CALIFORNIA STATE UNIVERSITY SAN MARCOS

THESIS SIGNATURE PAGE

THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE

MASTER OF ARTS

IN

PSYCHOLOGY

THESIS TITLE: Scratching as a Behavioral Indicator of Positive and Negative Arousal in Common Marmosets (Callithrix jacchus).

AUTHOR: Sarah Jo Neal

DATE OF SUCCESSFUL DEFENSE: 4/30/15

THE THESIS HAS BEEN ACCEPTED BY THE THESIS COMMITTEE IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF ARTS IN
PSYCHOLOGY.

Nancy G. Caine
THESIS COMMITTEE CHAIR

[Signature]

4/30/15

Marie Thomas
THESIS COMMITTEE MEMBER

[Signature]

4/30/15

Kimberly D'Anna Hernandez
THESIS COMMITTEE MEMBER

[Signature]

4/30/15
Scratching as a Behavioral Indicator
of Positive and Negative Arousal in Common Marmosets (*Callithrix jacchus*)

Sarah Neal

California State University San Marcos
Abstract

Negative emotional arousal is associated with a pattern of physiological and behavioral responses, such as increases in heart rate, blood pressure, and locomotion. In captive Old World monkeys and apes, self-directed scratching is a well-known behavioral indicator of negative arousal, with increased rates of scratching occurring in conjunction with simulated predation threats, social competition, cognitive challenge, and interactions with dominant conspecifics. Additionally, scratching in the context of negative arousal has also been found to be lateralized (i.e., scratching is directed to one side of the body or the other). For example, chimpanzees tend to prefer to use the right hand to scratch the left side of the body during anxiety-provoking circumstances. I tested the prediction that scratching in response to negative arousal generalizes to a sample of naturally-housed New World primates (common marmosets; *Callithrix jacchus*).

The second aim of my thesis was to determine if contexts of positive arousal (play, food anticipation, and foraging) are also associated with increased rates of scratching, a question that has not yet been addressed in the literature. Finally, I predicted that subjects would scratch more with the left hand than the right during negative arousal, and examined with which hand subjects would scratch more during positive arousal. Contrary to the first prediction, and contrary to the widely accepted assumption that there is a positive relationship between anxiety and scratching in primates, my results showed that scratching significantly decreased in response to all three negative arousal contexts. Contexts within positive arousal showed varying patterns of scratching between baseline, manipulation, and post-manipulation periods. There were no differences between the frequency of left and right limb scratches during negative arousal manipulations. There was a bias for right hand scratching in the positive arousal conditions, but the overall rates of scratching in all manipulations were too low to adequately address the prediction about
lateralized scratching. Overall, data from this study point to the conclusion that the anxiety-scratching relationship may be more complex than is generally accepted in the literature.

*Keywords:* scratching, arousal, marmoset, anxiety, laterality
Scratching as a Behavioral Indicator of Positive and Negative Arousal in Common Marmosets (*Callithrix jacchus*)

The term “arousal” is used in different ways in the psychological and neuroscience literature. At the most basic level, arousal refers to the on-off state of the brain (e.g., conscious versus unconscious), which is controlled by the reticular activating system (RAS) (Berlyne, 1960). Arousal is also used to describe the activation of the autonomic nervous system. When humans experience a stressful or exciting situation, the hypothalamus triggers activation of the sympathetic nervous system, which, among other reactions, increases heart rate and blood pressure (Berlyne, 1960; Comer, 2010). Additionally, the RAS, which exhibits EEG activation patterns, works with the sympathetic nervous system and inhibits parasympathetic activity to increase arousal (Berlyne, 1960).

In human studies, investigators can induce arousal, measure the resulting behavioral and physiological responses, and simultaneously ask participants to label what they are feeling. We assume that the physiological responses that accompany self-reported feelings of anxiousness in humans, including increased heart rate, blood pressure, breathing, and muscular tension (Comer, 2010), can be generalized to non-human animals. Furthermore, when animals engage in behaviors that humans exhibit during states of anxiety, such as increased agitation and vigilance/visual scanning (Koenig, 1998), we assume the animal is experiencing something equivalent to anxiety.

In humans, the physiological and behavioral correlates of arousal may look very similar for positive and negative arousal, but the self-reported emotional and cognitive correlates differ. For example, a person might exhibit increased heart rate, blood pressure, muscular tension, and agitation, but, depending on the circumstances, describe that arousal as either excitement (positive arousal) or anxiety (negative arousal). In non-human animals, there are some external
indicators as to whether the arousal may be positive or negative, including the presence of context-specific vocalizations, approach/avoidance behaviors, and signs of pain. For example, non-human primates issue alarm calls and contact calls in anxiety-provoking situations, such as confrontation with a predator or separation from the social group (Norcross & Newman, 1999). Additionally, like humans, animals tend to avoid unpleasant circumstances and approach or actively seek pleasant circumstances or stimuli (Clara et al., 2008; Mellou, 2006). In the absence of these indicators of negative arousal (i.e., alarm calls, avoidance, and pain), we can assume that the exhibited arousal is positive.

Understanding the neural substrates and behavioral correlates of arousal not only contributes to the body of knowledge in behavioral neuroscience, but also has important implications for improving the well-being of captive animals in research laboratories and zoos. Successful animal husbandry reduces stress (which can lead to negative arousal) and provides opportunities for enrichment (which can produce positive arousal). Thus, successful husbandry is dependent on a thorough understanding of the nature and indices of positive and negative arousal.

**Positive Arousal**

Positive arousal is less commonly studied than negative arousal, and, as described above, the distinction between positive and negative arousal is complicated by the fact that they share some physiological and behavioral correlates (Jacob et al., 1999; Schwartz, Weinberger, & Singer, 1981). For example, in comparing cardiovascular differences between the induced emotional states of happiness and fear, Schwartz et al. (1981) found that human subjects exhibited similar increases in blood pressure during fear and happiness. The authors also found an increase in heart rate during fear and happiness, although the increases were higher during
fear than happiness. This pattern of findings is consistent with other research that has found increases in heart rate and blood pressure during both positive and negative mood in humans (Jacob et al., 1991; Waldstein et al., 2000). In nonhuman animals, positive arousal is assumed to arise when there are indications of excitement (increased locomotion and attention) in the absence of aggression, fear-related vocalizations/postures/facial expressions, stereotypies, or pain.

**Play as Positive Arousal in Nonhuman Primates**

Play is widely considered to be an expression of positive arousal and well-being (Biben & Campoux, 1999; Lancy, 1980; Mellou, 2006). Animals often seek opportunities to play and will play for long periods of time (Mellou, 2006). Many studies of primates have shown that rates of play are greatly reduced during stressful situations (e.g., in the presence of predatory threat or food deprivation), leading to the conclusion that play is a good indicator of psychological well-being (Baldwin & Baldwin, 1974; Biben & Champoux, 1999; Lancy, 1980; Loy, 1970; Mellou, 2006; O’Neill-Wagner, Bolig, & Price, 1994; Spinka, Newberry, & Bekoff, 2001). There is even evidence that the mere observation of play is arousing. Parr and Hopkins (2000) had chimpanzees (*Pan troglodytes*) view a video of intense play and measured resulting tympanic membrane thermometry (tty) to assess overall brain temperature (higher brain temperature is indicative of higher arousal). They found that left tty increased while viewing the play videos. The inhibition of aggression and absence of injury during play (Poirier, Bellisari, & Haines, 1978) suggests that, despite its “rough and tumble” nature, the arousal associated with play is of a positive nature.
Positive Arousal in Feeding Contexts

Researchers have also examined positive arousal in appetitive contexts (i.e., contexts in which an animal anticipates and/or consumes highly desirable foods). Braesicke et al. (2005) had common marmosets (*Callithrix jacchus*) view preferred (marshmallows, raisins, and grapes) and non-preferred (laboratory pellets) foods through a small hole in a food box during two phases: an anticipation period, in which the subjects could only view the food, and a consumption period, in which the subjects were allowed to eat the food. The authors found that heart rate and blood pressure were higher when viewing and consuming preferred rather than non-preferred foods. Additionally, there is evidence for a dissociation between the pleasure caused by the anticipatory period and the consumption period in these appetitive contexts. The anticipatory period, or the “wanting,” activates the dopamine system; in fact, simply searching for food, or foraging, (i.e., the “wanting” of food) is sufficient to activate the dopamine neurotransmitter system. On the other hand, the consumption period, or “liking,” activates the opioid system (Boissy et al., 2007). Other research using the anticipatory period of food rewards has found increases in locomotor activity (an indication of arousal) in various species of captive animals, including mink, pigs, and rats (Boissy et al., 2007).

