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Man's other best friend: domestic cats (*F. silvestris catus*) and their discrimination of human emotion cues

Moriah Galvan[1] · **Jennifer Vonk**[1]

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Abstract The ability of domestic dogs (*C. lupus famaliaris*) to follow and attend to human emotion expressions is well documented. It is unknown whether domestic cats (*F. silvestris catus*) possess similar abilities. Because cats belong to the same order (*Carnivora*), but did not evolve to live in complex social groups, research with them enables us to tease apart the influence of social structure versus domestication processes on the capacity to recognize human communicative cues, such as emotions. Two experiments were conducted to determine the extent to which domestic cats discriminate between human emotion cues. The first experiment presented cats with facial and postural cues of happiness and anger from both an unfamiliar experimenter and their familiar owner in the absence of vocal cues. The second experiment presented cats with vocal cues of human emotion through a positively or negatively charged conversation between an experimenter and owner. Domestic cats were only modestly sensitive to emotion, particularly when displayed by their owner, suggesting that a history of human interaction alone may not be sufficient to shape such abilities in domestic cats.

Keywords Domestic cats · Human emotion · Communicative cues · Companion animal

✉ Jennifer Vonk
vonk@oakland.edu

[1] Department of Psychology, Oakland University, 2200 N Squirrel Rd., Rochester, MI 48309, USA

Introduction

It is surprising to find that achieving the status of the world's most popular pet (Bernstein 2007; The Humane Society of the United States 2011) does not assure you a seat at the main table in the current comparative scientific discussion. Despite the recent explosion of canine cognitive research and canine–human interaction studies (reviewed in Miklósi and Topál 2012; Udell and Wynne 2008), cats have yet to be a large part of the recent trend toward attempting to understand the cognitive abilities of domestic pets (for a recent review, see Vitale Shreve and Udell 2015). Understanding the cat–human relationship has the potential to challenge popular beliefs that sociality and coevolutionary processes are necessary conditions for the ability of companion animals to understand cues of human emotions. Although cats do not have the same domestication history as dogs, they have an evidenced bond with humans (Edwards et al. 2007; Zasloff 1996; Zasloff and Kidd 1994) that may be well served by an understanding of human communicative cues.

Although cats and dogs have different social histories, their early beginnings with humans are similar. Time lines for both species vary, but estimates indicate that the first domesticated dog dates back to 14,000–33,000 years ago (Druzhkova et al. 2013; Ovodov et al. 2011). Cat domestication may have taken place as far back as 10,000 years ago in the Fertile Crescent of the Middle East (Driscoll et al. 2007). By comparing the two species, both wild cats and wolves self-domesticated to early human settlements (Driscoll et al. 2009; Fogle 2007). Wolves were immediately useful to humans as alarm systems, hunters, and companions (Muller 2002), and they were subsequently selectively bred for tameness, obedience, and continued working service (Trut 1999), whereas wild cats found no

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such niche. It is likely that humans tolerated wildcats for their pest-controlling abilities, but had little use for them otherwise. Additionally, a "tamer, more obedient cat" was difficult to breed given that wild cats easily escaped human confines and reproduced freely outside of human establishments. Thus, the domestication process for cats took thousands of years longer than for dogs (Driscoll et al. 2009).

The two-stage hypothesis (Udell et al. 2010) proposes two critical elements necessary for a domesticated animal to sensitize to human cues: First, the nonhuman animal must be willing to accept humans as companions, a process that usually occurs during early ontogeny. Second, the animal should learn through conditioning to follow human actions in order to receive reinforcement. The sensitive period of socialization for kittens occurs from 2 to 7 weeks of age. If socially engaged during this period, kittens have the ability to imprint and recognize specific human handlers, which supports the idea that cats accept humans as social companions (Karsh 1983; Karsh and Turner 1988). Kittens socialized to humans during the sensitive period display less fearful responses to humans at later ages and become more social toward humans overall (Casey and Bradshaw 2008; Karsh and Turner 1988). Turner (1991) suggests that humans may even serve as stimulation for indoor cats in a mutually rewarding relationship, with each subject (human or cat) readily complying with the other's need for interaction. These findings suggest that increased levels of kitten socialization with humans lead to an increased desire for human connection later in adult cat life (Casey and Bradshaw 2008; Karsh 1983), and thus the acceptance of humans as social companions.

In support of the second stage of the two-stage hypothesis, cats also appear capable of learning to respond to some human actions. For example, there is evidence that cats are as capable as dogs at following basic human gestural cues (Miklósi et al. 2005). Miklósi et al. (2005) tested cat and dog subjects on four different types of human-presented communicative cues in the form of pointing gestures. The gestures were combinations of proximal (10–20 cm away from the bowl) or distal (70–80 cm away from the bowl) cues and momentary (the point position was held for 1 s and then removed) or dynamic (the point position was held for the duration of the trial until the subject made his/her choice) cues. If the animal understood the cue, it could utilize the cue to locate hidden food in one of two containers. The results indicated that cats were as proficient as dogs in their use of the four types of communicative cues, although the authors suggested that dogs may have the overall advantage in following communicative gestures due to their trainability and tendency to offer extended visual contact with humans. Notable, however, is that neither species demonstrated significant learning throughout the duration of the experiment, suggesting that both species were familiar with communicative cues and their potential meanings before the onset of the experiment. An ability to respond to human points need not imply anything about the underlying representation of a human's intentions, but it does imply that cats are able to use these cues to predict the presence of objects of interest.

The goal of the current study was to extend these findings to the domain of human emotion cues. As with the ability to follow gestural cues, an ability to respond differently or appropriately to varied cues of human emotion need not imply that cats have representations of the meaning of underlying emotion states, but it would again show that cats are able to interpret and predict different consequences based on cues provided by humans. In this case, cues provided by emotion expressions might be considered to be more subtle than overt point and gesture cues. Therefore, an ability to use human emotions as predictive cues to likely outcomes is unlikely to emerge in the absence of prolonged human contact, but we also questioned whether it would depend upon having evolved to live in social groups, in which case, dogs, but not cats, should have this ability. Domestic dogs have previously demonstrated the ability to differentiate human facial expressions. For example, Deputte and Doll (2011) found that dogs displayed more avoidant behavior and were significantly less likely to approach actors displaying angry expressions in comparison with actors displaying happy expressions. Buttelmann and Tomasello (2013) determined that dogs were able to utilize human facial expressions of happiness and disgust to locate hidden food. Merola et al. (2012) found that dogs did not regulate their behavior as a function of positive or negative emotional messages provided by humans in a social referencing paradigm, but did respond differently toward a potentially frightening object. Furthermore, a follow-up study found that dogs were better able to distinguish between emotions when their familiar owner, rather than a stranger, presented the cues (Merola et al. 2014). In this study, dogs could distinguish between their owners' fearful and happy expressions and use these cues to guide their explorations of boxes, but, as in Buttelmann and Tomasello (2013), had more difficulty differentiating neutral expressions from other emotional expressions. These findings support the idea that dogs interpret human emotion expressions in an adaptive manner allowing them to predict plausible outcomes, but that specific experience through human interaction is critical.

