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ABSTRACT

The study of animal emotions is of growing interest and has recently been established in a variety of scientific fields. To study the phylogenetic basis of empathic processing, non-human primates have been investigated, whereby the majority of research has concerned great apes and some Old-World monkeys. Little is known about New-World monkeys, even though this group is very interesting due to its early split from Old-World Monkeys in the primate phylogenetic tree. Common marmosets (*Callithrix jacchus*) are cooperatively breeding New World monkeys, renowned for their high social tolerance, and high levels of cooperative and prosocial behaviour. In this present study, I aimed to investigate (1) if it is possible to elicit different behavioural expressions of emotions in these monkeys through the presentation of external stimuli and (2) if they are able to gain emotional information through the presentation of a video with a conspecific showing a specific emotional expression. I predicted that if marmosets could pick up on the others' emotion via videos, they should subsequently show the same behavioural expression through the process of emotional contagion and differ in the amount of expression from a neutral control condition.

Concerning my first objective, I succeeded in eliciting different emotional expressions by confronting the monkeys with different stimuli. Their reactions were filmed and then used to create the video footage for the experimental conditions in the contagion experiment. In this second part of my study, I found little evidence for emotional contagion in common marmosets. Contrary to my expectation, I found no matching of the emotional expressions and less change in the observed behaviour in the affective test conditions than in the neutral control condition. These findings hint towards a 'freezing' response to emotionally loaded video footage, but could also be interpreted in various alternative ways. Although my predictions were not met, this project is the first exploration of emotional contagion in common marmosets and therefore has to be seen as a first step to unravel the complex phenomenon of empathic processing in New World monkeys.

ZUSAMMENFASSUNG

Die Erforschung von Emotionen von nicht-menschlichen Tieren weist mittlerweile eine große Tradition in verschiedenen wissenschaftlichen Disziplinen auf. Um die phylogenetische Basis der Rolle von Emotionen in Bezug auf empathische Prozesse zu erforschen, wurden bis dato speziell nicht-menschliche Primaten als Modell verwendet. Aufgrund dessen bezieht sich ein Großteil der Forschung auf diesem Gebiet auf Menschenaffen und Alte Welt Affen. Obwohl sie aufgrund ihrer frühen Abspaltung von anderen Primaten im evolutionären Stammbaum sehr interessant sind, ist diesbezüglich wenig bekannt über so genannte Neue Welt Affen.

Weißbüschelaffen (*Callithrix jacchus*), bekannt für die kooperative Aufzucht ihrer Jungtiere, hoher sozialer Toleranz und eines komplexen prosozialen Verhaltens, sind hierbei vermutlich ein guter Startpunkt um Basismechanismen von emotionaler Verarbeitung zu erforschen.

In der vorgestellten Studie untersuchte ich, (1) ob es durch die Verwendung externer Stimuli möglich ist, verschiedene emotional bedingte Verhaltensweisen in Weißbüschelaffen hervorzurufen und (2) ob diese mittels emotionale Ansteckung, dazu in der Lage sind, bei Betrachtung eines Videos mit einem Artgenossen der bestimmte emotionale Ausdrucksweisen zeigt, diese Verhaltensweisen spiegeln. Konkret erwartete ich, dass Weißbüschelaffen dieselben emotionalen Ausdrucksweisen, wie auf den Videos zu sehen, übernehmen und die Häufigkeit ihrer Reaktionen sich klar von der in einer neutralen Kontrollsituation unterscheidet. Der erste Teil des Experiments war äußerst erfolgreich. Hierbei gelang es mir durch die Präsentation verschiedener externer Stimuli, starke Anzeichen unterschiedlicher Emotionen hervorzurufen. Im zweiten Teil zeigten sich nur wenige Hinweise auf emotionale Ansteckung im Weißbüschelaffen. Die Tiere zeigten kaum Anzeichen für eine ähnliche emotionale Stimmung wie in den Videos; zudem fand ich weniger Reaktionen in den Emotions-Tests als im Vergleich zu der neutralen Kontroll-Bedingung. Das vorliegende Projekt ist die erste Untersuchung von emotionaler Ansteckung bei Weißbüschelaffen und kann daher als wichtiger Schritt zur Erforschung des komplexen Phänomens der emotionalen Verarbeitung von Neue Welt Affen gesehen werden.

INTRODUCTION

Emotions play a crucial role in our everyday life. We feel them, we are aware of them and in most cases, we know if the emotion we experience right now is positive or negative. By now the investigation of emotional experiences in humans has a long tradition and led to findings with significance for a lot of scientific fields like psychology, biology, economy, etc. But, also the study of emotional functions in non-human animals is of growing interest in the scientific community (e.g. Preston & de Waal, 2002).

Emotions can be described as:

“...intense but short-living affective response to an event (the duration of emotion is a much debated question but briefness seems widely accepted), and is materialized in specific body changes. An emotion is classically described through a behavioral component (a posture or an activity), an autonomic component (visceral and endocrine responses) and a subjective component (emotional experience or feeling)” (Desire, Boissy & Veissier, 2002)

Emotions thus coordinate the bodily and psychological workings of the individual towards a specific task that needs to be performed with highest priority (Spoor & Kelly, 2004). This underlines the very important role of emotions in relation to cognition. More precisely, an emotion helps to organize physiological, motivational and cognitive systems that facilitate adaptive responses to aid the survival of the organism. As such, emotion can be thought of as a process that facilitates appropriate responding to a wide range of situations, including predator avoidance, intra and inter-specific aggression, reproduction, child care, and maintaining stability within social groups (Parr, Waller & Fugate, 2005). In particular, emotions seem to play an important role in shaping the behaviour and the inner experience of socially living animals (Spinka, 2012).

Considering these definitions and explanations of emotions in general, the questions arises, if nonhuman animals are also able to feel, express and share emotional information. Although it is claimed that animals are sentient creatures, it is paradoxical that there is no exact knowledge of what their emotional experiences are

about (Boissey et al., 2007). Using the term emotion when considering non-human animals is often considered unscientific and to wrongfully implicate anthropomorphic assumptions of human-like experience (Boissey et al., 2007). What we so far know scientifically about emotions in (non-human) animals is much less extensive and less deep, than what science found out about human emotions (Spinka, 2012). However, this is largely due to the lack of studies; fortunately, the study of animal emotions is of growing interest in several scientific fields. Human appraisals of emotions may involve cognitive processes such as memory and anticipation that may or may not be found in other animals, but they can also be simple, rapid and automatic. It is thus conceivable that similar emotional processes occur in animals (Desire et al., 2002). The investigation of the emotional processing in non-human animals has not only important implications for the understanding of the evolution of empathic processing. In a modern society, the welfare of non-human animals should also be an important agenda. Therefore, a better understanding of emotions in animals is highly desirable in different disciplines including neuroscience, comparative psychology and animal welfare science (Mendl, Burmann & Paul, 2010).