Negative Arousal

Unlike positive arousal, negative arousal (usually referred to as anxiety in primates) has been given a great deal of empirical attention, especially in nonhuman primates, in part because it is used to assess well-being in captivity. Researchers have identified a number of physiological and behavioral indicators of anxiety, including stereotypies (Koolhaus et al., 1999), increased cortisol levels (Clara, Tommasi, & Rogers, 2008; Elder & Menzel, 2001; Higham, Maclarnon, Hesitermann, & Semple, 2009), increased heart rate (Boccia, Reite, &
Laundenslager, 1988), increased blood pressure (Parr, 2001; Parr & Hopkins, 2000), piloerection (De Almeida, De Paula, & Tavora, 2006; Dettling, Pryce, Martin, & Dobeli, 1998; Omedes, 1981), lowered skin temperature (Tomaz, Verburg, Boere, Pianta, & Belo, 2003), and self-directed behaviors (Diezinger & Anderson, 1986; Elder & Menzel, 2001; Maestripieri, Schino, Aureli, & Troisi, 1991; Leavens, Aureli, & Hopkins, 2004; Mason & Perry, 2000; Troisi et al., 1991). Of most importance for the proposed study is the literature on anxiety and a prominent form of self-directed behavior: self-scratching.

**Scratching as an Indicator of Negative Arousal**

Self-directed behaviors (SDBs), including scratching, grooming, yawning, body shaking, and rubbing, occur during anxiety-provoking situations, and are thought to reflect feelings of uncertainty, threat, or danger (Elder & Menzel, 2001; Leavens, Aureli, & Hopkins, 2004; Mason & Perry, 2000). Self-scratching (hereafter, “scratching”), defined as movement of the fingers in a repetitive, parallel scraping or raking motion across a body part or fur (Mootnick, Cunningham, & Baker, 2012; Troisi et al., 1991), is one of the most commonly used behavioral indicators of anxiety among nonhuman primates. Although scratching can occur in the context of self-grooming, many researchers believe that scratching as grooming and scratching as an indicator of anxiety are separate behaviors. For example, Mootnick et al. (2012) were able to distinguish grooming from scratching by more clearly defining the two behaviors. The authors defined self-grooming as manipulation of the fur using the thumb, with gaze directed at the groomed body part, whereas scratching does not include these specifications. In using these definitions, they were able to exclude self-grooming from their analyses of self-scratching across various primate species. Diezinger & Anderson (1986) concluded that skin care scratching and scratching as a SDB are causally different, and may have different determinants as indicated by the finding that
animals differentially direct these two activities across their bodies. Specifically, rhesus monkeys (Macaca mulatta) directed most scratching toward the legs, back, and thighs, whereas most self-grooming was directed toward the arms and legs, with the least amount of self-grooming directed toward the thighs.

**Scratching in social contexts.** Much of the research on scratching and anxiety in non-human primates has focused on social contexts because of the inherent tension resulting from the potential for conflict. Scratching rates increase with (the risk of) intra- and inter-group aggression, whereas rates of scratching decrease when social tension is reduced via allogrooming (Maestripieri et al., 1991; Schino, Maestripieri, Scucchi, & Turillazzi, 1990). Research from social contexts has primarily focused on anxiety and scratching in relation to dominance rank and risk of threat or aggression from conspecifics.

Pavani et al. (1991) examined scratching rates in response to inter-individual proximity (passive contact, close proximity, and solitariness) in conjunction with dominance rank in long-tailed macaques (M. fascicularis). They found that subordinate animals had higher scratching rates in general, and that females scratched more when in close proximity to a male. The authors reasoned that the increased scratching was indicative of anxiety stemming from conflicting motivation to approach and withdraw from the more dominant conspecific.

Diezinger and Anderson (1986) found that a sample of rhesus macaques of intermediate rank scratched nearly twice as frequently as dominant and low ranking individuals during feeding time. Low-ranking individuals did not attempt to obtain food until all higher-ranking individuals had already done so, thus reducing the potential for anxiety in that context. Intermediate-ranking monkeys, however, vacillated between approach to and avoidance of the
food in the presence of a higher-ranking group mate, thus increasing anxiety due to conflicting motivations.

Viewing or hearing conspecifics in a state of anxiety also induces scratching in great apes. For example, Japanese macaques (*M. fuscata*) are known to increase scratching (and other SDB) rates in response to viewing a strange conspecific in an alert posture. Nakayama (2004) called this a “contagion of scratching,” representing a transmission of arousal between the animals. Furthermore, chimpanzees need not see conspecifics in their physical environment in order for arousal transmission to occur. Even hearing a neighbor’s vocalizations (hooting, screaming, or banging/drumming) (Baker & Aureli, 1997) or viewing a video of agonistic encounters between a group of unknown chimpanzees (Hopkins et al., 2006) is effective in increasing scratching rates in chimpanzee subjects. Lastly, close proximity to an unknown conspecific can induce scratching. Schino et al. (1990) found that female long-tailed macaques increased overall rates of SDBs, including scratching, when placed near an unfamiliar rather than familiar conspecific. The authors conclude that this increased scratching was indicative of anxiety resulting from uncertainty and risk of aggression from the unknown conspecific.

**Scratching in non-social contexts.** Cognitive challenges can cause negative arousal, which has been correlated with rates of SDBs. Leavens et al. (2001) used a computerized match-to-sample (MTS) task, in which the subject was required to match a given symbol to a sample symbol using a joystick in both easy (simple discrimination between the symbols) and hard (difficult discrimination between the symbols) conditions. Subjects that transitioned from the easy to the difficult task exhibited more scratching overall than subjects that transitioned from the hard to the easy task. Using a very similar procedure, Leavens et al. (2004) also found that increased scratching rates in chimpanzees occurred with more incorrect responses in a MTS task.
Elder and Menzel (2001) had a female orangutan (*Pongo pygmaeus*) use a joystick to move a cursor on a computer screen. This task included three conditions varying in difficulty level: the subject had to (a) solve four problems at a time with a fast-moving cursor to receive a reward, (b) solve one problem with a slow-moving cursor to receive a reward, or (c) solve one problem with a fast-moving cursor with a delay inserted between solving the problem and receiving the reward. The subject exhibited the highest rates of SDBs during the inserted delay condition, suggesting that the subject was negatively aroused when an expected reward was not provided.

**Pharmacological evidence of the relationship between anxiety and scratching.**

Pharmacological studies also connect scratching to anxiety. The majority of these studies use anxiolytic and anxiogenic drugs to reduce or induce scratching or other SDBs. Barros et al. (2000) studied scratching and anxiety in Cerrado marmosets (*C. penicillata*) by creating a predator model of anxiety called the Marmoset Predator Confrontation Test (MPCT). In this model, the subject is placed into an eight-figure maze after administration of diazepam (valium) or saline, and subsequently confronted with a taxidermied model of a cat (*Felis tigrina*), a predator common to the marmoset’s natural environment. The authors found that 2 and 3 mg/kg doses were effective in reducing overall scratching rates compared to the saline control. These doses also increased the amount of time spent in the section closest to the model predator. This implies that the marmosets that received the anxiolytic drug were less anxious, as indicated by decreased rates of scratching as well as increased amount of time spent near what would normally be an anxiety-inducing stimulus. Furthermore, the Barros et al. data show that rates of scratching in the absence of arousal (i.e., when medicated with diazepam) are very low,
averaging less than 1 scratch per hour. This is an important indication of the extent to which scratching is related to arousal.

Cilia and Piper (1996) found similar results to Barros et al. (2000). Their sample of common marmosets exhibited decreased rates of scratching after 1.0 and 3.5 mg/kg doses of diazepam in response to an unknown conspecific. Furthermore, they found that the anxiolytic drug doses also decreased rates of other anxiety-related behaviors, such as aggression and self-grooming. Schino et al. (1996) examined the effects of both anxiogenic (FG 7142) and anxiolytic (lorazepam) drugs on the frequency of scratching and other anxiety-related behaviors (i.e., autogrooming and body shaking) in female macaques (*M. fascicularis*). They found dose dependent increases in scratching and other anxiety-related behaviors in response to the anxiogenic drug, and dose dependent decreases in scratching and anxiety-related behaviors in response to the anxiolytic drug. Schino et al. (1991) also demonstrated that lorazepam decreased scratching in female macaques, particularly those of low rank. These authors showed that lorazepam did not change the baseline rates of grooming, locomotion, and passive aggression, suggesting that possible sedation from the drug was not responsible for the changes in rates of scratching. Thus, the authors concluded that the decreases in anxiety due to administration of lorazepam were responsible for the observed reductions in scratching.

Taken together, the results of the aforementioned pharmacological studies suggest that scratching is associated with the internal state of anxiety. Drugs that are used to induce and reduce anxiety in humans are effective at inducing and reducing anxiety-related behaviors in non-human primates with concurrent productions and reductions in scratching.

**Physiological evidence of the relationship between anxiety and scratching.** Few researchers have attempted to correlate scratching with physiological indicators of anxiety such
as heart rate, blood pressure, and circulating levels of catecholamines and corticosteroids (Maestripieri et al., 1991). In fact, no studies have investigated correlations between scratching and blood pressure or circulating catecholamines, and only one study has indirectly examined heart rate in relation to scratching. As in humans, increased heart rate is suggestive of the internal state of anxiety in primates. Consistent with research linking scratching to anxiety in social agonistic encounters, Boccia, Reite, and Laudenslager (1988) found that the heart rate of a pigtail macaque (*M. leonina*) increased during agonistic encounters and decreased upon initiation of allogrooming. Because heart rate is a well-established indicator of anxiety, and because heart rate increases during agonistic encounters, researchers assume that agonistic encounters induce anxiety in the animal. Consequently, because scratching increases during agonistic encounters, the assumption can be made that scratching is an indicator of anxiety in the animal during these types of situations (Maestripieri et al., 1991; Manson & Perry, 2000; Pavani et al., 1991; Schino et al., 1990).

