Title: Cats (*Felis silvestris catus*) read human gaze for referential information

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Abstract
Companion cats often occupy the same anthropogenic niche as dogs in human families. Still, cat cognition remains an underrepresented research subject in ethology. Our goal was to examine whether two components that are crucial in dog-human communicative interactions (sensitivity to ostensive signals; gaze following) are also present in cats. In a two-object choice task, we used dynamic and momentary gazing in ostensive and non-ostensive communicative situations. We tested 41 cats at their owner's home. Cats on the group level achieved a 70% overall success rate, showing that they are capable of following human gaze as a referential cue. Cats' success rate was unaffected both by the type of gazing and the presence/absence of ostensive communication, showing that the subjects followed readily even the more difficult momentary cues. We found a trend (p=0.085), showing that young cats (max. 1 year old) may achieve higher success rate than adult animals. Ostension had a significant effect on the latency of eye contact, which was the shortest when the experimenter called the cat's attention with ostensive signals (p=0.006). Our results are the first that prove cats' ability to follow human gaze, which is considered to be one of the more difficult visual referential signals given during human-animal interactions. Although ostension did not affect the success rate of cats, we found ostensive human signals to be a more effective attention elicitor compared to non-ostensive vocalizations. Our study therefore provided the first insight to the existence of sensitivity to human ostension in another non-human species besides dogs. These results emphasize the possible relevance of the domestication process and responsiveness to socialization in the development of human-compatible socio-cognitive skills even in such animals as the cat, where the ancestor was not a highly social species.

Key words: cat, gaze following, referential signal, ostension

Introduction

In this article we investigated whether domestic cats would follow the gazing cues of an unfamiliar experimenter in a two-way choice situation, and whether human ostensive signaling would have an effect on the performance of cats. The potential usage of referential guidance signals (such as pointing, or gazing at particular targets by someone else) can be important factors regarding intelligent behavior, where animals are required to use various environmental (or social) information flexibly. Referential signals are often in the highlight of research for human language evolution (gestural/visual orienting signals: e.g. Leavens et al., 2004; non-verbal vocalizations: e.g. Slocombe & Zuberbühler, 2005). Additionally, ostensive behaviors (such as establishing eye contact, or using specific verbal utterances with an ostensive tone) are considered expressions of communicative intent, therefore their usage on either the sender's or the receiver's side, are also taken as signs of higher cognitive functions (Gómez, 1996).

The investigation of animal cognition is almost inseparable from the comparative approach where evidence is sought for the existence of key features of human cognitive functions in nonhuman animal species (i.e. Bates and Byrne, 2007). The scientific reasoning behind such interspecific comparisons is usually based on either the close phylogenetic relationship (i.e. studies on great apes, Deaner et al., 2007; MacLean et al., 2012), or the functional similarity (i.e. highly developed social system, Griffin et al., 2015; or complex environmental challenges, Fitch et al., 2010) between particular species and humans. The investigation of domesticated species offers another possibility for the study of animal cognition: namely the nurturing effect of the anthropogenic socio-cognitive niche (Miklósi & Soproni, 2006) that can affect the cognitive capacity of a species both on the proximate (i.e. through learning, Miklósi and Topál, 2013) and the ultimate level (i.e. through genetic selection, Kaminski et al., 2005). In the case of companion animals, especially the dog (*Canis familiaris*), it is hypothesized that the natural living environment of these animals is the human social group (Miklósi & Topál, 2013). Therefore, both natural and artificial selection could favor those socio-cognitive features in these species that enhanced their successful adaptation to the most influential agent in their new niche: humans.