A very interesting fact is that humans and probably some non-human animals are also able to share emotions. When we see another human with a particular emotional expression, in most circumstances we have the same or at least an attenuated form of this emotion in our self (for review, see Singer, 2006). As social animals, the ability to share emotions makes not only sense from a psychological point of view, but also from an evolutionary perspective. For example, it is essential for the survival of an infant, that the mother is able to identify the actual emotional expression. But also in other daily situations it is important to be aware of the feelings of others. Especially in threatening circumstances, a proper evaluation of the situation through the behaviour of other individuals can be lifesaving. The ability to detect and process emotions of other individuals is usually labelled as emotional contagion. According to Hsee et al. (1992), emotional contagion can be clarified as the ability to automatically mimic and synchronize emotional expressions, vocalizations, postures, and movements with those of another person's and, consequently, to converge emotionally. To date, there are already some studies, involving nonhuman animals in respect to emotional contagion (e.g. Osvath & Sima, 2014; Schwing et al., 2017; Huber et al., 2017). The investigation of the ability to perceive and in respect to that, express different

emotions is of growing interest in modern science. All these findings suggest that it can be very desirable to evaluate the possibility of shared emotions in nonhuman animals.

From the perspective of cognitive biology, the process of emotional contagion involves affective sharing but does not need self-other distinction which stands for the ability to distinguish between whether the source of the affective experience lies within ourselves or was caused by another individual (de Vignemont & Singer, 2006). In this respect, more simple forms of empathic attribution (like emotional contagion) may be one in which the noticed object (or object's situation) is evaluated, and more complex forms would be ones in which self and object evaluations are discriminated (Edgar et al., 2012). These findings and definitions can be used as explanations, why emotional contagion can also occur in individuals without higher cognitive skills, like human infants and nonhuman animals. According to Panksepp and Lahvis (2011), the available evidence indicates, that simple forms of emotional transfer may be common to all mammals, and possibly to other group-living species.

Through the observation of conspecifics in an emotional state, emotional contagion leads individuals to shift their own affective state in the same direction (Spinka, 2012). During this process, the perception of a behavioural change in one individual appears to automatically activate the same process in another individual (Panksepp & Lahvis, 2011). Especially by looking at social living mammals, the ability to detect emotions from others makes sense. According to Preston and de Waal (2002), juvenile and adult members of all group-living species show emotional contagion behaviours that facilitate group movements that are important for survival. Especially within highly social groups, emotional contagion can be an advantage in facing daily challenges. From an evolutionary point of view, neural and emotional systems of non-human primates have specialized to deal with the increasing challenges of more complex social organizations and inter-individual relationships (Parr, Waller & Fugate, 2005). Therefore, emotional contagion can be seen as one of the ways to learn environmental information from conspecifics (Nakahashi & Ohtsuki, 2015). Understanding the emotions of conspecifics can also be labelled as one of the most important factors involved in regulating social interactions in primates.

The term emotional contagion is often labelled as a basic mechanism of the complex phenomenon empathy (e.g. de Vignemont & Singer, 2006). In a nutshell, one can say that there is probably no empathy without emotional contagion, but emotional contagion (as basic form of empathic processing) can occur without empathy.

Although there are many definitions of empathy, a very useful description of this complex mechanism is presented by the Perception Action Model (PAM) from Preston & de Waal (2002). This model points out, that the perception of an object's state activates the subject's corresponding representations, which in turn activate somatic and autonomic responses.

An important distinction here is the difference between cognitive empathy and emotional or affective empathy. Cognitive empathy refers to the capacity of understanding another individual's emotional state (de Waal, 2008), whereas affective empathy refers to the ability to be influenced by and additionally, to share, another conspecific's emotional state (Edgar et al., 2011).

In this regard, the term behavioural contagion should also be mentioned as different to emotional contagion. Behavioural contagion is suggested to promote group coordination that may facilitate activity transitions, increased vigilance, and state matching and occurs automatically when a particular behaviour is observed by a conspecific (Massen et al., 2016). Although the visible outcome of this phenomenon can look quite similar to the perception and expression of emotions by conspecifics, there is no need of involved emotional processing in contrast to emotional contagion.

Regarding research of emotions in empathic processing, there are many studies involving great apes (e.g. Preston & de Waal, 2002; Parr et al., 2005; Campbell & de Waal, 2011; Koski & Sterck, 2009) and Old-World monkeys (Kuraoka & Nakamura, 2010; Paukner & Anderson, 2006; etc.). Little is, however, known about New World monkeys. In addition to observing these representatives of primates, the investigation of phylogenetically more distant species can give important insights into the evolution of emotional systems and the basic mechanism in empathic responses.

A representative of the New World monkeys is the common marmoset (*Callithrix jacchus*). They belong to the group of the smallest true monkeys and have a very characteristic appearance. They have multi-coloured fur with grey, brown, yellow and white patterns and a black and white alternating coloured tail. Common marmosets

(*Callithrix jacchus*) are native to Northeast, East and Southeast Brazil where they are able to inhabit a huge variety of forests (Grzimek, 2003). Marmosets are known for their cooperative breeding system, high social tolerance, and high levels of cooperative and prosocial behaviour (e.g. Burkart et al., 2007).

Although marmosets show higher cognitive skills than their brain size indicates (e.g. Strasser & Burkart, 2012), there is presumably a lack of advanced cognitive abilities like Theory of mind (which is necessary to show a full complex empathy) in this primate species (Burkart et al., 2007). Nevertheless, emotional contagion does not necessarily involve any kind of cognitive perspective taking (Edgar et al., 2012). Therefore, I hypothesize that emotional contagion is present and functional in marmosets.

In respect to their breeding system, these highly cooperative primates are also a good model-species for testing predictions of the cooperative breeding hypothesis (e.g. Burkart & van Schaik, 2010). This hypothesis argues that humans evolved as cooperative breeders, which lead to increased sensitivity and attention towards the emotional states of others. In this regard, the understanding of shared emotions as a building block of cooperative breeding, can give important advantages to this promising theory about the evolution of prosocial behaviour in humans and nonhuman animals. Although further studies are needed, a recent investigation argues that common marmosets could be able to demonstrate at least a sex biased form of inequity aversion (Mustoe et al., 2016). In this regard, it is interesting to mention, that some authors (e.g. Yamamoto & Takimoto, 2012) suggest that a sense of fairness and empathic processing co-evolved as underlying psychological mechanisms of pro-social behaviour. Here, the following study can help to give new insights into this complex evolutionary phenomenon.