The level of circulating cortisol is another physiological indicator of anxiety that has been investigated in the literature on self-scratching. Cortisol is often called the “stress hormone” because it is released during times of increased physiological or psychological demand (Axelrod & Reisine, 1984). In humans, increased cortisol levels are associated with high levels of anxiety and/or stress. However, research concerning cortisol levels, anxiety, and scratching in primates is inconclusive. In inducing frustration in a male orangutan, Elder and Menzel (2001) found lower cortisol levels during testing (computer tasks) days than during non-testing (baseline) days, whereas scratching rates were higher during testing than non-testing days. The authors mentioned the possibility that engaging in scratching may serve as a behavioral release of anxiety, consequently lowering cortisol levels and acting as a coping mechanism. Higham,
Maclarnon, Heistermann, Ross, and Semple (2009) also found no correlation between scratching rates and fecal glucocorticoid levels in female wild olive baboons (*Papio hamadryas nubis*). These authors speculated that scratching may serve as an effective coping mechanism for anxiety or stress (although it is entirely unclear how it could do so), and that scratching may be more related to low-level anxiety than chronic stress. Maestripieri et al. (1991) also stated that scratching (and other displacement activities) may function to regulate the animal’s psychological state. This regulation would consist of reducing anxiety by either redirecting attention to the body and away from noxious stimuli, or causing actual physiological changes, such as increased catecholamine release. In any case, research that simultaneously examines physiological correlates of anxiety and scratching is needed to further understand the source of the scratching-anxiety relationship in non-human primates.

The Neurological Basis of the Arousal-Scratch Association: Evidence from Lateralization.

There is ample evidence that scratching is related to anxiety, but the reason for this association is unclear. Hopkins et al. (2006) write that arousal may cause histamine release and/or piloerection, which, in turn, makes individuals feels “itchy.” These or other explanations await empirical confirmation. But data from studies of lateralized preferences for scratching have implicated the right hemisphere in the scratch response.

Lateralization refers to the specialization of the cerebral hemispheres for certain biological functions, including behavior. Two popular theories propose that the left and right hemispheres are equally, but differently, involved in emotions (Demaree, Everhart, Youngstrom, & Harrison, 2005). There is good evidence that the medial pre-frontal cortex (and some other regions) of the right hemisphere are selectively involved in autonomic responsiveness to stress in rats and humans (Denenberg & Yutzey, 1985; Wittling, 1997). The emotional-valence
hypothesis (Silbermann & Weingartner, 1986) posits that the right hemisphere controls responses to negative arousal, such as anxiety, and the left hemisphere controls responses to positive arousal, such as excitement. The approach-withdrawal hypothesis, put forth by Davidson (1992), states that approach-related behaviors (positive arousal) are associated with greater activity in the left hemisphere, whereas withdrawal behaviors (negative arousal) are associated with greater activity in the right hemisphere. Combined, these two theories have led to the assumption that animals placed in positively arousing situations (i.e., situations that induce happiness, approach, and excitement) should exhibit increases in left-hemisphere activity (Berlyne, 1960). Animals placed in negatively arousing situations (i.e., situations that induce anxiety or fear and avoidance) should exhibit increased activity in the right hemisphere.

Behavioral evidence supporting emotional lateralization and the valence and approach-withdrawal hypotheses includes data showing that fish, reptiles, and mammals, including non-human primates, prefer to view threatening stimuli with the left eye (Bisazza, Rogers, & Vallortigara, 1998; Bracinni et al., 2012; Rogers, 2010). Non-human primates have approximately 50% decussation of the optic fibers (Brooks, Komaromy, & Kallberg, 1999); however, the contralateral fibers are larger in diameter, and thus conduct more quickly than the ipsilateral fibers (Rogers, Ward, & Stafford, 1994). Thus, a left eye preference is indicative of greater activity in the right hemisphere. Studies have also investigated emotional lateralization in the form of motor biases. Austin and Rogers (2007) found that horses (Equus caballus) move farther away when confronted with an inanimate threatening stimulus from the left. Furthermore, Hook-Costigan and Rogers (1998) found that common marmosets display larger left-mouth movements than right-mouth movements when issuing alarm calls. These studies suggest that the
right hemisphere is more active during anxiety-provoking or stressful situations, that is, when animals are negatively aroused.

Leavens et al. (2004) found that a single chimpanzee subject preferentially scratched the left side of his body during poorer performance on a difficult cognitive task. Moreover, Hopkins et al. (2006) found that chimps who viewed videos of agonistic encounters of unknown conspecifics directed self-scratches toward the left side of the body. Both Leavens et al. (2001, 2004) and Hopkins et al. (2006) explained their findings in terms of nervous system organization. First, as explained above, the right hemisphere shows increased activity during negative emotional arousal. Second, ipsilaterally descending fibers traveling through the dorsal horns of the spinal cord inhibit pain and itch. If the right hemisphere is more active, sensation in the right cutaneous hemispace is more inhibited, causing the perception of increased sensitivity in the left hemispace. As such, animals in anxiety-provoking situations may scratch their left side more because of perceived greater arousal and sensitivity in the left hemispace.

However, the conclusions drawn by Leavens et al. (2004) are speculative. Hopkins et al. (2006) point to the need for more research in this area, stating that there are many physiological models that could account for the observed left-side scratching bias. Indeed, studies conducted with common marmosets present a perplexing case of lateralized scratching, as side and hand preferences during scratching are confounded. Neal, Rice, Ritzer, Wombolt, and Caine (2013) examined hand preferences during scratching in common marmosets with the specific aim of replicating the left side scratching bias in a different species. We found that subjects scratched significantly more with their left hand and on the left side of the body, regardless of overall hand preferences. If we focus solely on the findings of increased left hand scratching, it seems that scratching may be a result of contralateral motor biases under conditions of arousal. That is,
because the brain controls the limbs in a contralateral manner, and because the right hemisphere is more active during anxiety-provoking situations, the result may be increased motor activity on the left side (i.e., a left motor bias in the form of left hand scratching). However, if we focus solely on the left side scratching preferences, the data seem to support the Leavens et al. hypothesis of increased cutaneous sensitivity on the left side of the body during arousal. However, our data were collected without manipulating arousal in the marmosets.

**Summary**

In summary, scratching as a behavioral indicator of arousal in nonhuman primates is evidenced by behavioral and pharmacological research findings. However, all of these studies examine scratching in relation to negative arousal (i.e., anxiety). Although positive and negative arousal are assumed to be accompanied by different cognitive and emotional states, there are many physiological similarities between positive and negative arousal. For example, both positive and negative arousal involve increases in heart rate and blood pressure, as well as increases in locomotion (Engel et al., 2009). Some research has found that self-reported, experimentally induced levels of itchiness in humans are greater in response to negative than positive mood. Unfortunately, the authors did not compare the positive mood condition to a neutral emotion condition (van Laarhoven et al., 2012). If scratching is a result of general physiological arousal, it should be seen in both positive and negative contexts. However, if the right hemisphere is less engaged during positive than negative arousal, there might not be the same autonomic mechanisms at play, and hence less scratching. Finally, the different cognitive correlates of positive (excited) and negative (anxious) arousal might influence the behavior in as yet unexplored ways.
Furthermore, studies of scratching are primarily limited to laboratory housed apes and Old World monkeys. Even small differences in neuroanatomy and physiology may change the nature and behavioral correlates of arousal across species, and stressors used to cause arousal in laboratory settings (which are highly artificial in many ways) may be perceived and reacted to in ways that are not typical of free-living primates. Therefore, we need additional research to understand the scratching-arousal relationship.

**Current Study**

In my thesis I tested the prediction that negative arousal would be positively related to scratching in naturalistically-housed common marmosets. This prediction was based on studies of primates that have found this relationship. Because previous literature has examined scratching caused by arousal in relation only to negatively arousing stimuli (i.e., anxiety) in laboratory housed monkeys and apes, I extended the findings on scratching as a behavioral indicator of anxiety to naturalistically-housed common marmosets. I employed previously used negative arousal paradigms that have successfully induced scratching in laboratory monkeys and apes, including predation threat, food competition, and social isolation, to determine if previous findings concerning scratching generalize to naturally housed New World monkeys. I hypothesized that, consistent with previous research, marmosets would exhibit increases in scratching rates in negative arousal contexts as compared to baseline scratching rates (H1).

Additionally, I examined scratching under conditions of positive arousal to determine if scratching is specific to anxiety (i.e., negative arousal), a question that has not yet been addressed in the literature. If scratching is primarily a function of the fact that there is greater right hemisphere activation under conditions of negative (but not positive) arousal (Leavens et al., 2006), then there would be no reason to expect increased scratching under conditions of
positive arousal. However, if scratching is primarily a function of general physiological arousal, which occurs in both positive and negative contexts, then scratching might also increase during positive arousal (RQ1).

Because previous literature has found evidence for lateralized scratching (Hopkins et al., 2006; Leavens et al., 2004), and because previous studies in our lab have found that subjects scratch significantly more with their left hand and on their left side in everyday (i.e., not experimentally controlled) circumstances (Neal et al., 2013), I also examined hand and side preferences for scratching during both positive and negative arousal conditions. I predicted that subjects would exhibit greater left hand than right hand scratching during negative arousal (H2). I had no directional prediction about lateralized preferences in the positive arousal condition (RQ2).