In the last two decades researchers almost exclusively focused on studying the socio-cognitive capacity of companion dogs as the possible effects of domestication became interesting. So far there is ample evidence that dogs possess a complex set of skills that enables them to flawlessly co-exist with their human group members, such as attachment (Topál, Miklósi, Csányi, & Dóka, 1998), attention (Miklósi, Kubinyi, Topál, & Gácsi, 2003), interspecific communication (both visual: Pongrácz et al., 2013a; and acoustic: Pongrácz et al., 2011); and sensitivity to human ostensive cues (Topál, Gergely, Erdőhegyi, Csibra, & Miklósi, 2009). By employing the same or very similar experimental paradigms, the comparison between the socio-cognitive performance of dogs and human infants (e.g. Péter et al., 2015); and also between dogs and socialized individuals of dogs' closest living wild relatives, the gray wolf (*Canis lupus*), showed both socialization (i.e. associative learning – Udell et al., 2010; Hall et al., 2015) and domestication played an important role in the presence/onset of many of the highlighted skills (e.g. Miklósi and Topál, 2013).

The apparently smooth adaptation of dogs to the new, interspecific social environment with humans, is explained in both ontogenetic and evolutionary terms with the gregarious nature of the species, of its closest relative (the wolf), and its hypothetical wolf-like ancestor (MacLean et al., 2017; Lampe et al., 2017). From this aspect the emergence of a set of human-compatible socio-cognitive skills in dogs is taken as an exemplar of evolutionary analogy (or convergence), compared to homologies that are present between humans and non-human apes, respectively (Miklósi, 2014, p.18). However, there is another animal that rivals dogs as a companion of humans, both in its number and popularity (Downey & Ellis, 2008) – the domestic cat (*Felis catus*). Although cats were also domesticated many millennia ago (Driscoll et al., 2007), their

apparently good adaptation to the anthropogenic niche is theoretically less evident than in the case of dogs. The ancestor of cats (*Felis silvestris*) is a more or less notoriously solitary animal (Velli, Bologna, Silvia, Ragni, & Randi, 2015), and even African wildcats (*F. s. lybica*), the subspecies that is considered to be the closest relative of domestic cats (Driscoll et al., 2007), is characterized as exhibiting minimal contact between individuals in nature (Turner, 2014, p. 64, which mostly occurs between a mother and her juvenile offspring). Domestic cats can be considered as facultative social animals, where the availability and distribution of food and other resources can largely influence both the interactions between individuals and the number of cats living near to each other. Therefore there are somewhat differing empirical results about the nature of cat-cat interactions (e.g. Curtis et al., 2003; Crowel-Davis et al., 2004; Bradshaw, 2016) and the extent how exclusive/ strict is their home range usage (e.g. Corbett, 1997; Feldman, 1994; Vitale, Shreve & Udell, 2017). In any case, the facultative solitary/social cats may seem to be far from being ideal as a candidate for the role of "man's other best friend" (c. from Galvan and Vonk, 2016). The fact that domestic cats are highly successful in their role as a companion animal, presumes well developed inter-specific socio-cognitive skills of these animals, which in turn would be predicted unlikely for a species with the above mentioned ecological background.

Contrary to the above mentioned reservations, we now have evidence that even adult domestic cats show pro-social intraspecific behaviors, such as allorubbing or licking (Macdonald, Yamaguchi, & Kerby, 2000). Furthermore, there is a small number of papers that identify certain socio-cognitive abilities which also exist in the domain of cat-human interactions, such as the recognition of the owner's voice (Saito & Shinozuka, 2013); using the owner's expressions as social reference (Merola, Lazzaroni, Marshall-Pescini, & Prato-Previde, 2015); recognition of a human's attentional state (Ito et al., 2016) and following visual signals (pointing with arm) in a two-way choice situation (Miklósi, Pongrácz, Lakatos, Topál, & Csányi, 2005). The literature on cats' interspecific social capacity is still very narrow compared to similar research on dogs (for review see Miklósi & Topál, 2013), and there are indications that show cat-human communication might be less-developed than similar domains of human-dog interactions (weak emotion recognition by cats: Galvan and Vonk, 2016; humans do not attribute distinct meaning to cat vocalizations: Nicastro and Owren, 2003). The main goal of our research was to investigate such aspects of cats' understanding of human communication that are considered highly specific to complex social interactions and adaptation to the anthropogenic niche: gaze following and sensitivity to ostensive communication.

