

Cats (*Felis catus*) follow human communicative cues but pay less attention to human faces

Tessie van der Honing

1042405

MSc Minor Thesis Behavioural Ecology (BHE-80324)

December 2023

Supervisor: Bonne Beerda

Behavioural Ecology Group

Wageningen University

Abstract

It is currently unclear to what extent domestic cats (*Felis catus*) can understand human communicative signals, and whether they have a Theory of Mind. Using several two-choice tasks in which cats ($n = 12$) were rewarded for choosing the correct target, we investigated if cats could distinguish between human attentional states in a scenario where one person was facing them while the other was facing the opposite direction, or when one person was blindfolded while the other was not. Cats received a food reward when begging for food from the seeing person. Furthermore, we tested various directional cues (pointing, turning body, and gazing) to indicate the correct target, a baited cup. Data on success rates, chosen targets, paw preferences, tail position, and the reaction after choosing an empty cup were recorded for all trials. Cats performed above chance level during the begging experiments when the person was turned away from them, but not when the person was blindfolded. Moreover, cats were able to use each provided cue to obtain the food reward from the baited cup, but success rates were lower when the cues were less distinct, i.e. cats were better at following the pointing gesture than the body turn or gazing only. The results suggest that cats are able to follow human directional cues without having to learn them first and that cats have some understanding of the human perspective, supporting that cats have a Theory of Mind. However, they seem to pay less attention to human faces and cannot distinguish between two experimenters when the only difference is the covering of the eyes. This study contributes to a broader understanding of cat-human communication and Theory of Mind in cats, and further research on this subject can help improve welfare of pet cats.

Keywords: Attentional state, Cat-human communication, *Felis catus*, Social cognition, Theory of Mind

Introduction

Cats communicate with humans in various ways, like by slow eye blinking. Cats half-blinked and narrowed their eyes more frequently when their owner displayed a slow blink towards them, compared to a stranger displaying the same stimulus (Humphrey et al., 2020). Also, cats were more likely to approach an experimenter when they exhibited a slow blink interaction than when they kept a neutral expression, suggesting that slow blinking is a form of positive emotional communication between cats and humans (Humphrey et al., 2020). Another form of cat-human communication is through vocalisations. Cats can discriminate the content of human utterances based on phonemic differences and discriminate their name from other words when they are presented with a sequence of four different words or four different cat names before hearing their own name (Saito et al., 2019). They are also able to use vocal cues to distinguish between humans, and recognise their owners and in response to his/her voice orient their ears and head (Saito & Shinozuka, 2013). Moreover, cats can match pictures of faces projecting an emotion to the related vocalisations, especially when the emotions are of high intensity, such as anger. They were successful in matching pictures with vocalisations of both conspecifics (i.e. other cats) and humans, showing that cats have a general mental representation of the emotions of their social partners (Quaranta et al., 2020). Facial expressions of cats do not seem to play a major role in cat-human communication, however, since no specific facial movements affected the speed at which cats were adopted from a shelter (Caeiro et al., 2017). This is in contrast with dogs' facial expressions, which have been found to positively influence rehoming speed (Waller et al., 2013). Cats that displayed more rubbing (e.g. against a person, object, or conspecific) were adopted more quickly than cats that showed less of this behaviour, suggesting that humans are more affected by more obvious behaviours as opposed to (subtle) changes in facial expressions (Caeiro et al., 2017).

Cat owners often consider their cats to be a part of the family and use various ways to communicate with them, e.g. by using pointing gestures, verbal commands and imitating cat vocalisations (Pongrácz & Szapu, 2018). When given free access to food, toys, human interaction and a source of scent, most cats choose social interaction with a human over the other three stimuli. This was true for both pet cats and shelter cats (Vitale Shreve et al., 2017). It is therefore not surprising that they can develop separation anxiety when separated from their owner, resulting in inappropriate urination and defecation, excessive vocalisation and destructing behaviour (Schwartz, 2002). Cats showed more exploratory behaviour, less alert behaviour, and were more active when they were accompanied by their owner as compared to a stranger, confirming the attachment of the cat to its owner (Edwards et al., 2007). Additionally, Vitale et al. (2019) found that cats display the same attachment styles toward their human caregiver as human infants and dogs do. Spending time with those caregivers, alongside an enriched environment, can effectively reduce stress in cats (Rehnberg et al., 2015). The close bond between humans and cats makes it important to understand what cats can and cannot understand in social interactions, such as human gestures and perspective-taking. Research on these cognitive and social abilities focuses more on dogs and primates than cats, and for example, chimpanzees change their communicative behaviour depending on the attentional state of a human (Hostetter et al., 2001) and they follow a human's gaze and body orientation to find hidden rewards (Povinelli et al., 1999, 2002). Marmosets are also able to follow human gaze and use it to locate a food reward, even when distracting objects are in the way and targets are at a distance (Burkart & Heschl, 2006). When a human gazed at the ceiling, straight ahead or behind a barrier, orangutans, gorillas, chimpanzees and bonobos all placed themselves in positions from where they could see what the experimenter was looking at behind a barrier. The apes do not only orient to a target that another is oriented to, but they also attempt to take the other's visual perspective (Bräuer et al., 2005). Domestic dogs possess these communicative skills as well, and they understand the difference in knowledge between a human 'guesser' and 'knower' and follow the directions of the person who knows where a treat is hidden (Maginnity & Grace, 2014). This ability to take another individual's perspective and be aware of the information or mental state they possess is also known as 'Theory of Mind'. This concept has been researched in different species, for example, goats follow gaze direction of a conspecific, but not of a human (Kaminski et al., 2005), and hand-raised ravens follow human gaze and position themselves in a way that they can still follow the gaze around and behind visual barriers (Bugnyar et al., 2004; Schloegl et al., 2007). Moreover, fur seals follow directions given by a human when it involves the whole arm, but not when gazing is the only cue provided (Scheumann & Call, 2004). When it comes to cats, research on their use of human-given communicative cues is quite limited, and studies on Theory of Mind in cats are nearly non-existent. A

study by Ito et al. (2016) reported that cats used human vocal cues only when the human was looking at them, suggesting that cats may be able to distinguish between human attentional states, i.e. whether a human can observe the cat or not. To explore this topic further, the present study aims to determine whether domestic cats can distinguish between human attentional states and if they can understand three types of human-given directions (body turning, pointing, and gazing). During the first set of two experiments, cats will need to choose to beg for a food reward from either a seeing person or a blinded person. The blinding is achieved by either turning away from the cat so that the person is facing away and has their back turned towards the cat, or by wearing a blindfold. In the second set consisting of three experiments, cats will be provided with three different human-given cues (body turning, pointing, or gazing) in order to find a treat that has been hidden under one of two cups, which have a double-bottom containing food rewards to account for the cats' ability to rely on olfactory cues only when visual ones are absent (Mayes et al., 2015). The performance of the cats will be recorded and tested to determine whether they perform above the chance level of 50%. Side biases are considered, as this may influence the choices made by the cats. A better understanding of cat cognition and cat-human communication can help improve their welfare as pets.

Methods

Subjects

Thirteen domestic cats (*Felis catus*; 5 females and 8 males) participated in this study. The cats were housed in groups at research facility Carus at Wageningen University and Research, Wageningen, The Netherlands. The mean age of the cats was 7.73 years ($SD = 1.08$). Twelve out of thirteen cats had previously taken part in similar experiments. Behavioural experiments on Theory of Mind in (ToM) cats were conducted in the morning and cats were not fed until after the experiments to ensure motivation. All experiments took place in the same experimental room.