Merola et al. (2015) also recently tested domestic cats in a similar social referencing paradigm and found similar rates of looking between the owner and the ambiguous object as they previously observed in dogs (2012). This result contrasted with a previous study that reported lower rates of gaze to the owner from cats compared to dogs

(Miklósi et al. 2005) when food was placed out of reach. Furthermore, Merola et al. (2015) found only subtle behavioral differences when the owner reacted in negative versus positive ways to an ambiguous object (i.e., a fan). For example, cats were slightly quicker to start moving in the negative condition and gazed more at a possible exit. Thus, previous studies have suggested the possibility that cats will show more subtle effects of human emotion cues compared to dogs, but with only one existing study testing cats (Merola et al. 2015) it is important to examine cats' behavior in different contexts.

In the current study, we measured domestic cats' natural responses to humans exhibiting different emotion states in two experiments using facial, postural, (Experiment 1) and vocal (Experiment 2) cues of emotion. We hypothesized that cats with a close personal relationship to humans would alter their behavior in accordance with two basic human emotions: happiness and anger. In accordance with previous research finding that dogs (Merola et al. 2014) and cats (Collard 1967; Casey and Bradshaw 2008; Edwards et al. 2007) respond differently to familiar versus unfamiliar humans, we also manipulated familiarity of the human with the prediction that cats may be better able to differentiate the emotions of a familiar human caretaker compared to a stranger. The first experiment tested cats in a very familiar room of their home with a familiar and unfamiliar human using only emotion-related facial expressions and posture for the emotions of happiness and anger. The second experiment tested cats in a neutral laboratory with both their familiar owner and an unfamiliar experimenter using positive and negative emotional vocal cues (in the form of an emotionally charged conversation) to investigate their reactivity to an auditory cue of emotion versus a visual cue alone. In both experiments, we observed the cats' behavior and disposition, their latency to approach the (unfamiliar) experimenter or their (familiar) owner, and the duration in which they stayed in close proximity to either human. Additionally, in the second experiment, we added the variable of gaze direction and duration of gaze.

Experiment 1

In Experiment 1, we sought to determine whether cats would behave differently in response to two basic human emotion expressions without the use of verbal or dynamic movement cues. The two human expressions simulated for the cats were happiness (positive) and anger (negative, see Fig. 1). We predicted that cats would respond more positively, approach the human more quickly, and spend more time in contact with the human in the positive emotion condition compared to the negative emotion condition. We also expected that these effects might be more pronounced for the familiar owner, and that cats would generally approach the familiar owner faster than the unfamiliar experimenter. In contrast to the previously reviewed research, we were not interested in the ability of the cats to infer a communicative message with regard to a secondary object. Rather, we wished to measure a natural response to an indicator of emotional state, which might predict a direct behavioral consequence for the subject (i.e., an angry person is more likely to cause harm relative to a happy person). By reducing the extent to which the cat had to infer a goal or disposition on the part of the human toward an external object, we hoped to increase the potential to observe differential effects of the cats' behavior with regard to the human's differing emotion cues.

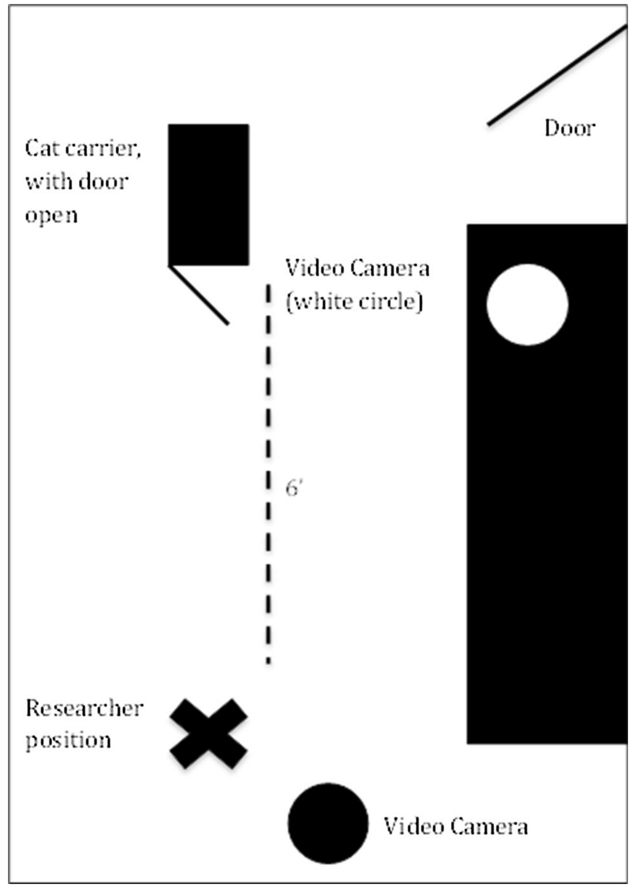

Fig. 1 Experimental setup for Experiment 1

Method

Subjects

Experiment 1 included 12 sterilized adult cats from five different households. Eight of the cats had participated in a pilot study, which was similar to the current study but involved releasing the cats from crates, and four of the cats were naïve to testing. Five different owners participated in this experiment. All of the cats were of mixed breed (seven males, five females) and ranged in age from an estimated 1–12 years. All were housed indoors and were "rescued" from shelters or as strays. All were described as affectionate with their owners.

Materials

Experiment 1 required two video cameras on tripods, a stopwatch, a measuring tape and placeholders, and a small food dish with treats. The video cameras on tripods were set in different places according to the testing room. However, each room had a video camera capturing the main footage of the session (the area in close proximity to the human, including the treat bowl and starting location of the cat), as well as a background video camera to capture areas not accessible by the main video where the cat may have investigated during the experiment.