Ostensive signals (such as the invocation – calling the receiver's name; eye contact; using specific words e.g. "Look!", "Listen!") serve an attention-eliciting purpose, which is widely present in human communication (Lloyd-Fox, Széplaki-Köllőd, Yin, & Csibra, 2015). Even newborn babies possess specific predisposition for recognizing others' communicative intent (Gergely & Csibra, 2013). Toddlers and infants were found to be very sensitive to ostension, as they were shown to be prone to commit perseverative errors in a two-object hiding game only when the hiding action of the assistant was highlighted with ostensive signals (Topál et al., 2008; 2009; Péter et al., 2015). And although ostensive communication seems to be a human-specific trait, it was found that companion dogs show a striking resemblance to children in their dependency on ostensive addressing by humans in various task situations. Besides the previously mentioned setups for perseverative erring (Topál et al., 2009; Péter et al., 2015), dogs also responded to ostensive signals in tasks of observational learning (Pongrácz, Miklósi, Timár-Geng, & Csányi, 2004) and gaze following (Téglás, Gergely, Kupán, Miklósi, & Topál, 2012). This type of behavioral plasticity in the dog is thought to be the product of natural selection along their domestication that favored the smooth acquisition of enculturation in dogs – i.e. the mastering of social rules and behavioral patterns of the human environment (Miklósi & Topál, 2013). In the case of cats however, there is no available information about their

possible sensitivity to human ostension. Meanwhile the long domestication history and the apparently successful companion status of cats would predict a dog-like dependency on ostensive signals; the lack of selection for cooperative work with humans (unlike in dogs, Gácsi et al., 2009a) and belonging to a family of mostly solitary species, would predict that cats will not show specific reactivity to ostensive signals.

The main paradigm of this paper is gaze following in cats – which would be the utilization of a visual communicative signal that is very typical in humans. The role of gazing as a means of communication includes the initiation of interaction; information sharing; sustaining of hierarchy; expressing of emotions and interest, etc. (Gobel et al., 2015; Reddy, 2015; Emery, 2000). When gazing indicates a point of interest, it becomes a referential signal, functionally similar to other pointing cues, such as someone points with hand or arm (Daum, Ulber, & Gredebäck, 2013). The sensitivity to referential signals can be detected in human babies from a very young age (Csibra & Gergely, 2009), and there are several studies proving that various non-human species possess the capacity for following various types of human pointing signals (e.g. dogs – Pongrácz et al., 2013b; wolves – Virányi et al., 2008; cats – Miklósi et al., 2005; apes – Bräuer et al., 2005; Leavens et al., 1996; bottlenose dolphins (*Tursiops truncatus*) – Herman et al., 1999; foxes (*Vulpes vulpes*) – Hare et al., 2005). It is important to note that specimens of all non-domesticated species involved in the aforementioned papers were socialized ('tame') animals that lived with humans in close proximity. In case of gaze (and glance) following, an additional difficulty exists for most nonhuman species: they may avoid eye contact because it represents an agonistic display. In the case of cats, staring at the other cat is considered as a 'challenging' behavior typical to confident individuals (Overall, 2013). So far there are few and contradictory indications regarding how widespread could be the utilization of gazing as a communicative signal between humans and cats. Miklósi and colleagues (2005) found that cats are less likely to gaze at their owner (i.e. initiating an interaction) when they face an unsolvable problem. From this aspect, cats behaved more similarly to socialized wolves than to dogs (Miklósi et al., 2003). On the other hand, in the experiment done by Merola et al. (2015), by looking at their owner, cats were able to get social reference from humans regarding the nature of an unknown object. Testing companion cats in a gaze following task would be another interesting aspect of the understanding of the possible effects of domestication on the ability of cats to adapt to the anthropogenic niche. Obviously, for fully understanding the above-mentioned question it would also be necessary to test socialized individuals of wild cats in comparable situations.