Procedures

Cats were tested for understanding that begging for food works only if it is seen by the person holding the food. Additionally, cats were tested for selecting a baited cup in two-choice set-ups. Prior to the test trials, the cats were trained to beg, and choose between 2 cups. All available cats ($N = 15$) participated in two training sessions consisting of two days each. The first two training days took part before experiments 1 and 2, the second two training days between experiments 2 and 3. One experimenter was present to provide directions to the cats during all training sessions.

The cats' ability of perspective taking was determined by the begging experiments. The read-out experiments 1 and 2 assessed if such 'begging' behaviour of the cats was particularly directed to an experimenter who could see the cats as compared to one who could not, because she had her back turned or was blindfolded. In the first training sessions, the cats were tested for begging behaviour and were taught to approach an experimenter and look up to her to receive a food reward. During these first training sessions, the cat was placed in a cage (Figure 1a). Two chairs were placed at an equal distance from the cage. The experimenter sat down on one of the chairs, holding a bag of food rewards (*Perfect Fit Indoor 1+*, dry kibble, chicken or salmon flavour). She shook the bag to gain the cat's attention and subsequently opened the cage door by pulling a string attached to the door. The cat could then leave the cage to approach the experimenter. Cats received a reward when they crossed the line in front of the chair (210 cm from the cage) or when they made sufficient eye contact with the experimenter, which was considered begging. This training procedure was repeated until every cat had completed four training trials on each training day.

In the second series of experiments, the cats could choose for a baited cup instead of an empty one, by following directions provided by the experimenter. These directions became less distinct with each experiment, and it was assessed whether cats understood the human-given cues to select the baited cup and not go to the empty one. A set of two training sessions prepared the cats for three different experiments. The cats were taught to select one of two cups by walking up to it and receiving a food reward if the selected cup was baited. In these training sessions, the cat was placed in the cage at the start of the experiment (Figure 1b). The experimenter sat down on the floor behind a line on which two cups were placed upside-down. To account for the possible effect of smell on the cats' choices, the cups had a double bottom containing three food rewards each. The experimenter obtained the cat's attention by dropping a food reward on the floor in front of the cups, after which she placed the reward under one

of the cups. She then opened the cage while tapping the baited cup with one finger. The cat approached the cups, making a choice for one of the two cups. A choice was made when the cat touched one of the cups with its paw or nose, or when it stopped moving while facing the cup, looking directly at it. The experimenter lifted the chosen cup, and the cat could take the reward when it had chosen the baited cup. When the empty cup was chosen, the experimenter showed the food reward under the baited cup, but the cat did not receive it. This training procedure was repeated until every cat completed four trials on each training day. Two cats were distracted during all training sessions and therefore did not participate in the following experiments.

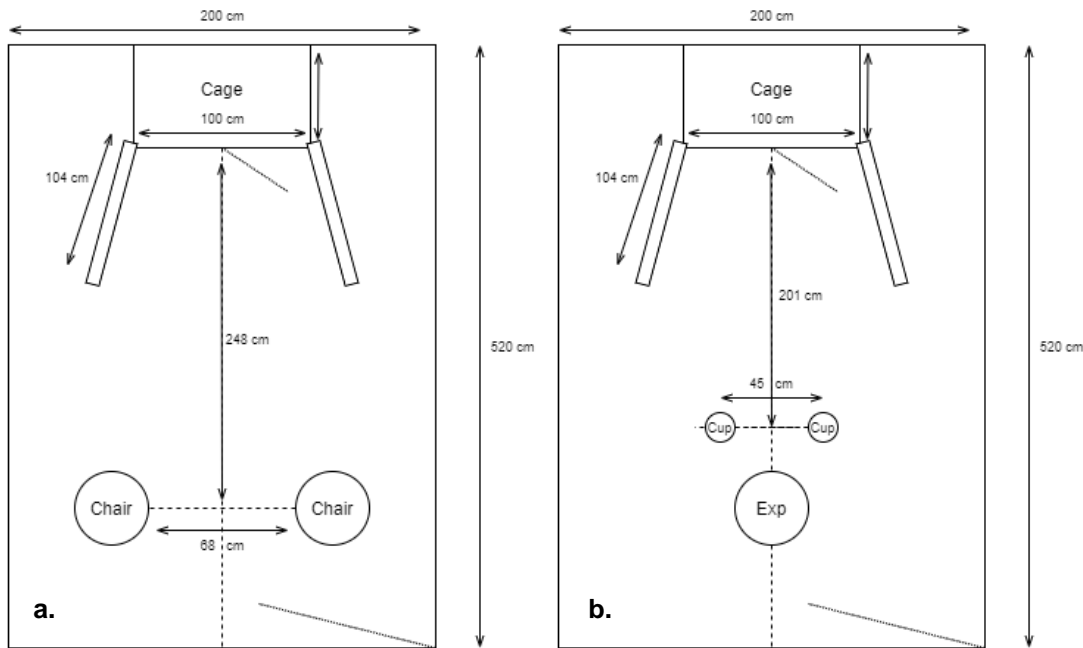


Figure 1 Experimental setup. Setup *a* was used during the first training session and the first two experiments: chair turn and chair blindfold. Setup *b* was used during the second training session and the other three experiments; cup point, cup body turn and cup gaze. Exp = experimenter.

Chair turn begging. The “Chair turn begging” experiment assessed whether cats were more likely to express begging behaviour towards a seeing experimenter than to an experimenter who had her back turned towards the cat. This should demonstrate the cats’ perspective taking ability. The setup of this experiment was the same as in the preceding training sessions, i.e. the cat was placed in the cage at the back of the experimental room and two chairs were present at an equal distance from the cage (Figure 1a). Two experimenters sat down on the chairs, both holding a bag of food rewards. In each trial, one of the chairs was turned around so that the experimenter was facing away from the cat, creating the ‘blind’ experimenter. The order in which the chairs were turned around was determined semi-randomly. The experimenters remained on the same chair on each experimental day but switched sides between days. After both experimenters had sat down, they started shaking their bag of food rewards to obtain the cat’s attention. The experimenter on the chair on the right opened the cage by pulling the string attached to the cage door. The cat then left the cage and approached one of the experimenters to beg for a reward. The cat received a reward when it approached or made sufficient eye contact with the seeing experimenter and did not receive a reward when choosing the blind experimenter. The experiment was conducted for three days, consisting of four trials for each cat.

Blindfold begging. The “Blindfold begging” determined the cats’ perspective-taking ability when the blinding of one of the experimenters was less conspicuous. The setup remained the same as in the Chair turn begging experiment, but now both chairs faced the cat at all times. The ‘blind’ experimenter wore a blindfold over her eyes. The seeing experimenter wore a blindfold on her forehead to account for the possible effect of the presence of a blindfold. The experimenter on the chair on the right (as seen from the cat’s perspective) opened the cage and the cat selected a target. Choosing the seeing experimenter was rewarded while choosing the blind experimenter was not. All cats completed four trials on each of the three experimental days.