Lastly, should both negative and positive arousal show increases in scratching, I predicted that increases in scratching during negative arousal would be greater than increases during positive arousal (H3). There are greater physiological responses to negative rather than positive arousal (Jacob et al., 1991; Waldstein et al., 2000), and as such, subjects may exhibit a similar pattern concerning scratching in negatively versus positively arousing contexts.

**Methods**

**Subjects and Study Site**

Subjects were eleven common marmosets (see Table 1 for ages and sexes) housed in outdoor enclosures at Animal Educators in rural Valley Center, California. One family group consisted of a mated pair and their offspring, while the other family group consisted of six siblings. The two family groups were housed separately in 25’x20’x7’ enclosures containing tree branches, shrubs, platforms, and enrichment items. The marmosets had free access to a heated
“bedroom,” approximately 2’x3’, that was connected to the main enclosure. A varied diet of commercial primate food, fruits, and vegetables was provided twice daily along with continually available fresh water. The marmosets were also supplemented with live invertebrate prey (e.g., meal worms) four to five times weekly.

General Procedure

To assess the relationship between scratching and arousal, I observed the marmosets under three contexts of positive arousal (play, introduction of widely-dispersed high-incentive foods for foraging and consumption, and anticipation of high-incentive foods) and three contexts of negative arousal (predation threat, food competition, and social isolation). Using three different manipulations within the positive and negative arousal conditions allowed me to avoid habituation and pseudoreplication. I observed the monkeys for 10 minutes prior to any data collection to ensure that there were no extraneous arousing events (e.g., a coyote in the area) within 10 minutes of the initiation of a trial.

Prior to the experimental manipulation, I recorded all occurrences of scratching (including the hand used and the side scratched) by the focal animal for 15 minutes. This served as the baseline measure. I then recorded all instances of scratching for four minutes in the presence of the arousing stimulus/event (eight minutes for the social isolation condition—see below). Based on pilot data and experience with the marmosets, a four-minute time frame allowed me to record scratching during maximal arousal without either frustrating or habituating the animals to the manipulation. Following the manipulation period in five of the six contexts, I recorded all instances of scratching in the focal animal during a 10-minute post-manipulation period (hereafter referred to as the “post” period). Although no predictions were made concerning scratching rates during the post period, I was interested in knowing if the scratching
rates quickly returned to baseline, if in fact the rates did change during manipulation. However, the post period was not appropriate and was not collected for the food anticipation context (see explanation below). See Figure 1 for condition breakdown.

A randomized list of focal subjects was developed, and trials were randomized within focal subjects, although it was not always possible to follow the randomized orders because various husbandry-related circumstances sometimes prevented a subject or manipulation from being used that day. Play was recorded opportunistically (see below). Trials took place four-five days per week, with one or two trials per day per group. When two trials were scheduled for a given day, one was conducted in the morning and one was conducted in the afternoon. Note that all of the arousing manipulations are common to the everyday experiences of these subjects. As such, my methodology did not generate excessive distress. Data collection took place from August 2013 to March 2014.

**Positive Arousal Contexts**

**Play.** I recorded scratching rates during naturally occurring play bouts. In this sense, the play trials were not “manipulations” but will be referred to as such for ease of description. Because breeding pairs in marmoset social groups rarely play, I excluded the breeding pair from play trials. Once a play bout began, I recorded scratching by the focal animal for four minutes, excluding the time during which the subjects were wrestling, which is incompatible with scratching due to motor demands. Each subject served as a focal animal in three play bouts.

Because I could not predict when play bouts would occur, pre-play bout scratching baselines were impossible to obtain. Instead, I recorded scratching using focal all-occurrences sampling in 15-minute increments on days when no trials were scheduled and when there were no obvious sources of positive or negative arousal in the groups. Each subject was observed in
three 15-minute baseline sessions, with each session being on a different day. The average rate of scratching across these three baseline periods served as the baselines for scratching rates during play.

**High-incentive food foraging/consumption.** Kix, Coco Puffs, and Cheerios are highly palatable and highly sought after food items for the marmosets. To avoid competition for food, I used a large quantity (the same quantity on each trial) of one of these food items in each trial. I dispersed the foods throughout the enclosure and all occurrences of scratching exhibited by the focal animal were recorded. Pilot testing showed that most of the food was found within four minutes. Each subject served as a focal animal three times.

**Food anticipation.** A research assistant prepared the subjects’ afternoon meal in front of the enclosure in view of the subjects. Prior to this experiment, the subjects had learned that, in the presence of certain cues (the key to unlock the enclosure, a certain food tray, gloves, etc.), they are about to receive their meal. The presence of these cues during the experimental manipulation ensured that the marmosets indeed anticipated that I was about to give them the food, thus eliminating any potential frustration (negative arousal) caused by the inability to obtain the food. All occurrences of scratching exhibited by the focal animal were recorded for four minutes. Each subject was observed as a focal animal twice using this manipulation.

During the time that data would have been collected for the post period, the focal was consuming its meal. Food consumption is a positively arousing context and we would not expect a return to baseline levels of scratching in that circumstance. Therefore, post period scratching rates for this context are not considered.
Negative Arousal Contexts

**Predation threat.** Common marmosets respond with antipredator behavior to models of cats (Barros, Boere, Huston, & Tomaz, 2000) and snakes (Clara, Tomasi, & Rogers, 2008; Hook-Costigan & Rogers, 1998). In addition, we have found in pilot studies that our colonies respond to models of owls.

A research assistant placed a predator model approximately five feet from the enclosure, where it was in view of either one or both family groups. I began recording scratching as soon as the first alarm call was issued. Data were collected for four minutes. Each subject served as a focal animal three times, one for each predator type (cat, snake, owl).

**Food competition.** Previous research has found that scratching resulting from social competition is induced when a limited amount of food is available to a social group (Diezinger, & Anderson, 1986). Highly palatable food items (roaches, crickets) were held in view of the focal animal and fed to other members of the family group to induce competition for this limited food item. Because these foods are highly desirable, competition between group members was inevitable. The manipulation began as soon as an agonistic vocalization associated with social competition was issued by any member of the family. All occurrences of scratching exhibited by the focal animal within the four minute period were recorded. Each subject was observed as a focal animal three times using this manipulation.

**Social isolation.** To induce anxiety due to social isolation, one research assistant lured the focal subject into the bedroom, which was then closed to create full physical and visual isolation, but not auditory isolation, from groupmates. All occurrences of scratching by the isolated subject were recorded in real time by a research assistant sitting unobtrusively near the bedroom enclosure. Focal subjects were isolated for an eight-minute manipulation period, as
pilot testing had shown that in the first few minutes the focal was unlikely to show signs of
distress such as contact calling. After eight minutes the focal animal was then released back into
the larger enclosure and reunited with the family group. Post manipulation scratching was
recorded for 10 minutes following this initial reunion with the family group. Each subject was
observed as the isolated individual on two occasions using this manipulation.

Analyses

**Scratching Rates.** Scratching rates are expressed as a number per minute. To obtain this
rate, the total number of scratches was divided by the number of minutes in each period.
Scratching rates were determined for each individual by averaging across trials in all of the
contexts within the positive and negative conditions. That is, for the statistical analyses, each
subject had a scratching rate for positive arousal that consisted of the average rate of scratching
across the play, foraging, and food anticipation contexts in the baseline, manipulation, and post
periods. The same was true for the negative arousal scratching rates, calculated from the
predatory threat, food competition, and social isolation trials. No predictions were made about
possible differences among the three contexts within the positive and negative conditions and
thus post-hoc comparisons were not made unless descriptive statistics revealed meaningful
variability across contexts, which was the case in the positive arousal condition but not the
negative arousal condition (see below).

**Statistical tests.** Due to a small sample size and non-normal distributions for scratching
rates, bootstrapped paired samples t-tests were used to analyze differences between scratching
rates during baseline, manipulation, and post periods under negative and positive arousal.
Bootstrapped paired t-tests were also used to analyze the difference between the number of left
and right hand scratches under positive and negative arousal.
Results

See Table 2 for a list of comparisons, mean differences, \( p \) values, and confidence intervals.

**H1: Subjects will exhibit increased scratching rates in response to negative arousal as compared to baseline scratching rates.**

Bootstrapped paired samples t-tests were used to analyze the difference between average baseline, manipulation, and post scratching rates under contexts of negative arousal. Results showed that subjects exhibited significantly lower scratching rates during the manipulation period (\( M = .13, SE = .03 \)) than during baseline (\( M = .26, SE = .04 \)), \( p = .002 \), or during the post period (\( M = .29, SE = .04 \)), \( p = .005 \). There were no significant differences between baseline and post scratching rates, \( p = .125 \). As Figure 2 shows, subjects showed the same change in scratching patterns across all three negative arousal contexts. Piloerection (an indication of arousal due to sympathetic nervous system activity) was recorded as a manipulation check using a yes/no tally. Results showed that subjects exhibited piloerection in 87% of trials during manipulation periods in the negative arousal condition. Anecdotally, subjects also exhibited high rates of locomotion during manipulations, alarm calls were consistently issued by all group members during predation threat, all focal subjects issued long calls (contact calls) during social isolation, and chattering was consistently issued during food competition.

