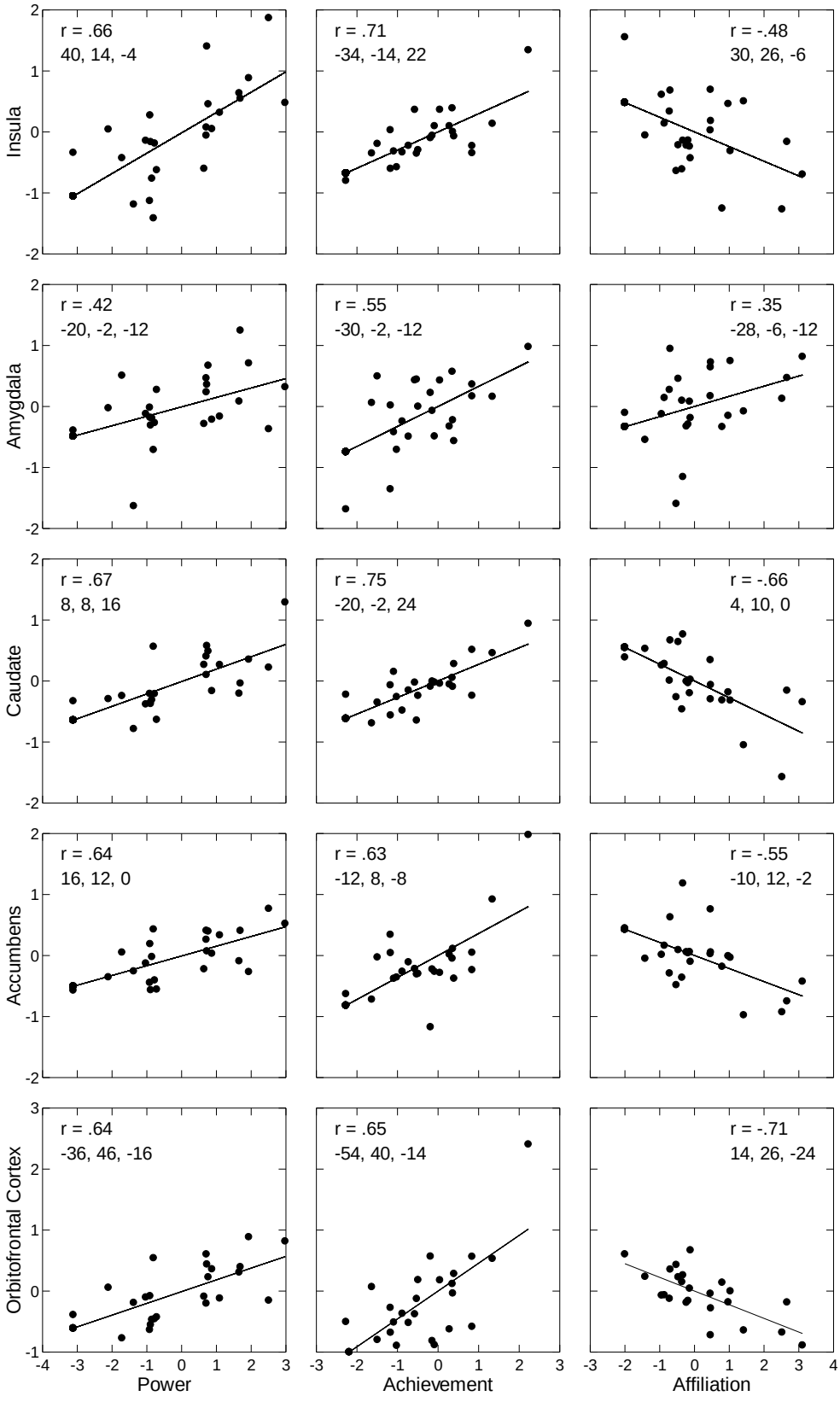
r = .66
40, 14, -4
r = .71
-34, -14, 22
r = -.48
30, 26, -6
r = .42
-20, -2, -12
r = .55
-30, -2, -12
r = .35
-28, -6, -12
r = .67
8, 8, 16
r = .75
-20, -2, 24
r = -.66
4, 10, 0
r = .64
16, 12, 0
r = .63
-12, 8, -8
r = -.55
-10, 12, -2
r = .64
-36, 46, -16
r = .65
-54, 40, -14
r = -.71
14, 26, -24
Insula
Amygdala
Caudate
Accumbens
Orbitofrontal Cortex
Power
Achievement
Affiliation

Figure 4