Cup point. In the “Cup point” experiment, we assessed the cats’ ability to follow human-given cues in order to find the baited cup. The setup was as on the second two training days (Figure 1b), with one experimenter providing directions to the cats. The cat was placed in the cage at the back of the experimental room. The experimenter sat down on the floor behind a line on which two cups were placed. In front of the cups, a wooden barrier was placed to block the cat’s view on the cups. The tops of the cups were still visible to the cat. The experimenter dropped a food reward on the floor in front of the cups to gain the cat’s attention. Once the cat paid attention, the experimenter lifted both cups one after the other while baiting only one of them. The cat could not observe which cup was baited, as baiting took place behind a wooden barrier. The order of baited cups was decided semi-randomly, so that the baited cup was not always on the same side. The experimenter then removed the wooden barrier. She tapped the baited cup with one finger to indicate which cup contained the food reward. Meanwhile, she opened the cage, and the cat could leave the cage and choose a cup. A choice was counted when the cat tapped one of the cups with its paw or nose, or when it stopped moving while facing the cup, looking directly at it. The experimenter lifted the chosen cup, and the cat received the food reward when it chose the baited cup. When the empty cup was chosen, the trial ended. The experiment was conducted on three days, containing four trials per cat each.

Cup body turn. The “Cup body turn” experiment assessed the cats’ ability to follow human-given cues that were more cryptic than those used earlier. We followed the same procedure as in the Cup point experiment, but instead of tapping on the baited cup, the experimenter now only bent her body towards it while directly looking at it. Cats received the food reward when choosing the baited cup and the trial ended when the empty cup was chosen.

Cup gaze. The “Cup gaze” experiment assessed the cats’ ability to follow human-given cues in the form of gazing, making the directions even less conspicuous than in the previous experiments. The same procedure was used as in the Cup point experiment, but now the experimenter only gazed at the baited cup with her eyes, without moving her head or body. Cats received the food reward when choosing the baited cup and the trial ended when the empty cup was chosen.

Data collection and analyses

For each experiment, it was recorded if a cat chose the correct target, which side it chose, and which paw it used to indicate a cup. All trials were recorded on video for later behavioural analyses. Using these videos, latency from opening the cage to choosing a target was measured. Furthermore, the tail position was recorded. Lastly, the reaction to choosing an empty cup, and thus not receiving a food reward, was noted.

Shapiro-Wilk normality tests were run and since the data did not have a normal distribution ($p < 0.05$), non-parametric statistical tests were used. Binomial tests were used to determine whether the cats’ performances in the two-choice trials were significantly above chance level (50%), with correct choices being when cats obtained a food reward. This was done per experiment across cats and per cat. Additionally, it was determined whether cats chose one side or target significantly more often than the other, and if they had a paw preference. A Kruskal-Wallis test was used to determine whether there were significant differences in latencies to choose between experiments, cats, and performance (successful/unsuccessful). Experiments were also tested separately for differences in latencies between unsuccessful and successful choices. Moreover, post-hoc pairwise comparisons using Dunn’s test were performed to compare latencies between experiments. Chi-square tests were performed to determine whether the factors experiment, experimental day, trial, and cat affected performance, and whether experiment, cat, and sex affected tail position and empty cup reaction. Lastly, a binary logistic regression model was performed to ascertain the effects of experiment, experimental day and trial on the likelihood that cats chose the correct target (seeing person or baited cup).

Results

Cats were observed in a variety of two-choice experiments where the correct choice earned them a food reward. It was tested whether cats understood the experimenters’ visual perspectives, meaning that they should only beg from someone who could see them. It was also tested if cats were able to follow three different human-given cues in order to select a baited target. One cat did not participate in enough experiments/trials to yield sufficient data and was therefore left out of the analyses, leaving a sample size of twelve cats.

Task performance

In the begging tests, a cat begged from the experimenter who could see the cat or from the one that could not, as she had her back turned towards the cat or was blindfolded. In the Chair turn experiment, the cats correctly chose the seeing experimenter 72 times out of a total of 108 trials (Binomial, $p < 0.001$). In the Blindfold experiment, cats ($N = 12$) chose 68 times correctly out of a total of 137 trials, meaning they performed at chance level (Binomial, $p > 0.1$). In the cup experiments, a cat chose between a baited and an empty cup while the experimenter provided direction towards the baited cup. In the Cup point experiment, the experimenter extended her arm and tapped the baited cup with her finger. Cats typically chose the baited cup, which occurred 119 times out of 144 trials (Binomial, $p < 0.001$). In the Cup body turn experiment, the experimenter turned her body towards the baited cup to indicate the correct choice. Cats chose correctly 102 out of 143 times (Binomial, $p < 0.001$). In the Cup gaze experiment, the experimenter only gazed with her eyes at the baited cup. Cats chose the baited cup 82 out of 144 times (Binomial, $p = 0.04$). Overall, cats performed above the chance level of 50% in all cup experiments (303 correct choices during a total of 431 trials) and in the chair turn experiment (72 out of 108 correct) (Figure 2).

Individual variation (i.e. the factor 'Cat') significantly affected performance during the Cup point experiment, with success rates ranging from 7 out of 12 to 12 out of 12 correct choices ($\chi^2 = 20.3$, $df = 11$, $p < 0.05$). Task performance did not differ significantly between cats in the other experiments (Chi-square, $df = 11$, $p > 0.05$). Accordingly, there was no overall association between 'Cat' and performance ($\chi^2 = 16.9$, $df = 11$, $n = 676$, $p > 0.05$).

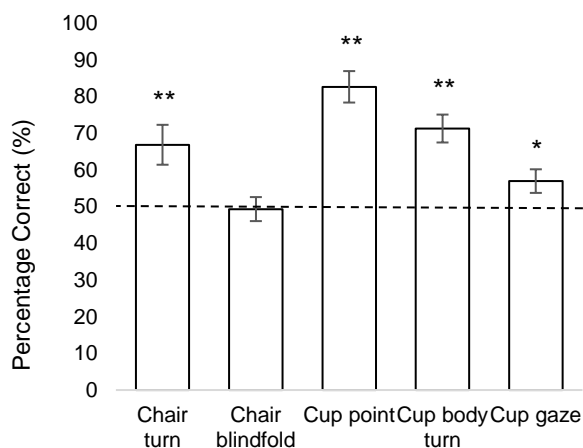


Figure 2 Means and standard errors of the performance of cats in a two-choice test where the choices consisted of begging from an experimenter on a turned chair or one on a chair facing the cat; a blindfolded experimenter or a seeing experimenter; choosing an empty cup or a baited cup which was indicated by one experimenter by either pointing at it, turning her body towards the cup, or gazing at it. Dotted line represents chance performance level (50%). * $p < 0.05$. ** $p < 0.001$.

Side bias

The presence of side bias among the cats was tested using data on the side they chose in each trial. These data did not consider whether a chosen side was correct or not, but only recorded which target side was chosen. Moreover, it was tested whether cats preferred to beg from one experimenter over the other during the 'blinded begging' tests (Saskia or Tessie).

Overall, i.e. considering the experiments altogether, seven out of twelve cats showed a bias to choose the target on their left, together choosing the left side 300 times out of 406 trials (Binomial, $p < 0.001$) (Table 1, Appendix I). None of the individual cats showed a bias to the right-side target (Binomial, $p > 0.05$). Testing for each experiment separately, with all cats included, showed that a left side bias was present in the blindfolded begging experiment, in which cats chose the left side 113 times out of 137 trials ($p < 0.001$). The left side bias was also present in the experiment in which the experimenter indicated the baited cup by turning her body towards it or by gazing at it, with cats choosing the left side 89 out of 143 times ($p = 0.001$) and 111 out of 144 times ($p < 0.001$), respectively. The cats did not show a preference to beg from either experimenter, choosing Saskia 76 times and Tessie 64 times in a total of 140 trials of both begging experiments (Binomial, $p > 0.1$).