In our study we tested companion cats with different types of human gazing signals in a two-way choice test. Our main goal was to find out whether cats would follow successfully such signals (i.e. choosing the indicated target above chance level). We used dynamic and momentary gazing signals, because our second goal was to test whether the nature of the referential signal would affect the cats' success rate. In the case of dynamic signals, the gazing posture is sustained until the subject makes a choice, therefore, based on pointing experiments done with dogs and wolves (Virányi et al., 2008), one could expect that cats would perform with a higher success rate when the gazing is dynamic. However, in the case of momentary gazing, when the signal consists of a brief look at the target, then the experimenter takes back her/his glance to the subject, the movement is more apparent, therefore one could also expect that for a predatory species (such as the dog and the cat), these cues would be more salient (i.e. Soproni et al., 2002). Finally, our third goal was to test whether the inclusion of ostensive cues to the gazing signals would affect cats' performance. Our prediction was that as cats were adapted successfully to the companion animal status, there is a high likelihood that they show similar capacity to dogs in being sensitive to human ostension. Besides the main factors, we also tested whether demographic variables, such as the age of the subjects and the source from where the cats were obtained would have an effect on their performance. Both variables could

theoretically affect the possibility of the given cat to learn about human signals, for example, young cats, or cats obtained from a shelter or former strays may had less opportunity to observe humans before the tests.

Materials and Methods

Subjects
We tested mixed breed companion cats (N=41: 5 males, 14 neutered males, 7 females and 15 spayed females) living with their owners. The average age of subjects was 5.5 years (SD=4.1), the youngest subject was 4 months old, and the oldest was 14.5 years old. During the recruitment of participants, we requested that cats which are strongly motivated by food be entered to the experiments. Besides this, we did not set any specific prerequisite for participation; with the exception of the successful completion of the preliminary test (see below). This test was done with the goal to assess whether a particular cat is willing to work with the experimenter. All subjects were naive, as they previously did not participate in any scientific experiment or official training. The subjects came from 26 different households. Each subject was tested in a semi-random, repetitive arrangement, in each testing condition.

Prerequisite of participation (preliminary test, Miklósi et al., 2005)
The preliminary test consists of three phases that follow each other in a consecutive order. The experimenter performed the preliminary test upon her first arrival to a particular subject's home. The experimenter was the same young female during the entire experiment, including the preliminary tests, pre-training and main experiment.
Phase 1: the experimenter calls the subject (with any suitable sound, verbal utterance, and/or the subject's name). The subject passes this phase if it approaches the experimenter on its own, without any forcing/ coercion (the latency of approach was also depending on the given home environment, but typically remained within the 1-5 min range).
Phase 2: The experimenter approaches the subject and attempts to pet it. The subject passes this phase if it did not leave the experimenter during this time.
Phase 3: The experimenter puts the test bowls in front of the subject and places a piece of food into each of them. Each subject was tested with a food reward that according to the owner's experience was that particular cat's favorite. The subject passes this phase if it eats the food from the bowls. We used two identical, blue colored plastic cereal bowls (7.5 cm high, 14.8 cm diameter). A subject was considered as 'suitable for experiment', if it passed at least two of these three phases. The third phase was also important from the aspect that the subjects were familiarized with the fact that both bowls may contain food. Each subject that were included to the final sample completing the whole test, did pass originally Phase 3.

General methods
At first each subject participated in a series of pre-training trials that utilized the pointing-with-arm gestures ('proximal dynamic pointing') described by Miklósi et al. (2005). This was followed by the main experiment, consisting of a series of head turn signals ('gaze following').

The experiments were always conducted at the home of the subjects. Most of the tested cats were kept at houses where they were allowed to enter the building. For these subjects and also for the exclusively indoor kept cats, we chose a sufficiently large room in the place of residence for the tests (i.e. there was enough open space for setting up the video cameras and running the tests unobstructed by furniture, etc.). In the case of six subjects (outdoor cats) the experiment was made in a fenced yard next to the owner's house – apart from this the indoor and outdoor testing conditions were identical. We asked the owners not to feed their cats a few hours (preferably minimum two hours) before the time of testing. For this reason, experiments

were either timed according to the feeding regime of the cats (the experimenter arrived just before feeding time); or in the case of those cats that were normally fed ad libitum, the cat's food was withdrawn a couple hours before testing.