In humans, it is clear that emotions can be experienced only through a thought or the perception of a past or future event or situation, and the investigation of emotional processing can be made via a lot of different research methods (e.g. self-report, fMRI, etc.). In non-human animals, where we cannot be sure how developed their ability of such complex cognitive challenges is, we usually have to work with external stimuli to investigate emotional reactions and expressions. According to Mendl, Burman & Paul (2010), emotional states occur in responses to stimuli or situations that are actually, or potentially, rewarding or punishing.

In this present study, I aimed to investigate (1) if it is possible to elicit different behavioural expressions of emotions in common marmosets through the presentation of external stimuli and (2) if these primates are able to gain emotional information through the presentation of a video with a conspecific showing a specific emotional expression. I predicted that if marmosets could pick up on the others' emotion via videos, they should subsequently show the same behavioural expression through the process of emotional contagion.

METHODS

Subjects and Housing

The experiments took place at the Animal care facility in the Department of Cognitive Biology from the University of Vienna, Austria. The subjects were 20 common marmosets (*Callithrix jacchus*) of six different family groups (Table 1). The age ranged from 1 year (two juveniles) to 14 years. The animals were kept in an indoor enclosure (250 x 250 x 250 cm) with access to an outdoor enclosure (250 x 250 x 250 cm). Within the indoor facilities the temperature was kept between 24 and 26°C. The humidity ranged from 40 to 60%. The dark:light cycle were kept stable in form of 12:12.

Around midday (usually 12:00 h) the marmosets were fed with different fruits, grains, pellets, dairy products, marmoset jelly, pellets, vegetables, and different protein and vitamin supplements.

Table 1. Composition of the groups.

Name	Group Name	Sex	Age	Relatedness
Zaphod	Kiri	Male	14 years	Breeder
Luna	Kiri	Female	3 years	Offspring/Sibling
Oli	Kiri	Female	11 years	Offspring/Sibling
Nemo	Kiri	Female	11 years	Offspring/Sibling
Aurora	Kiri small	Female	4 years	Offspring/Sibling
Jack	Kiri small	Male	10 years	Offspring/Sibling
Mink	Kiri small	Male	11 years	Offspring/Sibling
Fimo	Pooh	Male	14 years	Offspring/Sibling
Locri	Pooh	Male	13 years	Offspring/Sibling
Kobold	Sprichtel	Male	11 years	Father of Smart
Sparrow	Sprichtel	Female	10 years	Breeder
Smart	Sprichtel	Male	7 years	Breeder
Clever	Cleli	Male	7 years	Breeder
Veli	Cleli	Female	12 years	Breeder
Blinky Bill	Cleli	Male	1 year	Offspring
Wall-E	Cleli	Male	1 year	Offspring
Ernesto	V	Male	12 years	Breeder
Mathilda	V	Female	2 years	Offspring/Sibling
Melvin	V	Male	2 years	Offspring/Sibling
Vincent	V	Male	4 years	Offspring/Sibling

Procedure

The study took place between March 2016 and February 2017. First, I filmed the stimulus videos that were used in the experiments. The videos were thereafter edited so that they were as standardized as possible in every trial.

Obtaining the stimulus videos by eliciting the emotional expressions

To answer the first question of the study, if it is possible to evoke different emotional expression through external stimuli in marmosets, I elicited and recorded four different expressions of emotions ('anger', 'anxiety', 'fear', 'anticipation') through the visual contact with different objects (Table 2); in addition, I recorded a control condition for behavioural contagion (scent marking) and a general control condition (neutral resting position). Objects were chosen based on pre-trial experience of individual preferences and responses to frightening objects. Every individual was confronted with the objects alone and no visual contact to the familiar conspecifics. Except the scent marking videos (wooden board), no individual had physical contact with the external stimuli. This was done to avoid a direct reaction from the test-subject to the visible external stimuli in the video clip during the experimental phase. Except for the anger-condition, in which the individuals had to leave their home area, every video was recorded in an experimental compartment close to their home cages. To avoid the possibility of seeing the used stimuli during the tests of conspecifics, their home cages were concealed with grey curtains. For the anger-condition, every individual had to be transferred to an experimental cage in front of a strange group. To avoid too much stress, the time of visible confrontation took maximum five minutes.

Table 2. External stimuli to elicit the different expressions.

Condition	Emotional Expression	External Stimuli
Negative	Anger	Unfamiliar conspecifics
Negative	Anxiety	Human stranger staring at the individual for one minute
Negative	Fear	Visual contact with stuffed toy or a lychee fruit for max. 3 minutes
Positive	Positive	Presentation of a preferred food (banana/cricket) for max. 3 minutes
Control (positive)	Scent Marking	Wooden board in the experimental cage
Control (negative)	Neutral	No Stimuli

Preparing of the video clips

I filmed these stimuli videos of all the conditions from two individuals per family group to avoid pseudo replication. I chose the part of the clips with the highest amount of emotional expressions and edited clips with a duration of thirty seconds. To ensure that the individuals gain as much information as possible, the 30 sec. clips were repeated three times in a row every testing session, with a yellow screen for three seconds in between. Hence, every stimuli video clip had a total duration of 99 seconds. The video clips included the sound in the form of the different calls and surround sounds from their housing rooms. The editing and preparation of the video clips was done with the programs Microsoft Movie Maker and Avidemux.

Habituation of the subjects to the testing chamber

Although the individuals were largely habituated to the experimental room prior to the experiments, I further reinforced the habituation with two rounds of 10 minutes over a period of two weeks. This was done on an individual basis with every test subject.

Experimental procedure

The evoking and filming of the different emotional expressions took place in an experimental compartment (150 x 40 x 110 cm). Each experiment lasted max. eight minutes, of which 99 sec. the video was shown. Figure 1 depicts the experimental set-up. The subjects were invited to enter the experimental chamber from their home cages. They were alone in the chamber with no visual access to any other

conspecifics. Before the video was started, the animals were given max. five minutes to calm down and adjust to the situation. After that, the stimulus video started. I filmed the experiment with two cameras from two different angles with two cameras (Canon LEGRIA HF R806). One camera was fixated on the top of the video monitor. The position of the camera was orientated in a way, that as much space as possible got recorded. The second camera was held by the experimenter to follow the individuals during their movement (Figure 1). Except the scent marking condition, there was a wooden board in the experimental compartment, the individuals had no object close to them. After the presentation of the video, the individual was allowed to return to the home cage. After every trial, the compartment was cleaned to avoid a possible olfactory distraction.

In total, I tested 20 subjects with all six conditions: four emotionally charged video stimuli (anger, anxiety, fear, and positive anticipation), one behavioural contagion control (scent marking) and one general control (neutral state). Each subject was tested only once per condition. The stimuli videos were always of familiar group-members. The presenting of the videos to the subjects happened in a randomized order (Appendix Table A1).



Figure 1. Experimental compartment.