**H2: Subjects will exhibit more left hand scratching than right hand scratching in response to negative arousal.**

The number of scratches using only the hand during the manipulation period were too low for statistical analyses (\( N_{\text{manipulation}} = 0 - 14 \)), so hand and foot scratches were combined, creating a “limb” scratching measure. Total numbers of left and right limb scratches
were compared in two bootstrapped paired samples t-tests: one for right vs. left limb scratches during baseline and one for right vs. left limb scratches during manipulation. There were no significant differences between the numbers of right vs. left limb scratches during either the manipulation ($M_{right \ limb} = .47, SE = .11; M_{left \ limb} = .25, SE = .12, p = .11$), or the baseline period ($M_{right \ limb} = 1.80, SE = .30; M_{left \ limb} = 1.76, SE = .21, p = .83$).

It was originally planned that analyses based on computed z-scores for each individual under the negative arousal condition would be used to further assess differences in left and right hand/limb scratching. Z-scores for binomial data ($z = r(.5N) / \sqrt{.25N}$) reflect the strength of a left or right bias, with positive numbers indicating a right bias and negative scores reflecting a left bias. Differences between an individual’s z-scores at baseline and during manipulation might suggest different patterns of neural activity. However, the low rates of scratching in the manipulation periods made z-scores unreliable estimates of preference. These scores are presented in Figure 3.

**Research Question 1: Do subjects exhibit higher scratching rates in response to positive arousal as compared to baseline?**

Descriptive statistics revealed that each context under the positive arousal condition showed a different pattern of results (see Figure 4), and that the data in the play manipulation were possibly driving the results of the t-tests. Thus, results for each manipulation are presented separately.

**Play.** Bootstrapped paired samples t-tests were used to analyze differences in scratching rates during baseline, manipulation, and post periods. Results showed that rates during the manipulation ($M = 1.15, SE = .19$) were significantly higher than rates during both baseline ($M =$
SCRATCHING IN POSITIVE AND NEGATIVE AROUSAL

.28, $SE = .05$, $p = .008$) and post periods ($M = .41$, $SE = .08$, $p = .001$). There was no significant difference between scratching rates during the baseline and post periods, $p = .16$.

**Foraging.** Bootstrapped paired t-tests were used to analyze differences in scratching rates between baseline, manipulation, and post periods. Results showed that the manipulation rates ($M = .03$, $SE = .02$) were significantly lower than rates during baseline ($M = .24$, $SE = .05$), $p = .02$. A second bootstrapped paired t-test showed a trend toward lower scratching rates during the manipulation period than during the post period ($M = .27$, $SE = .08$, $p = .07$). There was not a significant difference in scratching rates between baseline and post periods, $p = .695$.

**Food Anticipation.** A bootstrapped paired t-test was used to determine the difference in scratching rates between baseline and manipulation. Results showed that manipulation rates ($M = .33$, $SE = .06$) were not significantly different from baseline rates ($M = .31$, $SE = .04$), $p = .779$. Recall that, during the time that data would have been collected for the post period, the focal was consuming its meal. Food consumption is a positively arousing context and we would not expect a return to baseline levels of scratching in that circumstance. Therefore, post period scratching rates for this context are not considered.

**Research Question 2: Do marmosets show a lateralized hand preference for scratching during positive arousal?**

Descriptive statistics showed that the number of scratches using only the hand were too low for statistical analyses ($N_{manipulation} = 0 – 26$), so hand and foot scratches were combined to create a limb scratching measure. Total numbers of left and right limb scratches for each individual were compared in two bootstrapped paired samples t-tests: one for right vs. left limb scratches during baseline and one for right vs. left limb scratches during manipulation. Results showed that subjects exhibited significantly more right than left limb scratches during the
manipulation period ($M_{\text{right limb}} = .98, SE = .24; M_{\text{left limb}} = .63, SE = .19, p = .025$). There was not a significant difference between left and right limb scratches during the baseline period ($M_{\text{right limb}} = 1.98, SE = .26; M_{\text{left limb}} = 1.67, SE = .15, p = .30$) in the positive arousal condition.

As was the case with negative arousal, total numbers of scratches with the left and right limbs were too low to calculate valid z-scores (see Figure 5).

**H3: Should subjects show significant increases from baseline in both the positive and negative condition, I predict that the change will be greater in magnitude in the negative than positive arousal condition.**

In none of the three negative arousal contexts did the subjects show increases in scratching during the manipulations. In the positive arousal contexts there was an increase in scratching while playing, a decrease in scratching rates from baseline to manipulation in the foraging context, and no change from baseline to manipulation in the food anticipation context. Therefore, no further analyses relative to H3 are warranted.

**Discussion**

The purposes of the current study were to: 1) generalize previous findings of increased scratching during negative arousal in laboratory-housed marmosets, Old World monkeys, and apes to a sample of naturally-housed common marmosets; 2) examine scratching under conditions of positive arousal to determine if scratching is specific to negative arousal or if it may be the result of general physiological arousal; and 3) examine hand preferences during scratching in hopes of elucidating the underlying neural control of scratching. The results are surprising and provocative.
Scratching and Negative Arousal

The prediction that subjects would exhibit increases in scratching rates from baseline to manipulation during the negative arousal condition was unsupported. In fact, data were in direct contradiction with the hypothesis: subjects from the current study exhibited significant decreases in scratching rates compared to baseline during all three negative arousal contexts. The facts that: 1) decreases occurred in all three negative contexts; 2) I used manipulations that have been used in other research; 3) 10 of the 11 subjects demonstrated these decreases; and 4) the monkeys demonstrated other signs of arousal such as piloerection and agitation, make it unlikely that my results reflect a statistical aberration, a failure of the manipulations to produce anxiety, or a methodological flaw.

The discrepancies between previous and current findings raise questions that led me to re-examine the literature that uses scratching as a measure of arousal or anxiety. One issue that emerged from this re-examination is that some studies that cite increases in scratching in relation to anxiety used composite behavioral scores, labeled “self-directed behavior” or “displacement activity” scores, that lump scratching together with other anxiety-related behaviors (e.g., scent-marking, self-grooming, rubbing, yawning) (Barros et al., 2004, 2007; Dettmer, Novak, Suomi, & Meyer, 2012; Elder & Menzel, 2001; Judge, Evans, Schroepfer, & Gross, 2011; Leavens et al., 2004; Manson & Perry, 2000; Schino et al., 1990, 1996). It is possible that one behavioral measure may have increased while others within the composite score did not change. This can make it difficult to differentiate between behaviors that are or are not related to anxiety.

When considering only those published studies that explicitly report scratching rates rather than a composite measure (N= 12 studies), we see that scratching may not have a simple relationship with arousal (see Table 3). Surprisingly, only six of these twelve studies show
explicit increases in scratching during anxiety-provoking circumstances (video of agonistic encounters: Hopkins et al., 2006; neighbor vocalizations: Baker & Aureli, 1997; behavioral transitions: Buckley & Semple, 2012; viewing conspecific in alert posture: Nakayama, 2004; inter-individual proximity and dominance rank: Pavani et al., 1991; MTS task: Leavens et al., 2001). Of the other six studies, one shows evidence of increases in scratching in some contexts but not in others (Diezinger & Anderson, 1986). Three studies show no changes in scratching during anxiety-inducing circumstances (social crowding: Judge, Griffaton, & Finke, 2006; intragroup conflict: Aureli, 1997; Duboscq, Agil, & Engelhardt, 2014). Another shows that common marmosets exhibited no changes in scratching during social isolation or during administration of an anxiogenic drug even though subjects exhibited concurrent increases in tsik-eggs calls, which are indicative of anxiety (Kato et al., 2014). Furthermore, although non-significant, subjects showed decreases in scratching (but increases in tsik and tsik-eggs calls) during visual presentation of fear-inducing photographs of predatory stimuli (leopard and cat) compared to the habituation session and sessions of non-picture (gray rectangles) stimuli. Finally, one study shows increases in scratching during grooming bouts, despite the fact that grooming is generally associated with states of low anxiety (Semple, Harrison, & Lehman, 2013).

The authors of these particular studies explain their unexpected scratching data in different ways. For example, Judge et al. (2006) found that hamadryas baboons (*Papio hamadryas*) showed no changes in post-crowding rates of scratching compared to baseline rates; however, rates of other displacement activities (i.e., yawn, self-groom, and pace) did increase significantly during post-crowding compared to baseline. The authors stated that the behavioral mechanisms used by subjects during crowding were effective in reducing social tension to the
point that scratching did not increase. Aureli (1997) found that post-conflict scratching rates in long-tailed macaques did not differ from matched control rates when analyzed across the full duration of the experimental timeline. However, the authors noted that there were certain time periods within the full trial where scratching increased. By focusing on those time periods that showed the predicted relationship between scratching and anxiety, they rescued the expected effect. Similarly, Diezinger & Anderson (1986) found that dominant, subordinate, and immature macaques exhibited no changes in scratching between baseline and feeding competition, but because the monkeys of intermediate rank did show the expected effect, the other data were largely ignored in the conclusion. Duboscq, Agil, & Engelhardt (2014) examined natural agonistic encounters between female crested macaques (M. nigra) and found no difference between baseline and post-conflict mean scratching frequency. They explained their findings by stating that the anxiety-scratching relationship may be weak in such a “tolerant” species. Lastly, Semple, Harrison, & Lehmann (2013) found that scratching rates after grooming bouts in female Barbary macaques (M. sylvanus) dramatically increased compared to baseline. As mentioned above, grooming typically reduces anxiety and has been shown to correlate with decreases in self-scratching in other studies (Maestripieri, Schino, Aureli, & Troisi, 1991; Troisi, 2002). The authors stated that certain unmeasured conditions in the study (e.g., signaling of relationships to group members though grooming, termination of grooming, behavioral transitions) may have increased anxiety, causing increases in scratching rather than decreases.