Paw preference

It was tested whether cats showed a paw preference for either paw during the cup experiments. This was done using the recorded data on which front paw the cats used to indicate the cup of their choice during the cup tests. During the cup experiments, cats used one of their front paws to indicate the cup of their choice in 182 trials and showed a preference for using their left paw, using it in 109 of these trials (Binomial, $p < 0.01$). Cats significantly differed in their paw preference ($\chi^2 = 35.0$, $df = 10$, $n = 182$, $p < 0.05$). Three out of eleven cats (one cat did not use its paws in any of the trials), of which two females and one male, showed a significant preference for using their left paw to indicate their cup of choice (Binomial, $p < 0.05$). These three cats were among those that showed a left side bias in the aforementioned side bias analysis. However, there was no overall association between the chosen side and the paw that was used ($\chi^2 = 1.6$, $df = 1$, $n = 182$, $p > 0.05$). Next, the data was tested for a possible difference in paw preference between sexes. Females used their left paw 63 times during 98 trials ($p = 0.001$), causing a significant left paw bias in this sex. Males, however, did not show a preference for either paw as they used their left paw 46 times and their right paw 38 times during the total of 84 trials ($p > 0.1$). Unexpectedly, 'sex' did not affect the sidedness of paw use in the chi-square analysis ($\chi^2 = 1.7$, $df = 1$, $n = 182$, $p > 0.05$).

Latency

The latency of cats to select a target, i.e. either an experimenter or a cup, after the cage door was opened was measured through video analysis. The recorded data was compared between experiments, as well as between cats and it was tested whether there was a difference in latency between correctly and wrongly made choices. The overall average (\pm SD) latency was 3.30 ± 3.03 (based on 587 choices made by 12 cats). Cats significantly differed in their latency to choose (Kruskal-Wallis $H = 254.2$, $df = 11$, $n = 587$, $p < 0.001$), with mean latencies ranging from 1.80 seconds (SE = 0.05) to 4.99 seconds (SE = 0.34). A Kruskal-Wallis test showed that latency differed significantly between experiments ($H = 14.4$, $df = 4$, $n = 587$, $p < 0.01$) (Figure 3). Post-hoc pairwise comparisons using Dunn's test with Bonferroni correction showed significant differences in latency between the turned chair and cup pointing experiment ($p < 0.05$) and between the turned chair and cup gazing experiment ($p < 0.01$). Cats took an average of 4.24 seconds to make a choice in the chair turn experiment (SE = 0.40). In both the cup pointing and cup gazing experiment, cats made their choice faster than that, with an average of 2.82 seconds (SE = 0.14) and 2.86 seconds (SE = 0.12), respectively.

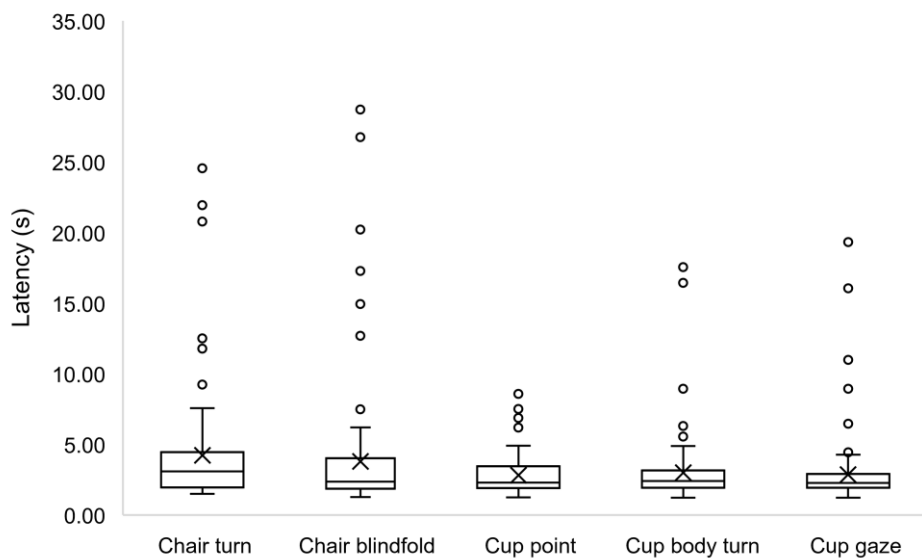


Figure 3 Boxplot of the latency of cats to choosing after the cage had opened for each two-choice experiment, in which the choices consisted of begging from an experimenter on a turned chair or one on a chair facing the cat; a blindfolded experimenter or a seeing experimenter; an empty cup or a baited cup which was indicated by one experimenter by either pointing at it, turning her body towards the cup, or gazing at it. Bold horizontal lines denote median values; boxes extend from the 25th to the 75th percentile of each group's distribution of values. Vertical extending lines denote the most extreme values within 1.5 interquartile range of the 25th and 75th percentile of each group. Open dots denote extreme values.

There was no overall effect of success on latency to choose ($H = 0.1$, $df = 1$, $n = 587$, $p > 0.05$). However, the latencies of successful and unsuccessful performances differed significantly in the cup pointing experiment ($H = 9.5$, $df = 1$, $n = 108$, $p < 0.01$). Successful choices were made faster than unsuccessful choices ($M = 2.68$, $SE = 0.15$ and $M = 3.41$, $SE = 0.30$, respectively).

Tail position

The position of the tail was recorded during every trial using video recordings, with three possible positions (down, moving, and up) and one mutually exclusive score per trial. The 'moving' position was assigned when the tail neither remained up nor down during the trial, but rather moved or stayed somewhere in between. These data were analysed using chi-square tests to determine the presence of significant differences between experiment, between cats, and between sexes. The total scores for the tail positions were 208 (down), 96 (moving) and 285 (up). Tail position significantly differed between experiments ($\chi^2 = 28.1$, $df = 8$, $n = 589$, $p < 0.001$). The tail was more often down with increasing difficulty of the baited cup experiments (Figure 4). The tail position also differed significantly between cats ($\chi^2 = 451.1$, $df = 22$, $n = 589$, $p < 0.001$) and between sexes ($\chi^2 = 77.5$, $df = 2$, $n = 589$, $p < 0.001$). Females usually had their tail down (137 out of 246 trials), whereas males had their tails up more often (207 out of 343 trials). There was no significant difference in tail position between successful and unsuccessful choices ($\chi^2 = 1.9$, $df = 2$, $n = 589$, $p > 0.05$).