Coding and statistical analysing of the recorded behaviour

The coding of the study-relevant reactions has been carried out with the Solomon Coder Version beta (Andras Peter). I defined 33 behavioural parameters of nine different categories (Table 3). Single reactions with a short temporal character were

coded as frequencies. Behaviours with more complex sequences like moving and orientation were coded as durations (Table 3).

For the preparation and analysis of the data I used Microsoft Excel 2016 and IBM SPSS Statistics Version 24. The first part of the statistical analysis was to run a Principle component analysis (PCA) to get an overview about the present data. This resulted in four factors. In the next analytical step, I ran a generalized linear mixed model (GLMM) to compare the stimulus versus the neutral conditions per factor. This happened in regarding of sex, age, breeding status and the stimulus effect.

Table 4. Categories and Definitions of the study-relevant behaviours and reactions.

Category	Definition	Frequency (f)/Duration (d)
Behaviour:		
Look behind screen	Individual is looking behind the monitor	f
Leg stand	Individual is standing on his hind legs	f
Archback display	Individual is showing his curved back	f
Slit stare	Individual is staring with slit eyes	f
Scratching	Individual is scratching his body	f
Stretching	Individual is stretching his whole body or body part	f
Showing tongue	Individual is showing his tongue	f
Activity:		
Moving within body length	Individual is moving within one body length in front of the screen	d
Orientation:		
Orientation towards screen	Orientation with the head or the full body towards the video screen	d
General:		
Moving general	Individual is moving with the whole body	d
Resting general	Individual is resting without moving	d
Resting:		
Resting within body length	Individual is resting within one body length	d
Vocalization:		

Alarm-call		f
Whirr-call		f
Twitter-call		f
Chirp-call		f
Gecker-call		f
Phee-call		f
Tsik-call		f
Tsik-ek-call		f
Ek-call		f
Excretion:		
Defecate	Individual is defecating	f
Urinate	Individual is urinating	f
Agonistic:		
Grab	Individual is grabbing at the monitor	f
Pilo-tail	Individual shows pilo-errection with the tail	f
Pilo-all	The whole body is pilo-errected	f
Grin face	Individual shows a grin face	f
Presenting	Individual is presenting his genitals	f
Ear tuft-moving	Individual is moving his ear tufts	f
Scent marking:		
Scent marking	Individual is scent marking on an object	f
Gnawing	Individual is gnawing on the wooden board	f
Sternal scent marking	Individual is scent marking with his sternum	f

RESULTS

Principle Component Analysis (PCA)

Fourteen out of thirty-three behavioural categories occurred never or very rarely. Therefore, I used the sixteen frequently showed categories in further analyses. To reduce the data and make possible correlations visible, we first calculated a Principle Component Analysis (PCA). These calculations resulted in four factors which were labelled as arousal, scent marking, interest and negative arousal (Table 5).

The first factor (arousal) includes loadings of behaviours twitter-call (0.471), whirr-call (0.632), duration of moving in general (0.917) and duration of the moving within the body length (0.816). The second factor (scent marking) consists of the behaviours scent marking (0.728), gnawing (0.773), defecate (0.489) and sternal scent marking (0.730). The third factor (interest) consists of grabbing (0.487), looking behind the screen (0.752), leg stand (0.675), duration of the orientation towards the screen (0.701). The fourth factor (negative arousal) is formed by pilo-errection of the tail (0.555), tsik-call (0.672), tsik-ek-call (0.634) and ek-call (0.559).

Table 5. Rotated Component Matrix of the behavioural categories which form the factors labelled arousal, scent-marking, interest and negative arousal.

Behaviour	Arousal	Scent Marking	Interest	Negative Arousal
Twitter-Call	0.471			
Whirr-Call	0.632			
Duration Moving in General	0.917			
Duration Moving within Body Length	0.816			
Scent Marking		0.728		
Gnawing		0.773		
Defecate		0.489		
Sternal scent Marking		0.730		
Grabbing			0.487	
Looking behind the Screen			0.752	
Leg Stand			0.675	
Duration of Orientation			0.701	

towards the Screen				
Pilo-Erection of Tail				0.555
Tsik-Call				0.672
Tsik-Ek Call				0.634
Ek-Call				0.559

Generalized Linear Mixed Model (GLMM)

In the next analytical step, I compared the video stimulus versus the neutral condition per factor in regarding of sex, age, breeding status and a possible stimulus effect in which each factor was tested in a separate model.

Anger vs. Neutral condition

I found no significant effects or interactions in the anger condition (for an overview of the result see table 6). In this condition, the subjects did not show any behavioural differences in the test condition compared to the neutral control condition.

Table 6. Results from the Generalized Linear Mixed Model (GLMM) in the comparisons of the Anger condition versus the Neutral condition in regards of sex, age, breeding status and a stimulus effect ($N = 20$, $\alpha = 0.05$).

Factor	Sex	Age	Breeding Status	Stimulus Effect
Arousal	$F = 2.431$ $p = 0.127$	$F = 0.741$ $p = 0.395$	$F = 1.649$ $p = 0.194$	$F = 0.876$ $p = 0.355$
Scent Marking	$F = 2.334$ $p = 0.136$	$F = 0.338$ $p = 0.565$	$F = 1.441$ $p = 0.239$	$F = 0.264$ $p = 0.611$
Interest	$F = 0.140$ $p = 0.710$	$F = 0.991$ $p = 0.325$	$F = 0.665$ $p = 0.421$	$F = 0.397$ $p = 0.533$
Negative Arousal	$F = 0.017$ $p = 0.897$	$F = 0.556$ $p = 0.461$	$F = 3.042$ $p = 0.090$	$F = 0.355$ $p = 0.555$

Anxiety vs. Neutral condition

In the anxiety condition, I did not find any overall behavioural differences compared to the neutral test condition. Regarding the factors scent marking and interest, I found no significant results (table 7). In the arousal factor, there was a visible trend with the breeding status ($F = 3.242$, $p = 0.05$) and in the negative arousal factor, there was a

significant negative age effect, meaning that younger individuals showed more negative arousal independent of test condition ($F = 5.718$, $p = 0.022$).

Table 7. Results from the Generalized Linear Mixed Model (GLMM) in the comparisons of the Anxiety condition versus the Neutral Condition in regards of sex, age, breeding status and a stimulus effect. Inclusive a visible trend in respect to factor one* and a stimulus-independent negative age effect** ($N = 20$, $\alpha = 0.05$).