Testing environment

The cats had a room in their house where they spent the majority of their time. These rooms were used as the testing spaces for the experiment. They were all approximately equivalent in size ($\sim 4 \times 4$ m) with at least one window and a door to keep subjects in the testing space during testing. All items (cat furniture, human furniture, toys, water bowls, etc.) were left in the testing space to maintain the normalcy of each room, but each room contained enough empty space to make it possible to conduct the experiment. The basic setup is depicted in Fig. 1.

Procedure

Eight of the cats participated in eight trials (two individual trials per day) across four test days. Given observed consistency in behavior over time and based on the availability of the additional three owners, the remaining four cats participated in four trials (one of each condition) in one test day. The order of presentation of emotion expressions was counterbalanced across and between cats, such that every cat participated in four happy emotion expression trials and four angry emotion expression trials (two of each with the familiar owner and unfamiliar experimenter), but no cat received the same order of presentation of expressions. Although the unfamiliar experimenter was no longer completely unfamiliar given that she had participated in four trials with eight of the cats in the pilot, she was still unfamiliar in comparison with the familiar owner (with whom each cat had lived for several years). Thus, there were four test conditions for Experiment 1: familiar happy, unfamiliar happy, familiar angry, and unfamiliar angry. Facial expressions were based on Ekman and Friesen (1975). Each was presented while the experimenter was sitting cross-legged, in direct sight line with the subject. The facial expressions were based on descriptions and images of human facial expression and emotion given by Ekman and Friesen (1975) and are depicted in Fig. 2. The experimenter had amateur theatrical experience, but to ensure that she was exhibiting the appropriate facial expressions for the designated trials, a naïve coder verified the intended emotion on 96 % (70/73) of the trials by observing the trials on video.

Angry emotion expression In the angry emotion expression condition, the experimenter sat cross-legged, with arms tense and hands clenched in fists resting on her/his knees. Posture was upright, tense, and slightly leaning forward. The face was clenched, with eyebrows furrowed and pinched together. The mouth was firmly set, lips puckered in, with chin slightly protruding. As with the

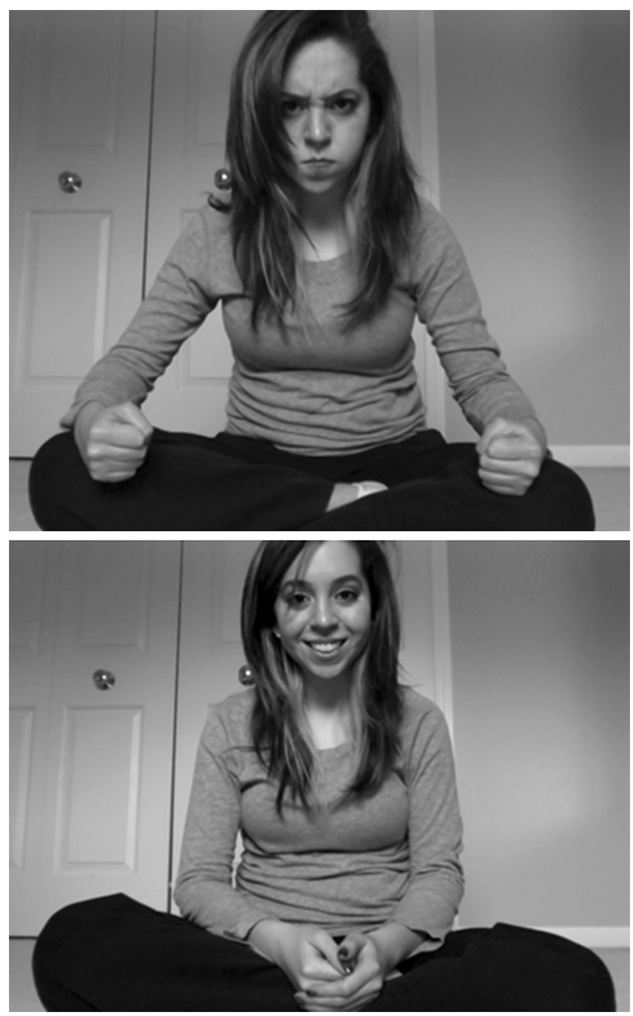

Fig. 2 Facial expressions for Experiment 1: angry (*top*) and happy (*bottom*)

happy condition, direct gaze was given to the subject for the duration of the trial.

Happy emotion expression In this condition, the experimenter sat cross-legged, with arms resting loosely on her knees or in her lap. Posture was upright, but relaxed. The face was relaxed, eyes slightly narrowed, with soft gaze directed toward the subject for the duration of trial. The experimenter was smiling (which alternated during a trial between showing teeth or not to prevent strain) and maintained relaxed breathing.

On each test day, the experimenter (female, 23 years) arrived at the home of the cats with all necessary materials. She wore neutral clothing. She went directly to the room that the owner indicated the cat should be tested in and set up the equipment. In each testing room, the measurements were identical. The experimenter marked .5 m from the entrance into each testing room as the location for the experimenter to sit. The treat bowl was marked 2 m from the experimenter's location, toward the center of the room. The treat bowl was used as motivation to lure the cats into a consistent starting position 2 m away from the experimenter (unfamiliar or familiar). When first placed, this worked to reposition the cats from the door to the room to the start position, allowing the experimenter to enter.

On each trial, the owner turned on the video cameras, placed several treats into the bowl, and placed the cat in front of the bowl before exiting the room. If the cat approached the bowl and immediately began eating, the owner indicated to the experimenter to enter the room, sit, and begin the trial by displaying the emotion expression. When the experimenter was in position, the owner shut the door and started the stopwatch. The trial lasted 3 min. If the cat did not approach the treats immediately after they had been set down, the owner would exit the room, start the stopwatch for 1 min, and then indicate to the experimenter to enter the room and begin the trial as described previously. At the end of 3 min, the owner would knock on the door, indicating the end of the trial. This signaled to the experimenter to stop the video cameras, open the door, and release the cat back into the main living area. These roles were reversed if the owner was participating in the trial (familiar condition). The order in which the cats were tested was randomly determined across all test days. In the multi-cat house, all of the cats rotated through their first trial before beginning the second trial. This allowed for maximal time between trials for each cat in an attempt to counteract any possible habituation effects.