A handful of studies with marmosets show very distinct increases in scratching when subjects are given anxiogenic drugs (but see Kato et al., 2014) and decreases in scratching when subjects are given anxiolytics (Barros et al. 2000; Cilia and Piper, 1996; Schino et al., 1991, 1996). However, we should be circumspect in our interpretation of these results, as the
physiological and cognitive side effects of such drugs may influence scratching independently of changes in anxiety. It has been argued that decreases in scratching are not simply a by-product of the muscle-relaxing and sedative properties of benzodiazepines because some studies have found decreases in scratching during administration of anxiolytics without concurrent decreases in locomotor activity (Schino et al., 1991, 1996). However, decreases in scratching have also been observed with concurrent and significant decreases in locomotor activity during administration of diazepam (Barros et al., 2000; Cilia & Piper, 1996). Side effects of benzodiazepines, such as alterations in cutaneous sensitivity, behavioral inhibition, and avoidance responses, may also influence scratching rates. In short, caution should be applied when examining and interpreting the anxiety-scratching relationship found in drug studies.

The failure to reliably uncover a positive relationship between scratching and anxiety is also reflected in the literature on scratching and cortisol. For example, Higham et al. (2009) observed overall levels of SBDs (including scratching) and found no correlation with fecal glucocorticoid levels in female baboons. Additionally, Elder and Menzel (2001) found a negative correlation between SDBs and cortisol levels in orangutans during computerized tasks. The authors explain this by stating that engaging in SDBs may have released the frustration caused by the task, thus reducing cortisol release, or possibly that there may be a distinction between stress and anxiety, such that cortisol release is related to stress, whereas SDBs are related to anxiety. However, they also point out that the frustration may not act on brain regions associated with the HPA axis, and thus, SDBs may not be related to cortisol levels in general.

It is possible that the widespread belief in primatology that scratching is a very reliable measure of negative arousal/anxiety has made that relationship a foregone conclusion, such that any empirical deviations from that relationship are either ignored or explained away. My data,
and data in published studies that, upon close examination, fail to confirm the relationship, suggest that scratching does not always increase with arousal, and that the assumption of the relationship prevents us from asking a much more interesting set of questions about what scratching tells us about underlying physical and emotional states. Furthermore, using scratching as a de facto indication of anxiety could lead to incorrect conclusions that misinform not only theory, but also decisions about captive animal welfare.

**Accounting for the variability.** Assuming that the manipulations did indeed cause arousal in the studies cited above and in my own study, what might be the factors that account for the variability we see in the scratching-arousal relationship? One possibility is that degree or intensity of arousal is important, but studies have not reported (and probably have no way to measure) the extent to which their subjects were aroused. In fact, Troisi et al. (1991) suggested that scratching and anxiety may be related in an inverse-U fashion, with high levels of scratching being expressed only during moderate levels of anxiety, and low levels of scratching being expressed during low and high levels of anxiety. Additionally, it could be that any change in scratching from baseline is important; that is, the specific direction of change is not as important as the change itself. Indeed, any alteration in the cortisol response (a measure of stress) is considered detrimental on health outcomes, regardless of the direction of the alteration (e.g., whether the cortisol pattern is blunted or highly increased compared to baseline patterns) (D’Anna et al., 2012). It may also be important to examine the possibility of transient changes in scratching throughout manipulation periods by examining scratching minute-by-minute during anxiety-provoking circumstances, as different rates of scratching can be exhibited throughout exposure to a stressor (Aureli, 1997). Additionally, Barros et al. (2004) point out that it may be especially important to dissociate fear and anxiety when measuring scratching, as anxiety-related
behaviors, including scratching, tend to decrease when fear-related behaviors increase (freezing, withdrawal). A second possibility is species differences in the physiological mechanisms (see below) that underlie the arousal-itch-scratch pathway. Third, monkeys tested in social groups may experience and therefore express arousal differently than monkeys tested alone. There is evidence for a social buffering effect that reduces HPA activity in marmosets (Cross & Rogers 2006; Smith, McGreer-Whitworth, & French 1998), but whether or not it affects how anxiety is expressed is not known. Similarly, housing conditions (indoor, outdoor, pair housing, natural social groups, etc.) and the subjects’ experience with experimental manipulations of various sorts may influence scratching in ways we do not yet understand. Furthermore, the type of circumstance used to create arousal might be of importance in explaining the variability across studies. Studies showing increased arousal-related scratching in great apes often utilized non-social contexts, including cognitive challenges such as match-to-sample tasks, to induce anxiety or frustration in subjects (Elder & Menzel, 2001; Leavens et al., 2001, 2004). These types of computerized tasks are very different from the more naturally-occurring situations used in the current study to induce negative arousal, such as food competition, social isolation, and predation threat. It is intriguing that the studies reported above that showed no change or a decrease (including the current study) in scratching took place in more naturally-occurring contexts, such as crowding (Judge et al., 2006), agonistic encounters (Aureli, 1997; Duboscq et al., 2014), and competition for food (Diezinger & Anderson, 1986).

**Lateralized preferences while scratching in negative arousal.** Because scratching decreased to such low levels during manipulations, there was not an adequate number of left and right limb scratches to calculate valid z-scores. Therefore, it is not possible to speculate about
lateralized scratching preferences, and thus, emotional lateralization during negative arousal, using data derived from this study.

**Scratching and Positive Arousal**

To examine if scratching is related to both negative and positive arousal, I recorded scratching rates during three positive arousal contexts. Each of the three positive arousal contexts showed a different pattern of scratching rate results. During the play condition, subjects exhibited significantly higher rates of scratching during the manipulation period than during baseline and post periods. Subjects showed no significant changes in scratching rates during food anticipation condition, and significantly lowered their scratching rates during the foraging manipulation.

Given the surprising result regarding scratching and negative arousal, and the fact that those data call into question some basic assumptions about scratching and arousal, the data for the positive arousal condition do not allow for simple interpretation. Nonetheless, to the extent that scratching has a (complicated) relationship with arousal, the observed variability of scratching rates across the three positive arousal conditions suggest different types or levels of excitement in each of the three contexts. The one context, whether it be positive or negative, that elicited significantly higher rates of scratching during manipulation was social play. Play is a highly energetic, explicitly social, and cognitively challenging event whose causes and long-term consequences are not well understood. It is also the case that play was the one condition in my study that was not manipulated experimentally. Therefore, it is not clear if play represents a truly unique context with regard to understanding arousal and scratching, but future studies might benefit from exploring this possibility.
Lateralized preferences while scratching in positive arousal. As a second research question, I examined scratching hand preferences during positive arousal. Because the positive arousal contexts showed a different pattern of scratching rate results, the positive arousal data concerning lateralized scratching should be interpreted with caution. Additionally, although scratching rates under the positive arousal condition did not decrease significantly, overall numbers of scratches were low, and thus, z-scores computed may not be valid. In any case, four individuals exhibited a number of scratches that may yield valid z-scores. Three of these individuals exhibited no significant change in their z-scores from baseline to manipulation, and one subject exhibited a switch from significantly right handed scratching during baseline to significantly left handed scratching during manipulation. However, the low overall number of subjects as well as low numbers of scratches makes it difficult to draw conclusions concerning lateralized scratching during positive arousal.

Underlying Mechanisms that May Produce Scratching

If we are to fully understand the relationship between scratching and arousal, we must identify the physiological mechanisms that underlie scratching as a self-directed behavior. These mechanisms have not been identified. It is difficult to explain why subjects do not scratch when we do not understand why they do scratch.

There are a number of well-known neurochemicals that are associated with pain, itch, anxiety, and/or stress that might help us understand the pathway to the scratch response. For instance, Substance P (SP) is involved in pain and itch, as well as anxiety regulation. Studies have found that, depending on the dose and brain area, injection of SP can have either anxiogenic or anxiolytic effects, while other studies have found that anxiety-provoking stimuli can cause increases in SP in various brain areas (Barros et al., 2002; Ebner & Singewald, 2006). Given SPs
importance in both anxiety regulation and pain and itch transmission, and the fact that it can have
differential effects on anxiety, it is possible that SP has a role in regulating different levels or
types of anxiety, and this may be reflected in the expression of anxiety-related behaviors.