Factor	Sex	Age	Breeding Status	Stimulus Effect
Arousal	$F = 0.046$ $p = 0.831$	$F = 0.526$ $p = 0.473$	$F = 3.242$ $p = 0.05^*$	$F = 1.673$ $p = 0.204$
Scent Marking	$F = 0.510$ $p = 0.480$	$F = 1.105$ $p = 0.300$	$F = 0.818$ $p = 0.492$	$F = 0.034$ $p = 0.854$
Interest	$F = 1.514$ $p = 0.227$	$F = 0.838$ $p = 0.366$	$F = 0.627$ $p = 0.434$	$F = 1.673$ $p = 0.205$
Negative Arousal	$F = 0.885$ $p = 0.353$	$F = 5.718$ $p = 0.022^{**}$	$F = 0.648$ $p = 0.426$	$F = 0.139$ $p = 0.711$

Fear vs. Neutral condition

In the fear condition, I found a stimulus effect in scent marking behaviours but no significant results in the factors interest and negative arousal (table 8). In the factor arousal, the analysis showed an interaction of the sex and the stimulus. Here, males were less aroused when they saw a conspecific in fear than when seeing it in neutral position ($F = 6.391$, $p < 0.001$), while in females the difference between the conditions was not significant.

In the factor two (scent marking), the individuals showed more scent marking when they saw a conspecific expressing fear ($F = 8.371$, $p = 0.006$). Here, I found also an age/stimulus interaction. The individuals showed more scent marking with age when they saw a resting (neutral) conspecific ($F = 4.981$, $p = 0.012$). In addition, there was a significant breeding status effect which was independent from the stimulus, i.e. non-breeders showed more scent marking when seeing a conspecific in fear ($F = 4.969$, $p = 0.032$).

Table 8. Results from the Generalized Linear Mixed Model (GLMM) in the comparisons of the Fear condition versus the Neutral condition in regards of sex, age, breeding status and a stimulus effect. Inclusive a stimulus-independent breeding status effect* ($N = 20$, $\alpha = 0.05$).

Factor	Sex	Age	Breeding Status	Stimulus Effect
Arousal	$F = 6.391$ $p < 0.001$	$F = 2.333$ $p = 0.137$	$F = 2.089$ $p = 0.158$	$F = 1.468$ $p = 0.234$
Scent Marking	$F = 1.078$ $p = 0.306$	$F = 4.981$ $p = 0.012$	$F = 4.969$ $p = 0.032^*$	$F = 8.371$ $p = 0.006$
Interest	$F = 1.067$ $p = 0.309$	$F = 0.451$ $p = 0.506$	$F = 0.206$ $p = 0.653$	$F = 2.015$ $p = 0.164$
Negative Arousal	$F = 1.672$ $p = 0.204$	$F = 1.638$ $p = 0.210$	$F = 2.011$ $p = 0.165$	$F = 0.031$ $p = 0.861$

Anticipation vs. Neutral condition

In the anticipation condition, I found one significant sex/stimulus interaction in which females were less aroused when they saw a conspecific expressing a positive emotion ($F = 6.381$, $p < 0.001$). In the factor two (scent marking), I found a stimulus-independent age effect ($F = 4.500$, $p = 0.041$). In the factor four (negative arousal), I found a significant negative age effect which was independent of the stimulus ($F = 5.771$, $p = 0.022$). Regarding the other factors, I found no significant effects or interactions (see table 9).

Table 9. The results from the Generalized Linear Mixed Model (GLMM) in the comparisons of the Positive condition versus the Neutral Condition in regards of sex, age, breeding status and a stimulus. Inclusive a stimulus-independent age effect* in factor four and a stimulus-independent age effect in factor two** ($N = 20$, $\alpha = 0.05$).

Factor	Sex	Age	Breeding Status	Stimulus Effect
Arousal	$F = 6.381$ $p < 0.001$	$F = 3.906$ $p = 0.056$	$F = 3.744$ $p = 0.061$	$F = 1.327$ $p = 0.257$
Scent Marking	$F = 3.645$ $p = 0.065$	$F = 4.500$ $p = 0.041^{**}$	$F = 3.948$ $p = 0.054$	$F = 0.668$ $p = 0.420$
Interest	$F = 0.426$ $p = 0.518$	$F = 0.051$ $p = 0.822$	$F = 0.403$ $p = 0.530$	$F = 0.013$ $p = 0.911$
Negative Arousal	$F = 1.794$ $p = 0.189$	$F = 5.771$ $p = 0.022^*$	$F = 0.049$ $p = 0.826$	$F = 0.094$ $p = 0.761$

Scent marking vs. Neutral condition

As expected, I found a significant main effect in the scent marking behaviours, and a weak trend in arousal behaviours (table 10). Individuals scent marked more in the test condition compared to the neutral ($F = 5.600$, $p = 0.024$). In addition, there was a sex/stimulus interaction in factor one (arousal), in which males were less aroused when they saw a conspecific scent marking ($F = 4.204$, $p = 0.023$). Additionally, there was an age/stimulus interaction in the form of a negative age effect ($F = 4.709$, $p = 0.015$) in negative arousal behaviours, and a stimulus/breeding status effect, in which non-breeders showed less scent marking when they saw another individual scent marking ($F = 10.547$, $p < 0.001$). Regarding factor four (negative arousal), I found a significant negative age effect independent of the stimulus ($F = 9.696$, $p = 0.003$).

Table 10. The results from the Generalized Linear Mixed Model (GLMM) in the comparisons of the Scent marking condition versus the Neutral Condition in regards of sex, age, breeding status and a stimulus effect. Inclusive a stimulus-independent age effect* ($N = 20$, $\alpha = 0.05$).

Factor	Sex	Age	Breeding Status	Stimulus Effect
Arousal	$F = 4.204$ $p = 0.023$	$F = 1.238$ $p = 0.274$	$F = 2.871$ $p = 0.099$	$F = 3.483$ $p = 0.071$
Scent Marking	$F = 3.645$ $p = 0.065$	$F = 1.640$ $p = 0.209$	$F = 10.547$ $p < 0.001$	$F = 5.600$ $p = 0.024$
Interest	$F = 0.156$ $p = 0.695$	$F = 0.499$ $p = 0.485$	$F = 0.357$ $p = 0.554$	$F = 0.419$ $p = 0.522$
Negative Arousal	$F = 1.794$ $p = 0.189$	$F = 9.696$ $p = 0.003^*$	$F = 0.049$ $p = 0.826$	$F = 0.094$ $p = 0.761$

DISCUSSION

The aim of the present study was to show if it is possible (1) to elicit different emotional expressions in common marmosets through the confrontation with different objects and conspecifics and (2) if they show emotional contagion when confronted with the behavioural expressions of a conspecific (elicited in 1) on a video screen.

Eliciting of different emotional expressions

The first part was generally very successful. As expected, the monkeys reacted with different behavioural expressions by facing stimuli of different emotional valence.