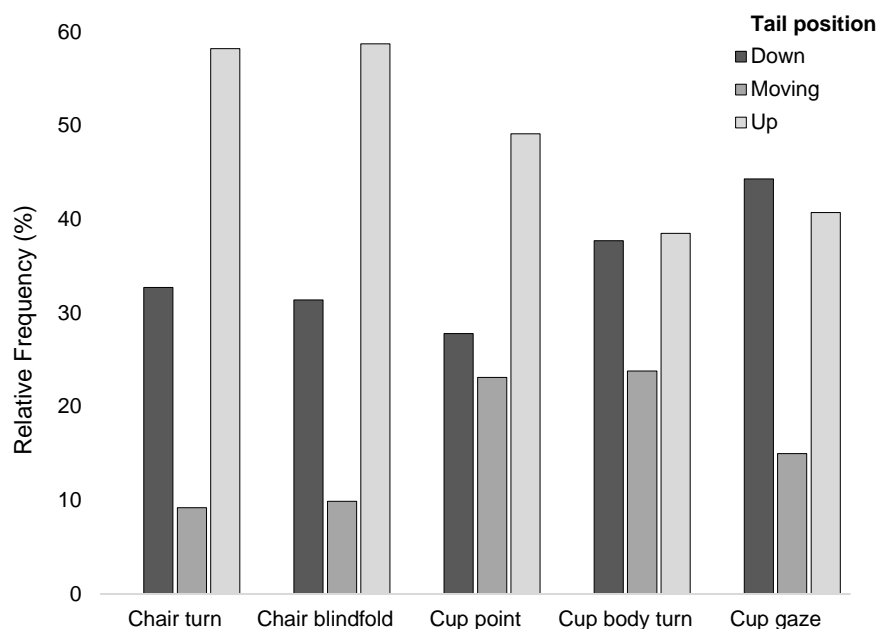


Figure 4 Relative frequency of tail positions of cats during each two-choice experiment in which the choices consisted of begging from an experimenter on a turned chair or one on a chair facing the cat; a blindfolded experimenter or a seeing experimenter; choosing an empty cup or a baited cup which was indicated by one experimenter by either pointing at it, turning her body towards the cup, or gazing at it. Tail position was considered 'moving' when it neither remained up nor down during the trial.

Empty cup reaction

During the baited cup experiments, it was recorded how the cats reacted to realising they had chosen the wrong, thus empty, cup. Three main reactions were found and recorded: looking at or into the cup, using a paw to reach inside the cup, or walking away. Chi-square tests were performed to test for differences between cats, sexes, and experiments. Cats significantly differed in the way they reacted to choosing the wrong cup ($\chi^2 = 46.047$, $df = 22$, $n = 114$, $p < 0.01$), including that males and females reacted differently to an empty cup ($\chi^2 = 6.664$, $df = 2$, $n = 114$, $p < 0.05$). Males were most likely to look at or into the cup (55 out of 62 trials), as were females (36 out of 52 trials), but females also tended to use their paws more often than males (9 versus 7 times out of 52 trials) or leave more often (13 versus 10 times out of 62 trials). Furthermore, there was a significant difference in reactions between experiments ($\chi^2 = 15.5$, $df = 4$, $n = 114$, $p < 0.01$) (Figure 5). Cats mostly looked at/into the cup in the gazing experiment (54 out of 60 trials), and less so in the experiments with pointing (15 out of 19 trials) and body turning (22 out of 35 trials). They rarely used their paw during the gazing experiment (1 out of 60 trials), and in the pointing experiment, they never walked away but instead rather looked at the cup or used their paw

to reach inside it. The most common reaction across experiments was looking at or into the empty cup, which happened in 91 of the 144 total completed trials.

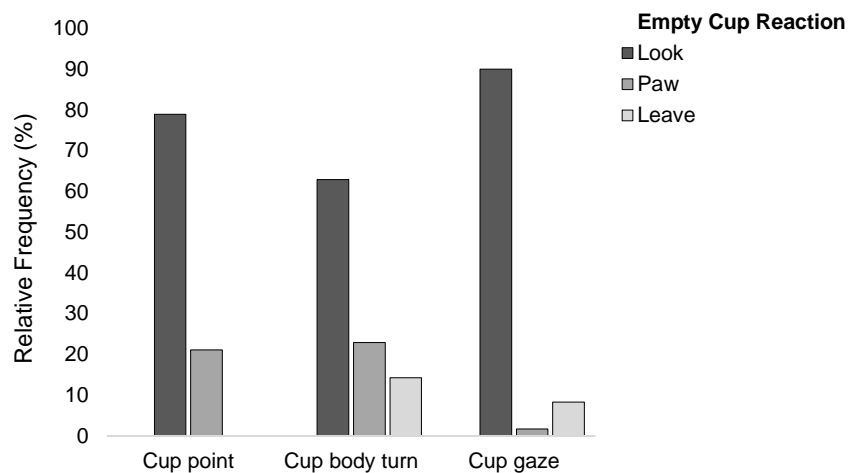


Figure 5 Relative frequency of cats' reactions to choosing an empty cup for each two-choice experiment, in which the choices consisted of an empty cup or a baited cup which was indicated by one experimenter by either pointing at it, turning her body towards the cup, or gazing at it.

Associative learning

It was tested whether cats performed better in later days and trials as compared to their earlier attempts. An increase in successful choices could indicate that the cats learnt to associate a stimulus with the correct choice, e.g. a finger on a cup indicates a baited cup. Associative learning would question the cats' insight and 'natural' cognitive capacity to solve these tasks. The analyses on associative learning were done per experiment, since performance differed between them and did not increase with each next experiment, as was previously described. Additionally, a binary logistic regression model was performed to determine whether the factors 'experiment', 'experimental day' and 'trial' could predict the cats' performance. There was no association between consecutive experimental day and performance in any of the experiments (Chi-square, $df = 2$, $p > 0.05$). This indicates that the cats did not learn to perform better on subsequent days. However, there was a significant relation between trial and performance in both the turned chair ($\chi^2 = 7.891$, $df = 3$, $n = 108$, $p < 0.05$) and blindfolded begging experiments ($\chi^2 = 12.455$, $df = 3$, $n = 137$, $p < 0.01$). In the turned chair experiment, the number of correct choices increased with later trials, from 13 out of 28 in the first trial to 20 out of 26 in the last trial (Figure 6a). Analyses per experimental day showed that this relation was not present on any of the specific days (Chi-square, $p > 0.05$). For the blindfolded begging experiment, the relation between trial and performance was only present on day one ($\chi^2 = 12.024$, $df = 3$, $n = 44$, $p < 0.01$). Moreover, the relation was not linear, as cats performed better during trial two and four (23 and 22 out of 35 correct, respectively) as compared to trial one and three (12 out of 33 and 11 out of 34 correct, respectively) (Figure 6b). This was the case for both performance on day one and overall performance during this experiment. Thus, it does not appear that cats learnt to perform better during this experiment, i.e. no associative learning was observed.