Behavior coding All behavioral data were coded from video by a naïve research assistant. Additionally, a second research assistant coded a random 25 % of the videos for reliability. The research assistants yielded a high inter-rater correlation for latency to exit the carrier ($r = 1.00$, $p = .01$), behaviors presented ($r = .93$, $p = .01$), and duration of time spent in contact with either human ($r = .98$, $p = .01$). The assistants measured approach latency, duration of contact, and types of behaviors presented by the cat (grouped as positive, negative, or neutral behaviors).

Dependent Measures Approach latency was measured as the time it took from the start of the trial for the cat to be within 10 cm of the experimenter's body. This time was recorded as the time to "make contact." The duration of time spent in contact with either type of human was the sum of the time(s) the cat spent "making contact" with a human. "Making contact" included behaviors such as rubbing against the experimenter, eating the treats, sniffing the experimenter within 10 cm of the experimenter's body, pawing at the experimenter, climbing in her lap, and other curiosity/attention-seeking behaviors.

Cat behavior(s) The behavioral ethogram depicted in the section "Appendix" was utilized to ensure that the research assistant could accurately gauge cat behavior and body language. The ethogram was based upon earlier work by Leyhausen (1979) with some modifications to suit the current research. The assistant was asked to watch each video in 15-s blocks (demarcated with a stopwatch) and indicate all behaviors observed at each interval using interval sampling. That is, they simply checked a box whether a behavior was present during that 15-s interval. After coding was completed, the behaviors were categorized as those that were explicitly positive and negative. For example, having ears forward and normal, relaxed body posture were considered positive behaviors, whereas slinking, tense body posture and a tightly tucked tail were considered negative behaviors. The frequencies of each type of behavior were summed.

Data analysis

Data (approach latency, duration of contact, and positive/negative behavior frequencies) were analyzed using repeated measures ANOVAs with familiarity (familiar, unfamiliar) and emotion (happy, angry) as repeated factors, using SPSS version 20.0. We used simple main effect tests (paired t tests) to examine significant interactions. We applied a Bonferroni correction for multiple analyses (.05/3) accepting a p value as significant at .017.

Results

A repeated measures ANOVA on approach latency with familiarity (familiar owner, unfamiliar experimenter) and emotion (happy, angry) as factors revealed no significant differences in approach latency based on emotion ($F_{1,11} = .00$, $p = .96$, $\eta^2 = .00$) or familiarity ($F_{1,11} = .06$, $p = .81$, $\eta^2 = .01$). There was no interaction of emotion and familiarity ($F_{1,11} = 2.10$, $p = .18$, $\eta^2 = .16$). Figure 3 shows the results for total duration of contact. There was no main effect of emotion ($F_{1,11} = .75$, $p = .41$, $\eta^2 = .06$) or familiarity ($F_{1,11} = 3.67$, $p = .08$, $\eta^2 = .25$), but there was an interaction between emotion and familiarity that approached our adjusted significance level ($F_{1,11} = 9.98$, $p = .01$, $\eta^2 = .48$). To probe the interaction, simple effect tests were conducted in the form of paired sample t tests to compare duration of contact in happy versus angry conditions for familiar owners and then for unfamiliar experimenters. The test was not significant for the unfamiliar experimenter; $t_{11} = -.98$, $p = .35$, CI −35.94–13.84. For the familiar owners, there was a tendency for cats to spend more time in contact with their owner in the happy ($M = 66.75$, SD = 63.11) versus angry condition ($M = 34.21$, SD = 38.69), $t_{11} = 1.96$, $p = .08$, CI −4.08–69.17). The results are depicted in Fig. 3.

Figure 4 shows the results for (a) positive and (b) negative behaviors. The behaviors were averaged across trials and were also analyzed using a repeated measures ANOVA including the factors of emotion and familiarity, as well as valence (positive, negative). There were significantly more positive behaviors exhibited by the cats than negative behaviors ($F_{1,11} = 29.03$, $p < .001$, $\eta^2 = .73$). There was a significant three-way interaction between valence of behaviors, emotion, and familiarity ($F_{1,11} = 10.69$, $p = .01$, $\eta^2 = .85$). The interaction was probed using separate repeated measures ANOVAs, split on the factor of valence (positive and negative). There was a significant interaction between emotion and familiarity only for positive behaviors ($F_{1,11} = 10.37$, $p = .008$, $\eta^2 = .49$). To

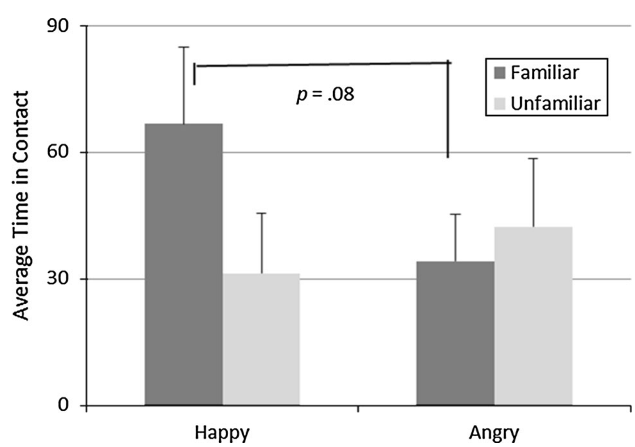

Fig. 3 Average time spent in contact with either human (familiar or unfamiliar) in both emotion conditions (happy or angry) in Experiment 1

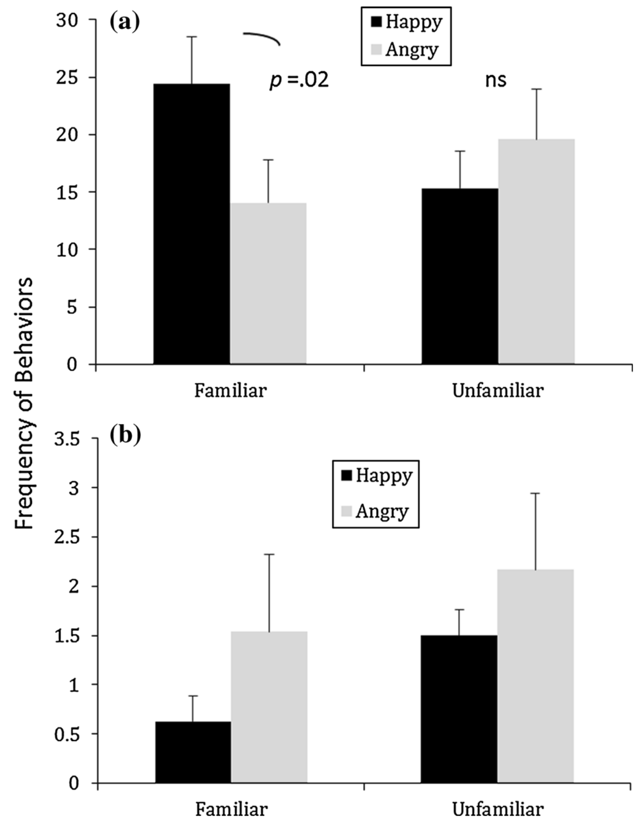

Fig. 4 **a** (*top*) Depicts the significant interaction between emotion and familiarity for positive behaviors in Experiment 1. **b** (*bottom*) Depicts the nonsignificant interaction between emotion and familiarity for negative behaviors in Experiment 1. Note the figures are presented on different scales for the sake of clarity