In the anger condition, I confronted the test subject with an unfamiliar group of marmosets. As soon as the individuals had visual and auditory contact, both the 'intruder' (test subject) and the unfamiliar group members engaged in variety of behaviours. The reactions went from rapidly moving around, pilo-erection of the whole body, trying to grab the others to loud agonistic vocalizations (alarm-calls, gecker-calls, tsik-ek-calls which can be labelled as mobbing calls).

To evoke anxiety, the individuals got confronted with a stranger person for a short period of time (one minute). On this occasion, all subjects showed a very typical behaviour, their so-called 'grin-face' (retracted lips and partially shown teeth). This response is typical for captive marmosets encountering unfamiliar humans, as for instance new staff in the laboratory. In contrast to the reactions in the fear-setting, they hardly made any vocalizations and also showed not much body movement.

In the fear condition, I used two different stimuli due of individual differences in the reactions. While most monkeys responded strongly to a stuffed predator, two individuals showed hardly any fearful reaction towards the stuffed toy. These two subjects were confronted with a skinned lychee fruit, which elicited strong fearful reactions. This phenomenon is well known in our lab, even though we cannot explain why the lychee skin works like a predator stimulus. I defined expressions of the emotion fear especially in contrast to those of anxiety (where I expected almost similar but less strong reactions). When showing fear, the monkeys moved around with at least a pilo-erected tail, ear tuft moving's and the individuals made stressful agonistic vocalizations like whirr-calls, tsik-ek and tsik-calls.

In the positive anticipation condition, I presented the monkeys two sorts of highly desired food (bananas and living crickets). According to Boissy et al. (2007), positive

emotions can be separated into the categories past (post-consummatory satisfaction), present (pleasant sensory activity) and future (e.g. positive expectation). Here, I tried to evoke a positive emotion through the expectation of a much-desired food reward. However, I would like to note that it is difficult to be sure about the valence (positive or negative) of an emotional expression in animals (e.g. Boissy et al., 2007). In the scientific literature, there is relatively little to find about the experience and expression of positive emotions in nonhuman animals. One reason for this could be that the expression of a negative arousal is much easier to interpret as compared to a positive state. In our study, the reactions towards the preferred food could also be interpreted as some sort of frustration about the fact that the food is not reachable. This idea is underlined by the fact that our test-subjects tried to grab the food outside the cage, made unclear vocalizations (food calls but also agonistic calls) and, in some cases, gave clearly negatively valenced calls (tsik-calls). Frustration can be described as an emotional state which arises when the animal fails to achieve some expected gratification (LeDoux, 1995). Nevertheless, I labelled and used the recorded material in that case as 'positive'.

The scent-mark condition was intended to serve as a control that allows me to distinguish between emotional and behavioural contagion. According to Massen et al. (2016), scent marking behaviour is contagious in common marmosets. My recordings confirmed that it can be elicited easily by providing a wooden board and does not go along with typical emotional expressions.

In the neutral condition, I recorded the individuals in a relaxed though attentive state. For these recordings, the marmosets were in the experimental cage without any distraction. I used the frame with the least expression of behaviours for the subsequent presentation in the experiment.

Evoking emotional contagion?

When presenting videos of the different behavioural expressions recorded in the conditions described above to individual monkeys, I found little evidence for emotional contagion. In general, I predicted that common marmosets would show high states of negative arousal in response to a conspecific expressing fear, anger and anxiety. Additionally, I expected high states of interest in the positive anticipation condition.

Anger Condition

In this condition, I found no significant differences compared to the neutral condition. Following the very strong reactions in the first part of the study (recording of the anger stimuli), I expected also strong reactions in the contagion experiment. One possible interpretation for my result is that marmosets hardly experience such an angry reaction from familiar conspecifics (members of their family group) in daily live. According to Mendl et al. (2010), a highly aroused negatively valenced state accompanied by a spontaneous impulse to flee can characterize fear while in contrast, a state of the same arousal accompanied by an urge to attack can characterize anger. In respect to this, we cannot be sure if the individuals probably got influenced by the emotion fear instead of anger.

Anxiety Condition

Here, I also found no significant results. As mentioned above, in the first part of the project, I differentiated anxiety and fear through the intensity of the expressed behaviour. It might be possible that the monkeys showed a contagious reaction, but that this reaction was very weak and fast and therefore not measurable in our setup. In general, the duration of an emotion is a much-debated question, but briefness seems widely accepted (Boissy et al., 2007). The measurement and analysis are always dependent on the used tools. According to this, working with more accurate instruments and coding programs could be helpful in future studies.

Fear Condition

In this condition, I found significant sex-differences. In particular, males were more aroused when seeing a familiar conspecific in fear. Another finding was that the individuals showed more scent-marking behaviour when they saw a conspecific expressing fear. Additionally, I found an age-stimulus interaction. The scent marking behaviour in this condition increased with the age of the individuals. One possible explanation for the sex effect could be the different emotional processing in males and females. From human-studies it is well known, that there are some differences in respect to the experience of emotions (e.g. Kring et al., 1998). Although, there is still a lack of such studies in nonhuman animals, similar phenomena might be possible. Interestingly, scent marking plays a prominent role in our fear condition and potentially could be explained as stress induced behaviour (e.g. Bassett et al., 2003). Further studies need to test whether this is the case.

Anticipation Condition

In this 'positive' emotion setup, I found a stimulus-sex effect. Interestingly, females showed less arousal when they saw a conspecific expressing a (potentially) positive emotion. As mentioned above, it can be very challenging to investigate positive emotions in nonhuman animals and it is not clear, if we really measured positive emotions. Like in the fear condition, sex differences in emotional processing can be also considered here as possible explanation of such a sex effect. Although, common marmosets are well known for their cooperative breeding system, it could be possible that females have in general more contact with juveniles and they are therefore more experienced in the confrontation with these types of 'positive' emotions in the foraging context.

Scent Marking Condition

In this condition, I found a significant stimulus effect. The individuals showed in general more scent marking when they saw another familiar marmoset showing this behaviour. Interestingly, males responded less than females and older individuals showed less scent marking than younger ones. Finally, there were also differences in respect to the breeding status. In particular, helpers showed less scent marking behaviour than breeders when they experienced a scent marking conspecific. Maybe these finding can be interpreted with an influence of the hierarchical social structure. It could be possible that non-breeding individuals are showing less scent marking because of their low status within the group.

That I found significant changes in this condition underlies the validity of our experimental setup. Obviously, the individuals reacted to the presented video clips in a meaningful way, which corroborates that they could perceive at least some relevant information from the video images. This finding also supports the idea of contagious scent marking in common marmosets as described by Massen et al. (2016).