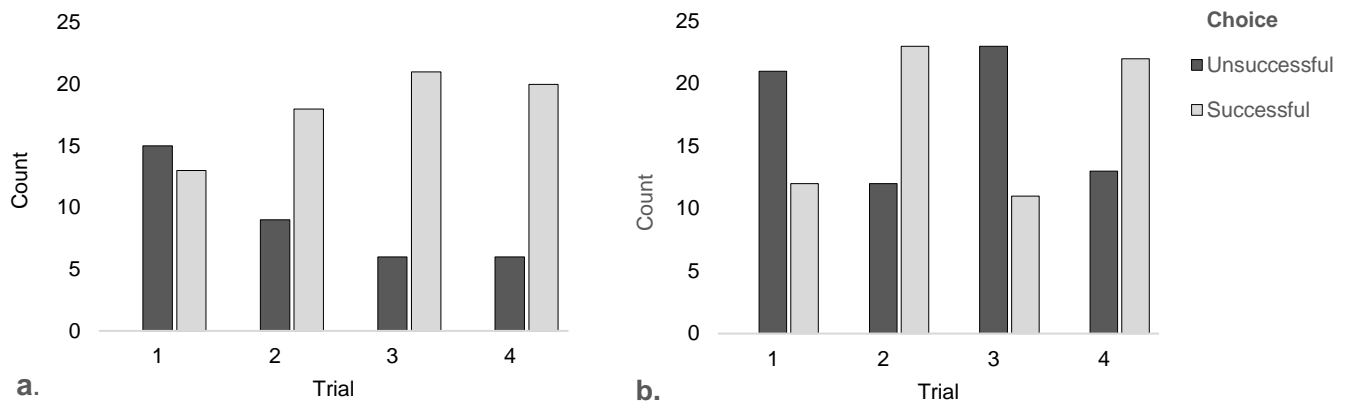


Figure 6 Counts of unsuccessful and successful choices made by cats when choosing to beg from either a seeing experimenter and a blinded experimenter that either had her back turned towards the cat (a) or was blindfolded (b). Counts are provided per trial and are the total over three consecutive experimental days.

The binary logistic regression model ($\chi^2 = 45.3$, $df = 9$, $p < 0.001$) explained 8.9% (Nagelkerke R^2) of the variance in performance and correctly classified 68.6% of cases. Experiment was a significant variable (Wald = 38.919, $df = 4$, $p < 0.001$). Compared to the chair turn experiment, cats were 2.30 times less likely to choose correctly in the blindfold experiment (Wald = 6.959, $df = 1$, $p < 0.01$) and 2.40 times more likely to choose correctly in the cup pointing experiment (Wald = 8.419, $df = 1$, $p < 0.01$). There were no significant differences between the chair turn experiment and the cup body turn experiment (Wald = 0.669, $df = 1$, $p > 0.05$) and between the chair turn and cup gaze experiment (Wald = 2.354, $df = 1$, $p > 0.05$). There were no significant differences between experimental days and trials ($p > 0.05$), supporting the previous finding that associative learning was absent.

Discussion

The understanding of mental states in others and having a Theory of Mind (ToM) starts with reading signals that others provide, unintentionally like facial expressions or intentionally like pointing towards a target. To what degree animals have such social skills is subject to research and this study investigated whether domestic cats could correctly identify human attentional state and if they were able to use various directional cues provided by a human to find a hidden treat. The cats differentiated between a 'seeing' and a 'blinded' person when the latter was facing away from the cat, but not when she was facing the cat while wearing a blindfold. The cats seem to understand human body orientation, in the context of communication, but they do not seem to pay attention to the eyes specifically and may not understand that a person cannot observe them when their eyes are covered. The cats successfully used the experimenter's directional cues towards a baited cup (either pointing, turning body towards the cup, or gazing), performing above chance level for all cues, but the success percentage decreased when cues became less distinct (from 83% success for pointing to 57% for gazing). Cats follow human-given communicative cues, which has also been shown for apes, monkeys and dogs (Burkart & Heschl, 2006; Kaminski et al., 2005; McKinley & Sambrook, 2000; Scheumann & Call, 2004), but struggle with reading cues from human eyes or possibly their entire faces. The findings support ToM in cats, in that they understand visual perspectives and intentions in humans. They underperform in reading human faces compared to dogs, which could be due to a lower level ToM or less focus on human facial cues.

Cats recognize human attentional states and both pet and shelter cats spent more time near an attentive human who could make contact with the cat as compared to an inattentive human who ignored the cat and looked at the floor (Vitale & Udell, 2019). Shelter cats spent more time near an unfamiliar inattentive human than pet cats did and also meowed more often, possibly as a way to get the human's attention. This difference between shelter and pet cats was also found in dogs, with shelter dogs spending more time near a passive unfamiliar person than pet dogs (Barrera et al., 2010). The dogs also showed more fear-appeasement behaviours such as having their tail and ears down and crouching. These results were explained by the stressful conditions the dogs experience in the shelter and the limited amount of human contact that dogs receive in the shelter, while they do appear to need social interaction with people (Barrera et al., 2010). It could be argued that the cats that participated in this study fall somewhere in between pet and shelter cats, as they do not live with an owner like pet cats do, but do

have caretakers with whom they're all familiar. This should, however, not affect the results of the study since both pet and shelter cats preferred spending time near an attentive person rather than an inattentive person. One might expect that the cats would meow at the inattentive experimenter as a way of begging for the food reward, however, meowing hardly occurred during trials. Perhaps the time between making a choice and the end of the trial was too short for such attention-seeking behaviour.

Cats only use human vocal cues directed at them in situations in which humans are looking at them, as opposed to when they are facing down (Ito et al. 2016). We did not use vocal cues to gain the cats' attention in the present study, but used the noise created by shaking the bag of food rewards, which is also a human-created sound directed towards the cat to gain its attention. However, this would not interfere with the results as the cats' ability to make the distinction between inattentive and attentive humans is not affected by human sounds, since both experimenters made the same noise. Ito et al. (2016) combined head and gaze orientations as visual cues, and therefore, could not conclude if cats can use these cues separately from each other or need a combination of the two cues to recognise the human attentional state. They suggested having an experimenter face the cats either with eyes closed or with an averted gaze. We did this by blindfolding one of the experimenters as the 'eyes closed' condition in the second chair experiment, as well as using gaze alone as a directional cue in the third cup experiment. Our cats used gaze as a separate directional cue to find a hidden treat, but they did not recognise the attentional state of a human with their eyes obscured (i.e. blindfolded). Cats have been found to follow human gaze in a two-choice experiment in order to find a hidden treat, regardless of the type of gazing (momentary or dynamic) (Pongrácz et al., 2019). The average success rate of the group in that study was slightly above 70%, which is above our success rate (57%). It is important to note that face masks were worn during all experiments according to COVID regulations, and this could potentially affect the way our cats perceived a human face. Additionally, both experimenters wore glasses during the chair turn, pointing at cup and turning body towards cup experiments, and had taken them off during the experiments involving a blindfold or gazing. The presence of glasses might affect cat-human communication, although the exact effects have, thus far, not been tested (Humphrey et al., 2020). Pongrácz et al. (2019) also showed that young cats were more successful than adult cats, while there was no difference between adult and old cats. The cats in the present study were all considered adult (between 1 and 8 years of age, but none of the cats were younger than 6 years) or old cats (older than 8 years). It was not tested whether age differences were present since most of the cats were around the same age, but according to the study by Pongrácz et al. (2019), no age differences are to be expected.

Dogs and cats performed similarly in following four different pointing gestures (proximal dynamic and momentary pointing; distal dynamic and momentary pointing) that were provided by a human experimenter during a two-choice task (Miklósi et al., 2005). Cats did better when the pointing was performed near the bowl and dynamically, i.e. moving the arm and remaining in the pointing position until a choice was made, than when momentary pointing was used, meaning the experimenter lifted their arm for a couple of seconds to point at the baited bowl and putting their arm down again before the cat was released. This applied to both proximate and distal momentary pointing (Miklósi et al., 2005). The pointing gesture used in the present study with the baited cups was similar to the proximal dynamic pointing in the aforementioned study and a cat could observe the experimenter moving her arm towards the correct cup and the arm remained in the pointing position until the cat had made a choice. Both the aforementioned study and the present study found a convincing success rate in these similar experiments (92% and 83%, respectively). In the same study by Miklósi et al. (2005), subjects were presented with a problem that would provide access to a food reward when solved. When the problem was made unsolvable, dogs tended to look at the human and back to the food, once they did not manage to solve the problem by themselves, whereas cats did not give up as quickly and paid little attention to the human's face. The majority of the dogs (85%) displayed gaze alternation, while only 42% of the cats did (Miklósi et al., 2005). Thus, cats can be considered socially intelligent animals, but seem to pay less attention to human faces.