examine the interaction, two paired samples t tests were conducted, one for familiar owner and another for the unfamiliar experimenter. For the experimenter, emotion was not significant, $t_{11} = -1.44$, $p = .18$. For the owner, however, emotion approached significance, $t_{11} = 2.76$, $p = .02$. The cats displayed more positive behavior when their owner was displaying a happy ($M = 24.42$, SD = 14.08), rather than an angry, expression ($M = 14.08$, SD = 12.83).

Discussion

Although the cats did not appear to alter their approach to their owner based on the emotion condition, they did alter their overall behavior by responding more positively to their owner in the happy condition. With regard to the duration of time the cats spent in contact with either type of human, the cats spent more time with their owner in the happy than in the angry condition, whereas they showed no significant difference with the unfamiliar experimenter. Thus, these cats were more sensitive to emotions when displayed by the owner—being more likely to engage in positive behaviors and spend time in contact with her when she appeared to be happy than when she appeared angry. These findings are consistent with findings that dogs find it easier to discriminate familiar emotions with familiar humans (Merola et al. 2014). It should be noted that relatively subtle changes in cats' behavior as the result of emotional cues given by familiar humans are also consistent with previous research (Merola et al. 2015). Taken together, these findings at least suggest that cats prefer positive emotion states in humans when these emotion states are conveyed by familiar humans with which they have established social bonds. We had deliberately controlled for sensitivity to auditory cues of emotion in the first experiment, but, given the relatively subtle effects with only visual cues present, we decided to include vocal cues in a follow-up experiment.

Experiment 2

In this experiment, we presented cats with vocal cues, in the form of an emotionally charged conversation (positive or negative) to increase the saliency of the cue and potentially the likelihood of the cats differentiating the two conditions. Vocal cues were selected given cats' sensitivity to auditory information (Fay 1988; Warfield 1973) and recent research by Saito and Shinozuka (2013) that demonstrated that cats differentiate and respond more to the voice of their owners than to the voices of novel humans. Cats were transported to a novel research site for this experiment; thus, carriers were introduced to both (a) protect the cats during travel and (b) provide a consistent starting position for both trials. If the cats could discriminate the vocal emotion cues, we expected that they should alter their latency to exit their carrier such that they would be more hesitant to leave the carrier during the negative emotion condition and faster to exit the carrier in the positive emotion condition. Additionally, the cat's overall disposition during the trial should reflect the condition, i.e., an increase in negative behaviors in the negative condition and an increase in positive behaviors in the positive condition. We also expected cats to spend more time in contact with the owner and experimenter during the positive condition, and we thought that this effect might be even more pronounced for the experimenter.

In Experiment 2, we also measured frequency of gaze toward both humans based on a recent finding that cats may utilize social referencing (Merola et al. 2015), in which an individual utilizes the perceptions and behaviors of another to shape their understanding of a situation (Feinman 1982). Given that the cats were placed in a novel environment in Experiment 2 and could use the owner as a reference when approaching the unfamiliar experimenter, gaze was a more useful cue here than in Experiment 1 where there was only one human present in a familiar environment. Social referencing is a known phenomenon in dogs (Merola et al. 2012, 2014), whereby dogs will alter their "looking" behavior and locomotion toward a novel object based on their owner's reaction. More than 80 % of the dogs in Merola et al.'s (2012) study looked referentially toward their owner. Additionally, they altered their behavioral approach and avoidance of the novel object based on their owner's own negative-avoidance response. The same research team recently found cats capable of social referencing under the same conditions (Merola et al. 2015). Therefore, in this study, it was hypothesized that the cats might spend more time exploring the room (perhaps closer to the experimenter) during the positive condition, whereas they might gaze more frequently at their owner in the negative condition when the atmosphere would be tense. The hypothesis of Experiment 2 was that understanding the cues of positive human emotion would signal relaxation to the cats, whereas understanding the cues of negative human emotion would signal fear and hesitancy to engage in contact with the cats.

Method

Subjects

Experiment 2 included 26 sterilized adult cats (15 males, 11 females). Twenty-three of the 26 cats lived exclusively indoors at the time of testing, two cats lived primarily indoors but had access to the outdoors, and one cat lived exclusively outdoors. The cats came from 16 households; therefore, 16 owners participated in the experiment. The average age of the cats was 5.53 years, with the average age of adoption as 1.19 years. On average, the cats had cohabitated with their current owner for 3.93 years before participating in this experiment. Before being adopted, 11 of the cats were identified as strays, six were adopted from shelters with unknown prior histories, five were house cats for the duration of their lives, two were exclusively outdoor cats, and one was a farm cat. None of the cats were considered feral, indicating that all of them had received some early socialization with humans such that they accepted and were responsive to the presence of humans. The cats were solicited via social media (Facebook), on campus recruitment (handing out flyers in psychology classes), and word of mouth. To participate, cats had to be physically healthy and easy to handle. The owner was required to bring the cat in a travel carrier, with the ability to replace the cat in the carrier several times throughout the duration of the experiment. The owners were given a five-dollar gift card for participation, with intended use for supplies for their cat.

Materials

The laboratory room was equipped with two video cameras on tripods, a table for the cat and carrier, place markers for the humans to stand on, and a stopwatch for timing the trials. The owner completed informed consent forms and demographic surveys before the trial began.