Neutral Condition

Like the scent marking condition, these presentations served as a control setup. However, it is possible, that the videos with a conspecific being "inactive", i.e. showing hardly any movement, could be very unnatural for marmosets. By observing a marmoset group in their home cages, it quickly becomes clear that they are active almost all the time: they play with each other, run around, show grooming behaviour etc. Hence, in their everyday live, except from resting, a conspecific like in our recordings hardly ever occurs. Also, when the test-subjects were in the experimental

cage, they moved around, made vocalizations and showed high amounts of different behaviours. Maybe a lack of any movement in the video prevented them from focussing on the monitor.

General Discussion

Interestingly, I found less change in the observed behaviour in the affective than in the neutral conditions. One possible explanation of this unexpected result could be lying in a possible freezing effect. It is well known from human stress research about the processing and perceiving of strong negative emotions that individuals may react with some sort of freezing when faced with strong and probably dangerous stimuli (e.g. Hagenaars, Oitzl & Roelofs, 2014). Such freezing behaviour can also be observed in nonhuman animals as an indicator for the processing of negative emotions (e.g. Gonzales-Liencre et al., 2014). In rats, for example, the shared distress of a conspecific through emotional contagion can result in strong fear and immobility unless one's own distress is down-regulated (Bartal, Decety & Mason, 2011). It is possible that such a phenomenon also occurs in nonhuman primates like common marmosets. This could help to explain why my test-subjects reacted at rates that were not measurable in most conditions of the experiments. Further studies should investigate the freezing behaviour in primates, and marmosets in particular, under more naturalistic conditions.

Another possible explanation for my results lies in the fact that, even in well-controlled experiments, behavioural or physiological responses to conspecific distress may indicate nothing else than interest and an unspecific arousal (Edgar et al., 2012). In our study, it could be truly possible that the individuals showed interest and unspecific arousal rather than emotional contagion. This could also help to explain the unspecified results I got. In contrast to human studies, where for example the test-subjects are able to tell about their feelings, the study of the emotional processing in nonhuman animals is dependent on measurements without the possibility of verbal reports. In principle, I cannot be sure, if I really investigated animal emotions in our study. Nevertheless, behavioural and physiological continuities between humans and different non-human animals are considerable similar, which allows an exploration of affective states in animals regardless of whether or not they may be consciously experienced (Paul, Harding & Mendl, 2005).

Studying complex emotions and empathic processing usually can be done with cognitive (e.g. cognitive bias) and physiological tests (for review see Preston and de Waal, 2002). Various studies concluded, that beside humans, different other species are able to show an automatic motor mimicry of emotional expressions, which additionally can also automatically generate physiological components of the mimicked emotion (Edgar et al., 2012). A deeper understanding of different emotions needs an awareness of the neural and endocrine systems necessary for the detection and response to bodily states (Porges, 1997). In the present study, there is an obvious lack of physiological and cognitive measurements. In sheep, for example, emotional valence can be differentiated by both behavioural and physiological measures like surface humidity and body temperature (Reefmann, Wechsler & Gyga, 2009). In general, skin temperature can be a promising physiological marker for emotional processing in nonhuman animals. In recent studies, the use of thermal imaging cameras provided a very useful and valid method to investigate a possible linkage between skin temperature and emotional experiences in different species like chickens (Edgar et al., 2011), rhesus monkeys (Kuraoka & Nakamura, 2010) and chimpanzees (Parr, 2001). Such an approach could also be very promising in further studies on common marmosets. Therefore, in follow-up studies, measurements of physiological markers (e.g. cortisol levels through saliva samples, heart rate monitoring, etc.) should be included. One possible disadvantage of physiological measurements is the question, if witnessing a conspecific causes the emotional reaction, or the method itself leads to negative emotions (e.g. collection of blood samples, heart rate monitoring, etc.). In this respect, further improvements of non-invasive methods to measure physiological markers for emotional processes in nonhuman animals are highly desirable.

There is some evidence that motor mimicry of facial expressions occurs in several primate species (Edgar et al., 2012). To differentiate this from emotional contagion, a deeper analysis of the faces would be needed. From human-studies it is well known, that emotions can be distinguished through different facial expressions even when the behaviour of the person looks similar (Ekman & Friesen, 1971). In contrast, observing and quantifying facial expression can be very difficult in animals, even when the animal shows a big variety of expression as in monkeys and apes (Desire, Boissy & Veissier, 2002).

Another valid method for experimentally pinpointing emotional expressions is the cognitive bias test or 'judgement bias' test. The idea behind this approach is that animals in a specific negative emotional state will tend to respond to ambiguous cues as if they predict the negative event (pessimistic judgement), than animals in a positive state (Mendl et al., 2009). In my case, such tests could have helped to see if the tested animals are really showing emotional expressions and it could have also led to a better differentiation between negative and positive emotions. Human studies suggest that the measurement of cognitive skills like attention, memory and judgement biases can often be the indicator for the person's emotional experience. If this is similar in non-human animals, such an approach can offer several advantages to behavioural and physiological indicators of emotions (Mendl et al., 2009).

According to a recent study from Siegel et al. (2018), emotional feelings have a large individual variance in humans. Therefore, individuals can feel and in addition express the same emotion differently. Likewise, in nonhuman animals, different individuals may perceive (appraise) the same situation differently (Mendl et al., 2010). Such differences could probably be explained by different shaping's of individual personality traits. Currently, there is some evidence about the existence of different personality traits in common marmosets (e.g. Koski & Burkart, 2015; Šlipogor et al., 2016). In respect to that, integrating investigations of emotional processing and personality traits in common marmosets could be very advantageous in future studies.

In this project, I worked with the emotions anger, anxiety, fear and a relatively unspecific positive emotion of anticipation. Because of the huge variety of emotions, the observation and investigation of other emotional expressions (e.g. play behaviour as representative positive expression) is highly necessary to make valid conclusions about the emotional spectrum in New World monkeys. Further studies with a wider range of emotions are therefore important and promising.

Intensity, salience and valence of the emotion displayed by the target might have a great influence on the intensity of empathic response (Carter et al., 2009). Although I elicited valid emotional expressions in the first part of the study, it is conceivable that stronger emotional reactions and in addition possible stronger contagious effects might have been possible. Nakahashi and Ohtsuki (2018) assume in their model that

only strong reactions to serious cues are copied, because such reactions are induced by strong emotions with high neural and physiological costs. Therefore, it is possible that the stimuli used in the first part of the present study were too weak and a strong notable reaction did not occur.

In this study, I used a video screen to present the test-subjects the recorded frames with a conspecific showing emotional expressions. Here the question may arise, if marmosets in general are able to gain such an important social information through a 2-D video image. In respect to that, a further experiment with the presence of a familiar conspecific in real live could have some advantages (especially in context of the validity). However, an experiment by Gunhold et al. (2014) demonstrated that even wild common marmosets are able to socially learn from video sequences. This provides a strong argument for the obvious ability of these primates to gain information in such an artificial setting. Interestingly, in contrast to the recordings of the anger condition, the individuals showed no aggressive behaviour, when they saw a familiar conspecific in the video-screen. In my opinion, this suggests that the marmosets were able to figure out, that they were familiar with the depicted subject in the movie sequence. Here, a control setup with the presentation of video clips involving unfamiliar animals could be very interesting for possible further studies.