Cats that chose the empty cup in the signalled two-choice object discrimination tasks typically looked at or into the cup, with reactions differing slightly between the provided cues. Cats never walked away after failing to follow the pointing cue but instead looked at or into the empty cup or used their paw to reach inside the cup as if to check whether the cup was truly empty. Cats anticipated to find a treat under the cup and did not seem to believe that the cup was not baited. Anticipatory behaviour in cats has been

described to be in line with their 'sit-and-wait' tactic when looking for prey, as opposed to an increase in hyperactivity found in e.g. rats, who actively search for their food while foraging (Spruijt et al., 2001; Van Den Bos et al., 2003). Anticipatory behaviour could not be observed during these experiments, as the cup was lifted instantly after a cat had chosen it. None of the cats walked away during any of the unsuccessful trials during the pointing experiment, while this did happen in the later body turn and gazing trials. This could be explained by the more distinct and therefore more understandable directional gesture of pointing directly at the cup, whereas turning the body towards the cup or gazing at the cup are more difficult for cats to understand, as evident from the lower success rates. Moreover, females and males differed in their reactions. Females more often used their paw in general, and their left one specifically, than males did, but both sexes most often looked at or into the cup. There was also a difference between cats, which could be explained by their different personalities, since more confident, affectionate, active and friendly cats have a stronger paw preference than those that scored lower on those traits (McDowell et al., 2016). Female cats showed a preference for using their left paw, while males did not show a preference for either paw. This is in contrast with earlier findings where female cats mainly used their right paw, whereas males preferred to use their left paw when reaching for food, and also when stepping down a set of stairs and stepping over a raised object (McDowell et al., 2018). However, the experiments in the present study were not designed to record paw use specifically, as it was always the cats' choice to use their paw or not, and therefore the data for this analysis was limited. The left side bias that was found in the blindfolded begging, the cup body turn and the cup gaze experiment could possibly be explained by a lower confidence in making the right choice as the human cues were more vague than in the chair turn begging and cup point experiment. The door of the cage in which the cats started their trials swung open from the left to the right, so cats always left the cage slightly starting from the left side, especially when they were eager to leave the cage. The left cup would then be the quickest to reach and would be a logical choice when the cat is not able to follow the human cue. The tail position differed between cats as well as sexes. Females usually had their tail down when approaching a target, whereas males had their tail up. Moreover, cats more often had their tail down with increasing difficulty of the baited cup experiments (from 28% of the trials for cup pointing to 44% for cup gazing). Cats displaying the tail-up position when approaching a human most often rubbed themselves on the human's leg, indicating a positive interaction (Deputte et al., 2021). However, there was no difference in tail position between successful and unsuccessful choices, so it is unclear whether cats that had their tail up anticipated to receive a reward. More research on the relation between personality and anticipation behaviour could confirm whether there is a link between the two. In addition, it would be interesting to analyse whether more successful cats showed more anticipation behaviour than less successful cats after choosing an empty cup.

The results provide insight in the understanding that cats have of the human perspective, and we showed that cats are more likely to approach a person that is facing them rather than someone who is facing the opposite way. Cats are also able to follow human directional cues without having to learn them first, supporting that cats have a Theory of Mind. However, they could not distinguish human attentional states between a blindfolded and a seeing person, suggesting that cats pay less attention to human faces. This study contributes to a broader understanding of cat-human communication, which in turn can improve the welfare of domestic cats.

References

- Barrera, G., Jakovcevic, A., Elgier, A. M., Mustaca, A., & Bentosela, M. (2010). Responses of shelter and pet dogs to an unknown human. *Journal of Veterinary Behavior: Clinical Applications and Research*, 5(6), 339–344. <https://doi.org/10.1016/j.jveb.2010.08.012>
- Bräuer, J., Call, J., & Tomasello, M. (2005). All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology*, 119(2), 145–154. <https://doi.org/10.1037/0735-7036.119.2.145>
- Bugnyar, T., Stöwe, M., & Heinrich, B. (2004). Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society B: Biological Sciences*, 271(1546), 1331–1336. <https://doi.org/10.1098/rspb.2004.2738>
- Burkart, J., & Heschl, A. (2006). Geometrical gaze following in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*, 120(2), 120–130. <https://doi.org/10.1037/0735-7036.120.2.120>
- Caeiro, C. C., Burrows, A., & Waller, B. M. (2017). Development and application of CatFACS: Are human cat adopters influenced by cat facial expressions? *Applied Animal Behaviour Science*, 189, 66–78. <https://doi.org/10.1016/j.applanim.2017.01.005>
- Deputte, B. L., Jumelet, E., Gilbert, C., & Titeux, E. (2021). Heads and tails: An analysis of visual signals in cats, *felis catus*. *Animals*, 11(9). <https://doi.org/10.3390/ani11092752>
- Edwards, C., Heiblum, M., Tejada, A., & Galindo, F. (2007). Experimental evaluation of attachment behaviors in owned cats. *Journal of Veterinary Behavior*, 2(4), 119–125. <https://doi.org/10.1016/j.jveb.2007.06.004>
- Hostetter, A. B., Cantero, M., & Hopkins, W. D. (2001). Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology*, 115(4), 337–343. <https://doi.org/10.1037/0735-7036.115.4.337>
- Humphrey, T., Proops, L., Forman, J., Spooner, R., & McComb, K. (2020). The role of cat eye narrowing movements in cat–human communication. *Scientific Reports*, 10(1), 1–8. <https://doi.org/10.1038/s41598-020-73426-0>
- Ito, Y., Watanabe, A., Takagi, S., Arahori, M., & Saito, A. (2016). Cats beg for food from the human who looks at and calls to them: ability to understand humans' attentional states. *Psychologia*, 59(2–3), 112–120. <https://doi.org/10.2117/psysoc.2016.112>
- Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour*, 69(1), 11–18. <https://doi.org/10.1016/j.anbehav.2004.05.008>
- Maginnity, M. E., & Grace, R. C. (2014). Visual perspective taking by dogs (*Canis familiaris*) in a Guesser–Knower task: evidence for a canine theory of mind? *Animal Cognition*, 17(6), 1375–1392. <https://doi.org/10.1007/s10071-014-0773-9>
- Mayes, E. R. E., Wilkinson, A., Pike, T. W., & Mills, D. S. (2015). Individual differences in visual and olfactory cue preference and use by cats (*Felis catus*). *Applied Animal Behaviour Science*, 173, 52–59. <https://doi.org/10.1016/j.applanim.2015.01.003>
- McDowell, L. J., Wells, D. L., & Hepper, P. G. (2018). Lateralization of spontaneous behaviours in the domestic cat, *Felis silvestris*. *Animal Behaviour*, 135, 37–43. <https://doi.org/10.1016/j.anbehav.2017.11.002>
- McDowell, L. J., Wells, D. L., Hepper, P. G., & Dempster, M. (2016). Lateral bias and temperament in the domestic cat (*Felis silvestris*). *Journal of Comparative Psychology*, 130(4), 313–320. <https://doi.org/10.1037/com0000030>
- McKinley, J., & Sambrook, T. D. (2000). Use of human-given cues by domestic dogs and horses. *Animal Cognition*, 3(1), 13–22. <https://doi-org.ezproxy.library.wur.nl/10.1007/s100710050046>
- Miklósi, Á., Pongrácz, P., Lakatos, G., Topál, J., & Csányi, V. (2005). A comparative study of the use of visual communicative signals in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. *Journal of Comparative Psychology*, 119(2), 179–186. <https://doi.org/10.1037/0735-7036.119.2.179>
- Pongrácz, P., & Szapu, J. S. (2018). The socio-cognitive relationship between cats and humans – Companion cats (*Felis catus*) as their owners see them. *Applied Animal Behaviour Science*, 207, 57–66. <https://doi.org/10.1016/j.applanim.2018.07.004>
- Pongrácz, P., Szapu, J. S., & Faragó, T. (2019). Cats (*Felis silvestris catus*) read human gaze for referential information. *Intelligence*, 74, 43–52. <https://doi.org/10.1016/j.intell.2018.11.001>