Testing environment

The laboratory space was rectangular (3 × 4 m), with one door and two windows. The laboratory and windows were painted black. The room held minimal distractions for the cats. Before testing began, the laboratory room was configured for testing. A 2 × 1 × .5 m table was placed lengthwise in the room. The video cameras were positioned to allow maximal video footage of the room. One video camera and tripod was erected facing the table where the carrier was placed with the front of the carrier facing the camera. This camera captured the cat's behavior and gaze as he/she remained in, or exited, the carrier. The second video camera and tripod was placed in the corner of the room, behind the table and carrier. This camera captured the cat's movements around the room after he/she exited the carrier. Place markers in the form of a masking tape "1" and "2" were placed on the ground .5 m from the end of the table where the cat carrier faced. The place markers allowed the experimenter to counterbalance the owner's position to eliminate any side biases the cat may have had. This meant for one trial, the owner stood on the number "1" and the experimenter on the number "2," while in the other trial the owner stood on the number "2" and the experimenter stood on the number "1." See Fig. 5 for a diagram of the laboratory setup.

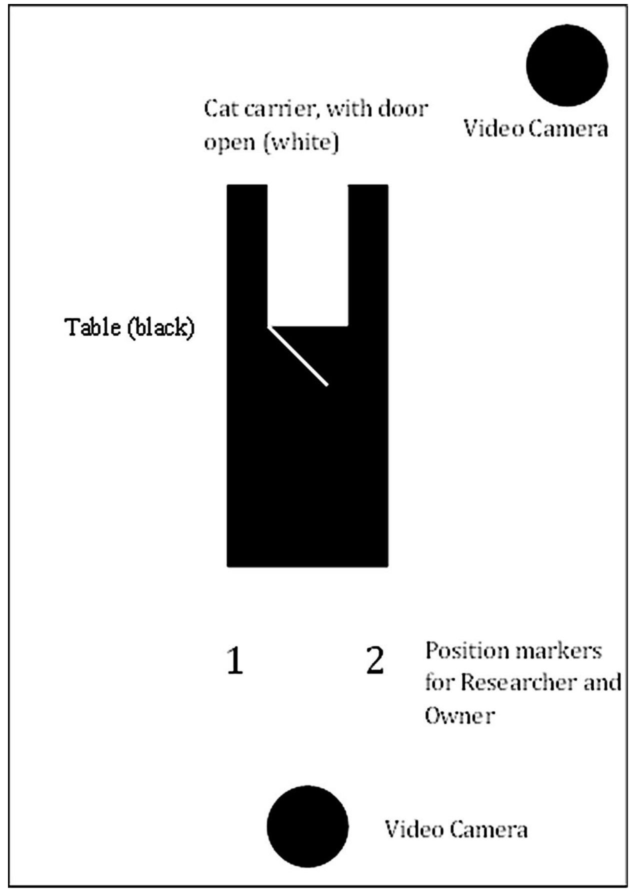

Fig. 5 Experimental setup for Experiment 2

Procedure

The cat was brought to the testing facility in a travel carrier and escorted to the laboratory space by the experimenter. Upon reaching the laboratory, the experimenter instructed the owner to place the carrier on the table with the carrier front facing the video camera. She then asked the owner to step into the hallway to allow the cat to acclimate to the testing space as well as to explain the trial procedure. The owner was instructed that the experimenter would be having two conversations with him/her. This procedure required acting on the part of the research team and the owners of the cats. The experimenter had amateur theatrical experience, but the owners were not known to. For this reason, the experimenter provided scripted phrases that served as emotion prompts for both the owners and the experimenter to use to convincingly convey the emotion in front of the cat. The owner was told that he/she was free to use the scripted prompts or to ad lib the conversation as long as the content maintained the emotion of the trial. The experimenter indicated that during the conversations, the owner was to keep a moderate and consistent vocal volume (no yelling or making loud noises that could startle the cat), to avoid touching or making eye contact with his/her cat should he/she approach, and to avoid excessive movement (e.g., waving arms, shaking a fist, or other movements that may frighten the cat). When the owner understood the procedure, the owner and experimenter equipped with a stopwatch to time the trial entered the laboratory. Exact movements and scripts were not controlled or standardized because the goal was to establish a natural conversation that varied in emotional tone, and corresponding expression and postures. In order to verify that the conversations were interpreted as positive and negative to a naïve human observer, a research assistant who was naïve to the purpose of the study coded the emotional valence of the trials from video. Her coding agreed with the intended valence on 100 % of the trials.

Each cat participated in two consecutive 2-min trials. Upon entering the laboratory, the experimenter initiated recording on both video cameras. The experimenter then asked the owner to open the cat carrier door and then stand facing the experimenter, on the number "1" or "2" taped on the floor. Position was counterbalanced across individual cats and across conditions. The trial started when the cat carrier door was open and the owner was standing on the appropriate positional number facing the experimenter. The experimenter started the stopwatch and engaged the owner in conversation with the appropriate emotional tone for that trial. One trial was deemed positive and the other negative with order of presentation randomized across cats.

When 2 min had elapsed on the stopwatch, the experimenter asked the owner to place the cat back in the carrier and secure the carrier door. While the owner collected the cat, the experimenter turned off the video cameras and then both humans exited the room to prepare for the next trial. To avoid the cat becoming familiar with the experimenter during the first trial and therefore exiting the carrier faster on the second trial, a research assistant (also female, though without theatrical experience) performed the second trial with the owner, following the same procedure as the first trial.

Behavior coding We measured the duration that each subject spent in proximity to the owner and experimenter/research assistant (measured by dividing the video screen into four equal quadrants), the cat's gaze direction during the trials (at the experimenter or owner), the latency to exit carrier and overall behavioral disposition (varying from stressed to relaxed) for each trial. Two research assistants who were naïve to the hypotheses of the study coded the video to assess these variables. They were instructed to keep the sound of videos muted to avoid any coding biases. The research assistants yielded a high inter-rater correlation for latency to exit the carrier ($r = .90$, $p = .03$) and for behavioral disposition ($r = .76$, $p = .002$)

Results

To measure the duration of time in proximity to owner/experimenter, the video for each trial was divided into four equal sized quadrants. The amount of time spent on the side (which was comprised of two adjacent quadrants) with the owner was summed, as was the amount of time spent on the side (comprised of the other two adjacent quadrants) where the experimenter was positioned. A repeated measures ANOVA with the factors of emotion (positive and negative) and familiarity (unfamiliar experimenter/research assistant and familiar owner) for the duration of time spent in proximity to both types of human was performed. There were no significant main effects of emotion ($F_{1,21} = .60$, $p = .45$) or familiarity ($F_{1,21} = 2.23$, $p = .15$) and no significant interaction ($F_{1,21} = .001$, $p = .98$).