By reviewing the measurement of empathic responses in domestic animals, Edgar et al. (2012), pointed out, that nonhuman individuals frequently witness negative affective states of conspecifics and the extent to which they are affected by, may depend on their capacity for empathy. Because of a lack of studies involving New World monkeys like marmosets in this regard, it is unclear in our case, which complexity of empathic processing they are able to show and express (e.g. behavioural contagion vs emotional contagion). Emotional contagion is believed to form one of the bases of empathy and it causes consistent group behaviour in many animals (Nakahashi & Ohtsuki, 2018). Common marmosets are known as highly social animals living in a complex environment. Nakahashi and Ohtsuki (2015) argue that some ecological conditions favour the evolution of emotional contagion and this could explain why this phenomenon is frequently observed in group-living animals. Emotional contagion can therefore be interpreted as one of the various ways to learn environmental information from conspecifics (Nakahashi & Ohtsuki, 2015). From this

perspective, I predicted that common marmosets have the ability to share their emotions. Even though we could not find strong evidence for this prediction, it is still conceivable that it is possible to identify emotional contagion in common marmosets.

The first part of the present study showed very well that common marmosets express different emotional states, but the ability to share these emotions is still unclear and cannot be answered through my results and findings. Therefore, further studies are highly desirable when it comes to the question, if New World monkeys and marmosets in particular, are capable of showing emotional contagion. This project is the first exploration of emotional contagion in common marmosets and therefore has to be seen as a first step to unravel the complex phenomenon of empathic processing in this species.

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APPENDIX

Table A1. Randomized presentation of videos to the test-subjects.

Group	Observer	Presented Individual	Expression
Kiri	Oli	Zaphod	Anger
Kiri	Nemo	Zaphod	Anger
Kiri	Luna	Oli	Anger
Kiri	Zaphod	Luna	Anger
Kiri small	Aurora	Jack	Anger
Kiri small	Jack	Aurora	Anger
Kiri small	Mink	Aurora	Anger
Pooh	Fimo	Pandu	Anger
Pooh	Locri	Fimo	Anger
Sprichtel	Kobold	Sparrow	Anger
Sprichtel	Sparrow	Smart	Anger
Sprichtel	Smart	Kobold	Anger
Cleli	Blinky Bill	Veli	Anger
Cleli	Wall E	Clever	Anger
Cleli	Veli	Clever	Anger
Cleli	Clever	Veli	Anger
V	Ernesto	Mathilda	Anger
V	Melvin	Mathilda	Anger
V	Vincent	Melvin	Anger
V	Mathilda	Melvin	Anger
Kiri	Nemo	Oli	Anxiety
Kiri	Luna	Zaphod	Anxiety
Kiri	Oli	Zaphod	Anxiety
Kiri	Zaphod	Oli	Anxiety
Kiri small	Jack	Mink	Anxiety
Kiri small	Mink	Aurora	Anxiety
Kiri small	Aurora	Jack	Anxiety
Pooh	Fimo	Pandu	Anxiety
Pooh	Locri	Pandu	Anxiety
Sprichtel	Sparrow	Smart	Anxiety
Sprichtel	Kobold	Sparrow	Anxiety
Sprichtel	Smart	Kobold	Anxiety
Cleli	Blinky Bill	Clever	Anxiety
Cleli	Clever	Veli	Anxiety
Cleli	Veli	Clever	Anxiety
Cleli	Wall E	Veli	Anxiety
V	Ernesto	Vincent	Anxiety
V	Mathilda	Ernesto	Anxiety
V	Melvin	Mathilda	Anxiety
Kiri	Luna	Oli	Fear

Kiri	Oli	Zaphod	Fear
Kiri	Zaphod	Nemo	Fear
Kiri	Nemo	Oli	Fear
Kiri small	Aurora	Jack	Fear
Kiri small	Jack	Mink	Fear
Kiri small	Mink	Aurora	Fear
Pooh	Locri	Fimo	Fear
Pooh	Fimo	Pandu	Fear
Sprichtel	Sparrow	Smart	Fear
Sprichtel	Kobold	Smart	Fear
Sprichtel	Smart	Sparrow	Fear
Cleli	Clever	Veli	Fear
Cleli	Wall E	Clever	Fear
Cleli	Blinky Bill	Clever	Fear
Cleli	Veli	Blinky Bill	Fear
V	Melvin	Vincent	Fear
V	Vincent	Melvin	Fear
V	Mathilda	Melvin	Fear
Kiri	Nemo	Luna	Scent Marking
Kiri	Oli	Luna	Scent Marking
Kiri	Luna	Zaphod	Scent Marking
Kiri	Melvin	Vincent	Scent Marking
Kiri small	Mink	Jack	Scent Marking
Kiri small	Jack	Aurora	Scent Marking
Kiri small	Aurora	Jack	Scent Marking
Pooh	Fimo	Locri	Scent Marking
Pooh	Locri	Fimo	Scent Marking
Sprichtel	Kobold	Sparrow	Scent Marking
Sprichtel	Smart	Kobold	Scent Marking
Sprichtel	Sparrow	Smart	Scent Marking
Cleli	Wall E	Clever	Scent Marking
Cleli	Clever	Veli	Scent Marking
Cleli	Veli	Clever	Scent Marking
Cleli	Blinky Bill	Veli	Scent Marking
V	Vincent	Melvin	Scent Marking
V	Mathilda	Vincent	Scent Marking
V	Ernesto	Vincent	Scent Marking
V	Melvin	Vincent	Scent Marking
Kiri	Nemo	Luna	Neutral
Kiri	Oli	Nemo	Neutral
Kiri	Zaphod	Nemo	Neutral
Kiri	Nemo	Luna	Neutral
Kiri small	Aurora	Mink	Neutral
Kiri small	Jack	Mink	Neutral

Kiri small	Mink	Jack	Neutral
Pooh	Fimo	Pandu	Neutral
Pooh	Locri	Fimo	Neutral
Sprichtel	Smart	Kobold	Neutral
Sprichtel	Sparrow	Smart	Neutral
Sprichtel	Kobold	Sparrow	Neutral
Cleli	Veli	Clever	Neutral
Cleli	Blinky Bill	Veli	Neutral
Cleli	Wall E	Veli	Neutral
Cleli	Clever	Wall E	Neutral
V	Ernesto	Vincent	Neutral
V	Vincent	Ernesto	Neutral
V	Melvin	Ernesto	Neutral
V	Mathilda	Ernesto	Neutral