Second, oxytocin is related to social bonding and affiliative behavior, and has been
implicated both agonistically and antagonistically with anxiety and the HPA axis. Recent studies
have found that increases in oxytocin can increase stress-enhanced fear responses in mice and
humans (Guzman et al., 2013; Theodoridou, Penton-Voak, & Rowe, 2013), whereas others have
found that oxytocin administration reduces anxiety behavior in rats when tested in an unfamiliar
environment (Windle, Shanks, Lightman, & Ingram, 1997). When highly social species
experience the stressor in the social group, oxytocin may be found in higher concentrations
relative to other species used in previous studies, which may change fear and anxiety-related
responses (such as scratching).

Lastly, enkephalins are involved in pain inhibition, and possibly itch induction.
Enkephalin is largely involved in inhibiting pain messages both centrally and peripherally.
Additionally, pain and itch have an antagonistic relationship, such that increasing pain messages
inhibits itch, and decreasing pain messages (e.g., taking opioids) often has the side effect of
increasing itch (Ikoma, Steinhoff, Yosipovitch, & Schmelz, 2006; Ward, Wright, & McMahon,
1996). However, other studies have posited that the same inhibition pathway for pain (involving
enkephalins) may also be involved in inhibiting itch (Mochizuki et al., 2003). Given that we do
not understand the full extent of the physiological relationship between inhibition of pain and
itch, it is difficult to say whether enkephalin (which, again, is involved in pain inhibition) may
increase or decrease itch. It is possible, and even likely, that SP, oxytocin, and enkephalins are
all involved in itch and anxiety-related scratching, but how these might fit together to explain
species and context-dependent differences in anxiety-induced scratching remains to be determined. Furthermore, it is unclear if anxiety-related scratching in primates reflects a perception of “itchiness” at all; scratching may be independent of the “itch” sensation and thus may not benefit from an understanding of a true “itch” sensation.

Conclusion

The current study showed that common marmosets did not exhibit the same pattern (in fact, an opposite pattern) of scratching as has been commonly reported in nonhuman primates under conditions of negative arousal. My data, and patterns that are revealed in a careful examination of the literature, suggest that the anxiety-scratching relationship may be more complex than typically reported and assumed. Furthermore, the relationship between scratching and states of positive arousal need further investigation, both to elucidate the similarities and differences between these two emotional states and to further examine the scratch-arousal association. In addition to the theoretical questions they pose, my results raise a potential concern about the use of scratching as an unqualified indicator of anxiety and well-being in captive non-human primates, with important implications for captive management.


http://dx.doi.org/10.1016/S0166-4328(99)00153-9


Higham, J. P., Maclarnon, A. M., Hesitermann, C. R., & Semple, S. (2009). Rates of self-directed behavior and faecal glucocorticoid levels are not correlated in female wild Olive...
 SCRATCHING IN POSITIVE AND NEGATIVE AROUSAL

baboons (*Papio hamadryas anubis*). *Stress, 12*(6), 526-532. doi:10.3109/10253890902756565


### Table 1

*Name, Age, Sex, and Group Number for Individual Subjects*

<table>
<thead>
<tr>
<th>Name</th>
<th>Age (months)</th>
<th>Sex</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ringo</td>
<td>12</td>
<td>M</td>
<td>1</td>
</tr>
<tr>
<td>George</td>
<td>12</td>
<td>M</td>
<td>1</td>
</tr>
<tr>
<td>William</td>
<td>30</td>
<td>M</td>
<td>1</td>
</tr>
<tr>
<td>Harry</td>
<td>30</td>
<td>F</td>
<td>1</td>
</tr>
<tr>
<td>Beatrice</td>
<td>18</td>
<td>F</td>
<td>1</td>
</tr>
<tr>
<td>Genie</td>
<td>18</td>
<td>M</td>
<td>1</td>
</tr>
<tr>
<td>Alfred</td>
<td>60</td>
<td>M</td>
<td>2</td>
</tr>
<tr>
<td>Annie</td>
<td>56</td>
<td>F</td>
<td>2</td>
</tr>
<tr>
<td>Achilles</td>
<td>30</td>
<td>M</td>
<td>2</td>
</tr>
<tr>
<td>Athena</td>
<td>30</td>
<td>F</td>
<td>2</td>
</tr>
<tr>
<td>Apollo</td>
<td>18</td>
<td>M</td>
<td>2</td>
</tr>
<tr>
<td>Condition</td>
<td>Positive Arousal</td>
<td>Negative Arousal</td>
<td></td>
</tr>
<tr>
<td>-----------------</td>
<td>------------------</td>
<td>------------------</td>
<td></td>
</tr>
<tr>
<td><strong>Contexts</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foraging</td>
<td>Positive Arousal</td>
<td>Negative Arousal</td>
<td></td>
</tr>
<tr>
<td>Kix</td>
<td>Base., Manip., Post</td>
<td>Snake</td>
<td></td>
</tr>
<tr>
<td>Cheerios</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td>Coco Puffs</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td><strong>Food Anticipation</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trial 1</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td>Trial 2</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td><strong>Play</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Trials</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Food Anticipation</td>
<td></td>
<td>Social Isolation</td>
<td></td>
</tr>
<tr>
<td>Trial 1</td>
<td>Base., Manip., Post</td>
<td>Mealworms</td>
<td></td>
</tr>
<tr>
<td>Trial 2</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td>Trial 3</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td><strong>Predation Threat</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snake</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td>Owl</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td>Cat</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td><strong>Food competition</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Roaches</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td>Crickets</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td>Mealworms</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td><strong>Social Isolation</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trial 1</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
<tr>
<td>Trial 2</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
<td></td>
</tr>
</tbody>
</table>

**Table:**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Positive Arousal</th>
<th>Negative Arousal</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Contexts</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foraging</td>
<td>Positive Arousal</td>
<td>Negative Arousal</td>
</tr>
<tr>
<td>Kix</td>
<td>Base., Manip., Post</td>
<td>Snake</td>
</tr>
<tr>
<td>Cheerios</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td>Coco Puffs</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td><strong>Food Anticipation</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trial 1</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td>Trial 2</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td><strong>Play</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Trials</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Food Anticipation</td>
<td></td>
<td>Social Isolation</td>
</tr>
<tr>
<td>Trial 1</td>
<td>Base., Manip., Post</td>
<td>Mealworms</td>
</tr>
<tr>
<td>Trial 2</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td><strong>Predation Threat</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snake</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td>Owl</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td>Cat</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td><strong>Food competition</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Roaches</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td>Crickets</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td>Mealworms</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td><strong>Social Isolation</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trial 1</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
<tr>
<td>Trial 2</td>
<td>Base., Manip., Post</td>
<td>Base., Manip., Post</td>
</tr>
</tbody>
</table>
### Table 2

**Comparisons and Respective Statistics from the Current Study**

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Mean difference</th>
<th>p</th>
<th>95% CI of Mean difference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>H1: Negative arousal scratching rates</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline vs. Manipulation</td>
<td>0.13</td>
<td>.002</td>
<td>[0.06, 0.19]</td>
</tr>
<tr>
<td>Manipulation vs. Post</td>
<td>-0.16</td>
<td>.005</td>
<td>[-0.27, -0.06]</td>
</tr>
<tr>
<td>Baseline vs. Post</td>
<td>-0.04</td>
<td>.125</td>
<td>[-0.09, 0.01]</td>
</tr>
<tr>
<td><strong>H2: Negative arousal right vs. left limb scratching</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline right vs. left</td>
<td>0.05</td>
<td>.83</td>
<td>[-0.41, 0.51]</td>
</tr>
<tr>
<td>Manipulation right vs. left</td>
<td>0.22</td>
<td>.11</td>
<td>[-0.6, 0.51]</td>
</tr>
<tr>
<td><strong>RQ1: Positive arousal scratching rates</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Food anticipation</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline vs. Manipulation</td>
<td>-0.02</td>
<td>.779</td>
<td>[-0.14, 0.10]</td>
</tr>
<tr>
<td>Baseline vs. Manipulation</td>
<td>.21</td>
<td>.02</td>
<td>[0.13, 0.29]</td>
</tr>
<tr>
<td>Manipulation vs. Post</td>
<td>-0.24</td>
<td>.074</td>
<td>[-0.41, -0.10]</td>
</tr>
<tr>
<td>Baseline vs. Post</td>
<td>-0.04</td>
<td>.695</td>
<td>[-0.20, 0.08]</td>
</tr>
<tr>
<td>Foraging</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline vs. Manipulation</td>
<td>-.87</td>
<td>.008</td>
<td>[-1.25, -0.46]</td>
</tr>
<tr>
<td>Manipulation vs. Post</td>
<td>0.73</td>
<td>.001</td>
<td>[0.42, 1.04]</td>
</tr>
<tr>
<td>Baseline vs. Post</td>
<td>-0.13</td>
<td>.16</td>
<td>[-0.29, 0.03]</td>
</tr>
<tr>
<td>Play</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline vs. Manipulation</td>
<td>-.87</td>
<td>.008</td>
<td>[-1.25, -0.46]</td>
</tr>
<tr>
<td>Manipulation vs. Post</td>
<td>0.73</td>
<td>.001</td>
<td>[0.42, 1.04]</td>
</tr>
<tr>
<td>Baseline vs. Post</td>
<td>-0.13</td>
<td>.16</td>
<td>[-0.29, 0.03]</td>
</tr>
<tr>
<td><strong>RQ2: Positive arousal right vs. left limb scratching</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline right vs. left</td>
<td>.31</td>
<td>.30</td>
<td>[-0.32, 0.94]</td>
</tr>
<tr>
<td>Manipulation right vs. left</td>
<td>0.36</td>
<td>.025</td>
<td>[0.06, 0.66]</td>
</tr>
</tbody>
</table>

*Note.* df (degrees of freedom), t (t-value), p (p-value), 95% CI of the Mean difference (95% Confidence Interval of the Mean difference).
Figure 2: Baseline, manipulation, and post scratching rates for the three negative arousal conditions.