- Povinelli, D. J., Bierschwale, D. T., & Čech, C. G. (1999). Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *British Journal of Developmental Psychology*, *17*(1), 37–60. <https://doi.org/10.1348/026151099165140>
- Povinelli, D. J., Dunphy-Lelii, S., Reaux, J. E., & Mazza, M. P. (2002). Psychological diversity in chimpanzees and humans: New longitudinal assessments of chimpanzees' understanding of attention. *Brain, Behavior and Evolution*, *59*(1–2), 33–53. <https://doi.org/10.1159/000063732>
- Quaranta, A., D'ingeo, S., Amoruso, R., & Siniscalchi, M. (2020). Emotion recognition in cats. *Animals*, *10*(7), 1–13. <https://doi.org/10.3390/ani10071107>
- Rehnberg, L. K., Robert, K. A., Watson, S. J., & Peters, R. A. (2015). The effects of social interaction and environmental enrichment on the space use, behaviour and stress of owned housecats facing a novel environment. *Applied Animal Behaviour Science*, *169*, 51–61. <https://doi.org/10.1016/j.applanim.2015.06.002>
- Saito, A., & Shinozuka, K. (2013). Vocal recognition of owners by domestic cats (*Felis catus*). *Animal Cognition*, *16*(4), 685–690. <https://doi.org/10.1007/s10071-013-0620-4>
- Saito, A., Shinozuka, K., Ito, Y., & Hasegawa, T. (2019). Domestic cats (*Felis catus*) discriminate their names from other words. *Scientific Reports*, *9*(1), 2–9. <https://doi.org/10.1038/s41598-019-40616-4>
- Scheumann, M., & Call, J. (2004). The use of experimenter-given cues by South African fur seals (*Arctocephalus pusillus*). *Animal Cognition*, *7*(4), 224–230. <https://doi.org/10.1007/s10071-004-0216-0>
- Schloegl, C., Kotrschal, K., & Bugnyar, T. (2007). Gaze following in common ravens, *Corvus corax*: ontogeny and habituation. *Animal Behaviour*, *74*(4), 769–778. <https://doi.org/10.1016/j.anbehav.2006.08.017>
- Schwartz, S. (2002). Separation anxiety syndrome in cats: 136 cases (1991–2000). *Journal of the American Veterinary Medical Association*, *220*(7), 1028–1033. <https://doi.org/10.2460/javma.2002.220.1028>
- Spruijt, B. M., Bos, R. Van Den, & Pijlman, F. T. A. (2001). A concept of welfare based on reward evaluating mechanisms in the brain: anticipatory behaviour as an indicator for the state of reward systems. *Applied Animal Behaviour Science*, *72*, 145–171. [https://doi.org/10.1016/S0168-1591\(00\)00204-5](https://doi.org/10.1016/S0168-1591(00)00204-5)
- Van Den Bos, R., Meijer, M. K., Van Renselaar, J. P., Van der Harst, J. E., & Spruijt, B. M. (2003). Anticipation is differently expressed in rats (*Rattus norvegicus*) and domestic cats (*Felis silvestris catus*) in the same Pavlovian conditioning paradigm. *Behavioural Brain Research*, *141*(1), 83–89. [https://doi.org/10.1016/S0166-4328\(02\)00318-2](https://doi.org/10.1016/S0166-4328(02)00318-2)
- Vitale, K. R., Behnke, A. C., & Udell, M. A. R. (2019). Attachment bonds between domestic cats and humans. *Current Biology*, *29*(18), R864–R865. <https://doi.org/10.1016/j.cub.2019.08.036>
- Vitale, K. R., & Udell, M. A. R. (2019). The quality of being sociable: The influence of human attentional state, population, and human familiarity on domestic cat sociability. *Behavioural Processes*, *158*, 11–17. <https://doi.org/10.1016/j.beproc.2018.10.026>
- Vitale Shreve, K. R., Mehrkam, L. R., & Udell, M. A. R. (2017). Social interaction, food, scent or toys? A formal assessment of domestic pet and shelter cat (*Felis silvestris catus*) preferences. *Behavioural Processes*, *141*(3), 322–328. <https://doi.org/10.1016/j.beproc.2017.03.016>
- Waller, B. M., Peirce, K., Caeiro, C. C., Scheider, L., Burrows, A. M., McCune, S., & Kaminski, J. (2013). Paedomorphic facial expressions give dogs a selective advantage. *PLoS ONE*, *8*(12). <https://doi.org/10.1371/journal.pone.0082686>

Appendix I

Table 1 Results of binomial tests run to test for the presence of side bias for each cat during all experiments. L = cat chose the left side target (either experimenter or cup), R = cat chose right side target. Chosen sides were recorded regardless of whether the cat made the correct choice or not. A p-value of <0.05 is considered significant.

Cat	Category	N	Observed Prop.	Test Prop.	Exact Sig. (2-tailed)
Bas	L	27	0.48	0.50	0.894
	R	29	0.52		
	Total	56	1.00		
Bella	L	39	0.70	0.50	0.005
	R	17	0.30		
	Total	56	1.00		
Edward	L	27	0.54	0.50	0.672
	R	23	0.46		
	Total	50	1.00		
Jack	L	37	0.66	0.50	0.022
	R	19	0.34		
	Total	56	1.00		
Jacob	L	33	0.61	0.50	0.134
	R	21	0.39		
	Total	54	1.00		
James	L	45	0.80	0.50	0.000
	R	11	0.20		
	Total	56	1.00		
Jill	L	40	0.67	0.50	0.013
	R	20	0.33		
	Total	60	1.00		
Kasko	L	28	0.51	0.50	1.000
	R	27	0.49		
	Total	55	1.00		
Roos	L	48	0.80	0.50	0.000
	R	12	0.20		
	Total	60	1.00		
Sally	L	52	0.87	0.50	0.000
	R	8	0.13		
	Total	60	1.00		
Sasha	L	33	0.60	0.50	0.177
	R	22	0.40		
	Total	55	1.00		
Siske	L	39	0.67	0.50	0.012
	R	19	0.33		
	Total	58	1.00		