Figure 6 summarizes where the cats were focusing their attention during the trial. A frequency of "looks" toward the owner, experimenter, or anywhere else in the room was acquired by tallying where the cats were looking at 10-s intervals for the duration of the trial. A repeated measures ANOVA was conducted on gaze frequency with the factors of emotion (positive and negative) and familiarity (unfamiliar experimenter/research assistant and familiar owner). Emotion did not have a significant impact on gaze frequency ($F_{1,25} = .72$, $p = .40$). However, the effect of familiarity approached significance based on our adjusted p value in that cats looked significantly more at their owner than at the experimenter ($F_{1,25} = 4.96$, $p = .04$). There was no interaction between emotion and familiarity ($F_{1,25} = 1.44$, $p = .24$).

The time until the cat exited the carrier in both trials was measured using a stopwatch. These times, grouped according to emotion (positive or negative), were compared using a paired samples t test. The results were non-significant based on emotion condition ($t_{25} = .34$, $p = .73$).

Lastly, to measure behavioral disposition, the research assistants were given a behavioral ethogram (see "Appendix" section) and asked to rate the cats on a Likert scale ranging from −2 (very stressed) to 2 (very relaxed) for the overall trial. A paired samples t test was conducted to compare the total scores based on condition (positive or negative). There was no significant difference between perceived emotional state/behavioral disposition based on emotion condition ($t_{25} = .42$, $p = .68$).

Discussion

The results from Experiment 2 indicate that the cats do not adjust proximity to their owner or the experimenter based

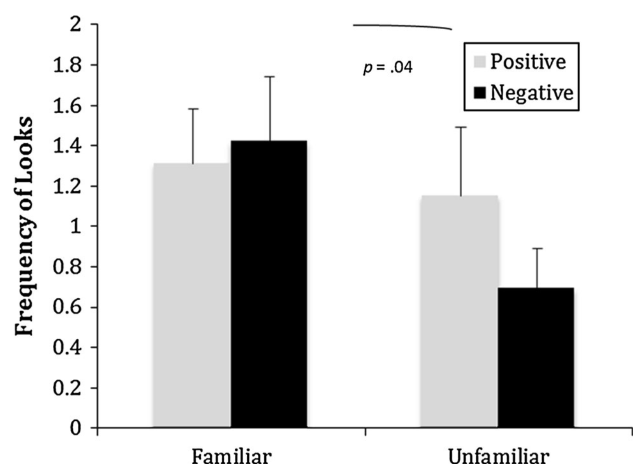

Fig. 6 Average frequency of "looks" toward owner (*familiar*) or experimenter (*unfamiliar*) in both the negative and positive emotion conditions in Experiment 2. There were significantly more "looks" toward the owner than the experimenter

on emotion condition, nor do they modify their latency to exit their carrier based on the emotion condition (positive or negative). Additionally, when a research assistant was asked to rate the cats on their overall disposition throughout the trial, it did not appear that the cats were reacting more negatively (stressed) under the negative emotion condition, or more positively (relaxed) during the positive emotion condition. This is unlikely to be due to high levels of distress from the experimental manipulation given that the average behavioral disposition scores were positive in both conditions. Finally, the cats gazed more at their owner than at the unfamiliar experimenter, suggesting that they may have been looking for cues, as in social referencing, from the owner. That the use of the owner as a source of reference was not differentiated based on emotion cues suggests that the cues provided were not salient to the cats and that cats viewed both experimental conditions as equally ambiguous. Thus, the results from this study may indicate their propensity for social referencing, consistent with Merola et al. (2015), such that cats look more toward their owners in novel situations regardless of the emotional atmosphere.

There are several reasons why emotional context may not have significantly impacted proximity to owner/experimenter, latency to exit carrier, and behavioral disposition. First, because the experimenters and owners were acting, the cats may have been unable to hear or feel a sincerely negative environment in the way they might perceive negative emotion in their home when their owner is truly upset. Furthermore, natural emotions may be associated with different chemical or olfactory signals that were not present in the contrived experimental conditions. However, Mayes et al. (2015) have shown that, in a food search task, cats appear to prioritize visual over olfactory cues, suggesting that the lack of chemical cues in this scenario may not have been responsible for preventing them from discriminating between conditions. Second, the laboratory setting was exciting to some cats and stressful to others. Whereas some of the cats eagerly exited their carrier to explore (regardless of what their owner and experimenter were doing), others appeared stressed, and their response to the emotion conditions may have been masked by their neophobia. Thus, individual differences in response to the situation may have exerted a stronger impact on behavior than the experimental manipulation.

General discussion

These experiments are among the first conducted on domestic cats to determine their discrimination of human emotion expressions. The results suggest that cats may alter their behavior in subtle ways based on the expressions of emotion, especially when a familiar owner is displaying the emotion, similar to the findings of Merola et al. (2015). For example, in Experiment 1, cats spent more time in contact with their familiar owners when those owners appeared happy than angry. However, unlike domestic dogs and their extensive, easily quantifiable usage of human emotive cues (Buttelmann and Tomasello 2013; Deputte and Doll 2011; Merola et al. 2012, 2014; Muller et al. 2015), cats do not appear to display the same type of responses when presented with the two most extreme human emotions (happiness and anger) presented through facial, postural, or vocal cues. For example, cats did not alter their approach based on human emotion expressions, but they did adjust their duration of contact and expression of positive behaviors in Experiment 1.

Behaviorally, the cats showed significantly more positive behaviors toward their familiar owner in the happy emotion condition versus the angry emotion condition. This could suggest that the cats' positive behaviors were somewhat influenced by the emotion of their owner, and that, perhaps, they may have equated their owner's positive disposition in the happy condition with a prior history of reinforcement (as happiness from the owner may have signaled affectionate or rewarding behavior toward her cats). This could be further substantiated by the fact that the cats performed significantly less positive behaviors in the angry trials and did not react to the emotions of the unfamiliar experimenter in any particular way. Although this result would need to be replicated, it fits well with the two-stage hypothesis, advanced by Udell et al. (2010) and with the current companion animal literature. Custance and Mayer (2012) found a similar effect in dogs, whereby dogs consistently approached and attempted to "comfort" their distressed owners as well as strangers. Custance and Mayer summarized the dogs' results less as true "empathy" and more as operant conditioning simply stating that the dogs were more than likely reinforced for approaching their distressed owners in the past such that they have learned to generalize the production of "comforting" behavior to any human (including strangers) in anticipation of reinforcement. Although the cats in Experiment 1 did not extend their positive behavior to the unfamiliar experimenter, this could be a by-product of domestication in that humans generally do not socialize their cats to the same extent they do their dogs, thus making the average cat more phobic of novel humans than the average dog (Bernstein 2007).