Pre-training

Although it was shown earlier that cats prefer visual cues over olfactory ones when they learn to locate food items (Mayes et al., 2015), to avoid odor-caused bias of choice throughout the entire experiment (including the preliminary test and pre-training), the food bowls were scented with the preferred food reward by smearing a small piece of this preferred food onto the inner wall of both bowls (a method used earlier by Pisa & Agrillo, 2009).

We included a pre-training session because we wanted to ensure that the subjects learned the connection between the experimenter as signaler (cue-giver) and the possibility of finding hidden food by following the cues coming from the experimenter. For this, we had to choose an already tested method for cueing the cats that was different from gazing which was planned to be used in the main experiment. Therefore, we chose the proximal dynamic pointing with arm that was previously proven to be the most effective pointing cue for cats by Miklósi et al., (2005).

At the beginning of the pre-training, the owner and the experimenter positioned themselves at the starting position. They were both sitting on the floor, facing towards each other from 2.5-3.0 m distance. During the trials the subject was held by the owner at a distance of 2–2.5 m from the experimenter. The experimenter held both bowls in one hand and put a piece of food into one of the bowls, meanwhile the subject was present, but it could not see which bowl the food was placed into. After this, with a simultaneous movement, the experimenter placed the two bowls in front of herself, equidistant left and right, 0.6 m apart. Then the experimenter directed the cat's attention to herself by calling the cats name, until the cat looked at her. This was immediately followed by performing a dynamic proximal pointing (the tip of the index finger of the pointing arm/hand is within a few centimeters of the indicated bowl) with the extended arm accompanied by gazing at the bowl that contained the food. The pointing cue was sustained until the subject chose one of the bowls. We asked the owners to release the cat only when the experimenter initiated the pointing cue. In the case of a correct choice, the subject could eat the reward, whereas if the cat approached the non-indicated bowl first ('wrong choice'), the experimenter picked up the bowls so that the subject was prevented from eating the hidden food. This procedure was then repeated with the opposite bowl. If the cat did not succeed on both sides trials 1 and 2, or it hesitantly made its choice (i.e. did not start moving towards the bowl within 10 s, stopped before reaching the bowl), the pre-training was repeated maximum two more times, with the baited bowl being balanced equally on both sides.

Main test (gaze following)

After the subject finished the pre-training, the gaze following test was started immediately. Before each trial the experimenter picked up the bowls and put a small piece of food into one of them. The cat did not know which bowl contained the food as before placing them back to the floor, the experimenter switched bowls left and right a few times in front of herself in the air. After this the experimenter simultaneously put back the two bowls to the same position where they were during the pre-training trials.

For providing head turn signals (gazing) to the cats, the experimenter would kneel on the floor 0.1 m behind the bowls, equidistant from each. The experimenter faced the subject from a distance of 2–2.5 m. Between trials the cat was gently restrained by the owner, who was given instructions when to release the subject according to the gazing cue of the experimenter. Before providing a gazing cue, the experimenter drew the subject's attention to herself. Half of the trials were preceded by ostensive attention elicitors, such as calling the subject's name,

'Look!', and using the specific cat-calling noises that are widely known and used in the area where the tests were run (a sort of "tse" "tse" sound). In the other half of the trials the experimenter used non-ostensive signals as attention-elicitors – these were clicking noises made by the tongue, often used for horses (Nishiyama et al., 2016), but never for cats. In the case of both the ostensive and non-ostensive trials, the gazing cue commenced only after the experimenter could establish eye contact with the cat. Half the trials used dynamic gazing (which was sustained until the subject made a choice between the bowls); the other half used momentary gazing. This cue consisted of a head turn towards the indicated bowl and back to the cat. The owner was instructed to release the cat only after the experimenter looked again toward the cat in the case of momentary gazing. In the case of dynamic gazing, the cat was released after the experimenter turned her head towards one of the bowls.