Figure 3: Scratching z-scores for each individual during baseline and manipulation time periods in negative arousal. Apollo, Beatrice, and George had z-scores of 0 (equal numbers of scratches by the left and right limbs) during manipulation. Two subjects did not scratch during the manipulation period, and are therefore not included on this figure.
Figure 4: Scratching rates during baseline, manipulation, and post periods in the three positive arousal conditions.

Figure 5: Scratching z-scores for each individual during baseline and manipulation time periods in positive arousal. George had a z-score of 0 (equal numbers of left and right limb scratches) during baseline, and Ringo had a z-score of 0 during manipulation. One subject (Annie) exhibited no scratching during manipulation, and thus does not appear on this figure. Because the positive arousal contexts showed a different pattern of scratching rate results, these positive arousal data concerning lateralized scratching should be interpreted with caution.
### Table 3

**Studies that Explicitly Report Scratching in a Non-Composite Measure**

<table>
<thead>
<tr>
<th>Authors</th>
<th>N and Species</th>
<th>Manipulation and Measures</th>
<th>Results</th>
<th>Authors’ Explanation of Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baker &amp; Aureli (1997)</td>
<td>81 chimpanzees</td>
<td>Scratching assessed before and after anxiety-inducing neighbor vocalizations.</td>
<td>Rough and gentle scratching increased after vocalizations compared to before vocalizations.</td>
<td>Authors state that results are consistent with previous research showing that anxiety and scratching are related.</td>
</tr>
<tr>
<td>Buckley &amp; Semple (2012)</td>
<td>17 ring-tailed lemurs</td>
<td>Scratching assessed before and after anxiety caused by behavioral transitions*</td>
<td>Scratching increased both before and after behavioral transitions.</td>
<td>Displacement activities (e.g., scratching) may serve as method to allow animals to divert attention from previous activity to next activity/ stimulus.</td>
</tr>
<tr>
<td>Diezinger &amp; Anderson (1986)</td>
<td>14 rhesus macaques</td>
<td>Scratching assessed at baseline and after 1) behavioral changes*, and 2) feeding contexts.</td>
<td>Scratching 1) increased during behavioral changes, and 2) was higher only in intermediates during feeding times compared to baseline (i.e., no change in scratching from baseline to feeding contexts in dominants, subordinates, or immature subjects).</td>
<td>1) Behavioral transitions are anxiety-provoking, as evidenced by increased scratching rates. 2) During feeding contexts, scratching may be considered a displacement activity, as an increase in scratching in intermediates may be due to frustration from attempts to obtain food, whereas dominant and subordinate individuals do not experience this frustration, and thus, do not scratch.</td>
</tr>
<tr>
<td>Hopkins, Russell, Freeman, Reynolds, Griffis, &amp; Leavens (2006)</td>
<td>89 chimpanzees</td>
<td>Scratching assessed at baseline and while subjects watched video of conspecific agonistic encounters.</td>
<td>Scratching increased while watching video compared to baseline.</td>
<td>Authors addressed results in context of lateralized preferences.</td>
</tr>
<tr>
<td>Study</td>
<td>Species/Subjects</td>
<td>Methodology</td>
<td>Results</td>
<td>Notes</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>------------------</td>
<td>--------------------------------------------------</td>
<td>-------------------------------------------------------------------------</td>
<td>----------------------------------------------------------------------</td>
</tr>
<tr>
<td>Judge, Griffaton, &amp; Fincke (2006)</td>
<td>9 Hamadryas baboons</td>
<td>Scratching assessed at baseline, during induced crowding, and post crowding.</td>
<td>No difference in scratching between baseline, manipulation, and post measures.</td>
<td>Authors stated that behavioral mechanisms used by subjects during crowding were effective in reducing social tension to the point that scratching did not increase.</td>
</tr>
<tr>
<td>Duboscq, Agil, &amp; Engelhardt (2014)</td>
<td>140 female crested macaques</td>
<td>Scratching assessed at baseline and post conflict and reconciliation.</td>
<td>No difference in scratching between baseline and post-conflict.</td>
<td>Three possibilities were presented in the discussion. 1) This is a “tolerant” species of macaque. Post-conflict interactions may serve a different function compared to other macaques/other species with despotic individuals, and thus, it is possible that scratching-anxiety relationship is weak in tolerant species. 2) Subjects were “too busy” to scratch. 3) Conflict must not have been perceived by subjects as very risky or costly given their lack of expression of anxiety-related behaviors.</td>
</tr>
<tr>
<td>Semple, Harrison, &amp; Lehman (2013)</td>
<td>12 female Barbary macaques</td>
<td>Scratching assessed at baseline and while subjects gave or received grooming.</td>
<td>Scratching increased after grooming bouts.</td>
<td>Authors rejected idea that self-scratching may <em>not</em> be indicator of anxiety due to results from previous studies with the same population of subjects showing increases in scratching. They explain the findings by stating that other situations that cause increases in scratching (e.g., behavioral transitions) may have been present to the extent that they overrode any decreases in scratching caused by grooming. Grooming may also be anxiety-provoking because it signals to other members certain preferences for individuals and relationships, and may also represent ending of a rewarding experience, which would cause frustration/anxiety.</td>
</tr>
<tr>
<td>Authors</td>
<td>Study Subjects</td>
<td>Methods</td>
<td>Results</td>
<td>Notes</td>
</tr>
<tr>
<td>--------------</td>
<td>----------------------</td>
<td>--------------------------------------------------------------------------</td>
<td>------------------------------------------------------------------------</td>
<td>-------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Aureli (1997)</td>
<td>31 long-tailed macaques</td>
<td>Scratching assessed post-conflict and in matched control observations.</td>
<td>Post-conflict scratching did not differ from scratching in matched control observations when assessed during the entire time period. However, when first the three minutes were analyzed separately, post-conflict rates were higher than matched control rates.</td>
<td>Authors stated that the disturbance of a valuable relationship due to previous conflict is the major cause of post-conflict anxiety. Authors did not address findings concerning no changes in scratching.</td>
</tr>
<tr>
<td>Kato et al. (2014)</td>
<td>6 common marmosets</td>
<td>Grooming (episodes of scratching) assessed in three fear and anxiety-inducing paradigms: isolation, anxiogenic administration, visual presentation of predator pictures.</td>
<td>No differences in scratching across five isolation sessions, no significant difference in scratching in the anxiogenic administration sessions, non-significant decrease in scratching during presentations of pictures of predators. However, subjects did show increased tsik-eggs calling in each condition, indicative of anxiety.</td>
<td>Scratching results were not addressed in the discussion, as the focus of the study was vocalizations.</td>
</tr>
<tr>
<td>Reference</td>
<td>Species</td>
<td>Methodology</td>
<td>Findings</td>
<td></td>
</tr>
<tr>
<td>-----------------------------------</td>
<td>---------</td>
<td>-----------------------------------------------------------------------------</td>
<td>---------------------------------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>Leavens et al. (2001)</td>
<td>chimpanzees</td>
<td>Gentle and rough scratching assessed during Match-to-Sample (MTS) task in easy and hard conditions.</td>
<td>Gentle scratching increased when subjects were presented with easy condition first compared to when subjects were presented with hard condition first.</td>
<td></td>
</tr>
<tr>
<td>Nakayama (2004)</td>
<td>Japanese macaques</td>
<td>Scratching assessed while subjects watched a monkey monitoring a third monkey that was a stranger to all other monkeys: stranger, and no stranger conditions.</td>
<td>Subjects who viewed the monitoring monkey in an alert state (i.e., during the stranger viewing condition) were more likely to scratch than during no stranger condition. Monitoring monkey also showed increased scratching in stranger than no stranger condition.</td>
<td></td>
</tr>
<tr>
<td>Pavani et al. (1991)</td>
<td>long-tailed macaques</td>
<td>Scratching assessed during inter-individual proximity and measured in relation to dominance rank.</td>
<td>Scratching was higher during close proximity to males compared to alone. Scratching was also higher in subordinates than high-ranking individuals.</td>
<td></td>
</tr>
</tbody>
</table>

Authors state that these results are consistent with the idea that scratching increases when subjects are anxious or frustrated.

Authors state that this shows a contagion of scratching in conspecific observers who experience negative arousal along with the monitoring monkey. This is indicative of a transmission of negative arousal.

Authors state that their results are consistent with the idea that proximity and lower rank creates anxiety due to internal conflict arising from possibility of agonistic encounters and constrained behavioral options of subordinates.

**Note.** Behavioral change/behavioral transition refers to scratching episodes occurring in a social context with a subsequent change in behavior; for example, scratching occurring between a change in behavior from grooming a conspecific to foraging.