Finally, Experiment 2 increased the sample and used vocal cues to determine whether cats would respond to emotionally charged conversations (positive or negative) in an uncertain situation (i.e., novel environment and humans). Overall, the cats were unaffected by the conversations in terms of their latency to exit their carrier, their spatial choices (proximity to owner or experimenter), and their overall behavior. However, based on gaze direction, the cats looked significantly more at their owner across conditions than at the experimenter, consistent with other recent research (Merola et al. 2015). These results could suggest rudimentary social referencing, whereby the cats looked at their owner for situational understanding, regardless of emotional context. Similar to Merola et al. (2015), the cats in this experiment were in a novel environment (compared to the familiar home setting used in Experiment 1), and only their owner was familiar. Whereas Merola et al.'s experiment included an ambiguous object which the pet and owner were orienting toward, in the current experiment, the unfamiliar experimenter could be viewed as an ambiguous element that might inspire referencing from the owner. Although we had expected the cats to reference the owner more in the negative context, if the emotion cues disambiguated the intentions or character of the experimenter equally in both conditions, similar patterns of gaze across conditions might be expected. Alternatively, the emotion cues may not have disambiguated the experimenter at all, also leading to equivalent patterns of looking, an interpretation that may be more consistent with the lack of differentiation of cats' behavior across conditions. Ideally, future studies would include a neutral condition in which no emotion information or context is provided.

Although the cats' behaviors in Experiment 2 did not provide clear evidence of discriminating between emotional valences in novel situations, it is possible that the subjects were assessing the situation based on different cues than those that were explicitly manipulated in this experiment, or expressed their understanding in more subtle behaviors such as ear orientation (as demonstrated by Saito and Shinozuka 2013), vocalizations, and other small body movements. We did not examine these subtle behaviors because we wished to test whether cats showed adaptive responses (movement toward or away) in response to cues that might predict a human's actions.

One possibility is that domestic cats may not have the ability to understand human emotion as a communicative cue given their relatively short period of domestication with humans. This conclusion would be in line with the Domestication Theory (communicative cue understanding as an evolved trait; Hare et al. 2002, 2010) but not the two-stage hypothesis (communicative cue understanding as the product of experience and reinforcement). It may be the case that cats need the interdependency of relationship that dogs and humans share, whereby dogs work for, obey, and look to humans for guidance in the vast majority of situations (Berns et al. 2012; Buttelmann and Tomasello 2013; Custance and Mayer 2012; Kaminski et al. 2013). Dogs have been selected and bred for their ability to quickly respond to humans in a highly visible and consistent way, whereas cats have never faced the same pressures. Although there is research consistent with the two-stage hypothesis (Casey and Bradshaw 2008; Karsh 1983; Karsh and Turner 1988; Miklósi et al. 2005; Turner 1991), the emphasis on coevolution of understanding between humans and domestic pets as part of the domestication process may be a critical component of cognitive capacities such as emotion cue understanding, and cats may not yet have coevolved with humans to this extent. An alternative explanation is that the pre-domestication evolutionary history of cats as solitary animals, in contrast to the rich social lives of wild dogs, has not prepared cats with the cognitive capacity to discriminate emotion cues to the same degree.

Future directions

Future work in this area should include investigation into what cues, if any, domestic cats use to predict differences in human behavior, and how these cues affect the cat–human relationship and attachment. Future studies should also compare the behavior of cats with different rearing histories. It is possible that cats reared by humans since birth (as opposed to the rescue cats that participated here) might respond differently in the same tests. A larger sample of cat–owner dyads would be ideal, as particular cat–human relationships may influence the results. Answering specific questions about the ways in which the cat–human relationship compares to and differs from that of the dog–human relationship could facilitate new training methods, more public understanding of cats, and better welfare practices. In the same way, the research into the dog–human relationship (Hare and Tomasello 2005; Joly-Mascheroni et al. 2008; Kaminski et al. 2013) has improved the way we view our dogs, and this small set of studies, along with the recent work of other researchers, has taken steps to further our understanding of the cat–human interaction.

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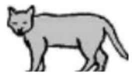
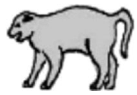
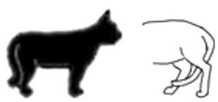
Appendix

See Table 1.

Table 1 Behavioral ethogram (modified from Leyhausen 1979)

Ears forward	
Ears out	
Ears back	
Body normal	
Body low	
Body arched	
Tail midline or up	
Tail tucked (around body, between legs)	
Tail below midline	
Sit	Cat's rear end is on the ground
Lay	Cat is not standing, or locomoting: may be resting on abdomen, side, or back, with legs extended or tucked under
Stand still	The cat is not in locomotion, but holds an upright posture
Walk-slink	Cat is locomoting with chest and abdomen close to the ground, legs not fully extended, may be pressed against walls or objects
Walk-normal	Cat is locomoting with legs extended and relaxed body posture
Rub	Cat presses its body, or head, against object or surface
Jump	The cat uses its legs and feet to vertically lift off of the ground
Purr	A "rumbling" sound which does not require the cat to open its mouth, often accompanied by other relaxed-type behaviors
Growl	A deep "groaning" sound often accompanied by stress-type behaviors
Hiss	A sharp exhale of air
Meow	A stacatto annunciated vocalization, onomatopeoic in sound "merrr-oww" or "rah-ooww"
Yowl/whine	A greater intensity meow often with the last vowel sound extended
Paw at door	The cat uses one or both front feet to manipulate the door
Eat treats	Cat ingests food
Behind E	The cat is behind the experimenter's body
Rub on E	Cat presses its body, or head, against the experimenter
Lick E	Cat uses tongue in repetition on the experimenter
Climb on E's lap	Cat locomotes onto the experimenter's crossed legs
Bite E	Cat closes its mouth and teeth around experimenter, may be seen when cat is behaving negatively (as in attack) or positively (as in "love bites")
Scratch E	Cat uses paw and claws in a swiping motion
Paw E	Cat uses paw(s) to manipulate an object or touch an object, without the use of claws

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