Within one trial, the momentary gazing cue was performed only once, with the exception of the following conditions (when the cue was repeated): (1) the cat did not leave the start position; (2) the owner released the cat too early (in this case the trial was started again); (3) after initial approach, the cat stopped and sat down half-way towards the bowls. The subject was allowed to visit only one bowl. If it chose the indicated bowl it could eat the food. In the event of choosing the non-indicated bowl, the experimenter picked up the bowls similarly to the pre-training. At the end of the trial the owner returned the cat to the starting position (by either calling, or carrying it back).

Each subject participated in 24 test trials. We used the following types of cues: 12 dynamic gazing, from these six ostensive (three to the left, three to the right); six non-ostensive (three to the left, three to the right); 12 momentary gazing, from these six ostensive (three to the left, three to the right); six non-ostensive (three to the left, three to the right). We used a predetermined trial order, where the indicated bowl could not be used more than two times on the same side in a row, and from the aspect of attention eliciting (ostensive/non-ostensive) and gazing type (momentary/dynamic), the same type of gazing could not follow each other more than three times. We had two different trial orders (see Appendix 1), where the experimenter started either with momentary ostensive gazing to the right, or with dynamic ostensive gazing to the left. In the case of both orders, the second gazing cue was the other gazing type and to the other direction compared to the first trial, but the second trials always used ostensive cues.

Each test was recorded with two video cameras (Sanyo Xacti CG10). Camera 1 was behind the experimenter in the middle, while the position of Camera 2 varied somewhat depending on the possibilities of the testing location, but preferably, we put it on one side, behind the owner. Camera 1 recorded the cat at the start position and during its approach towards the experimenter, while Camera 2 recorded the vicinity of the experimenter, including the cat's choice between the bowls. The footages recorded by the cameras were later synchronized with the help of the clapping noise the experimenter did at the beginning of each session when the cameras were started.

Exclusion of subjects and temporary suspending of the test

Only those cats were allowed to participate in the main test that successfully passed the preliminary test and the pre-training. Although it was possible to complete the 24 trials of the main test at one time, the 24 trials could also be divided into more than one session if the subject did not perform at least eight trials during the first occasion, however the subject was excluded from further testing and we did not use the results of its completed trials, if it performed less than 8 trials during the first occasion.

When a subject stopped choosing (i.e. the cat did not leave the start position after the signal was given) during the main test, the experimenter repeated the gazing cue belonging to that particular trial. If the subject still did not choose, but had completed at least eight trials, then the experiment was suspended, and we continued it on another occasion within a few days'

time. Compared to stop choosing, another reason for suspending the test was when a cat gave up the test after a few unsuccessful trials (i.e. repeatedly chose the non-indicated bowl, therefore missed the reward). We consider the cats' behavior as 'giving up', when the cat clearly withdrew itself from the testing context (e.g. laid down, left the testing area, performed replacement activities (cleaned itself), showed aggressive behavior if restrained). When this occurred the experimenter offered food to the cat as an attempt to lure it back to the test. If the cat responded to the food by taking it, we continued the trials. If the cat refused to take the food, but it had already completed at least eight trials, then we suspended the testing for that day. Otherwise the cat was excluded from the experiment. Another reason for suspending the test was if the cat was no longer motivated by the food reward. If that happened after at least eight completed trials with the given subject, we postponed the rest of the test to another day. However if the cat became unmotivated before eight completed trials, we excluded it from the experiment.

The experiment could be postponed only once, any subject that refused to cooperate twice would be excluded. At the end of all the trials, we did not exclude any cat for this reason, as each subject completed all twenty-four trials within a maximum of two occasions. When the second occasion started, we repeated the pre-training with the cat before the test trials were continued.

The experimenter altogether visited 99 possible subjects, from these eight cats had to be excluded because they failed the preliminary test. A further six cats did not pass the pre-training. From the remaining 85 cats, 24 subjects failed to perform any of the gazing trials, so the gaze following test was done on 61 cats. From these 61, 20 cats were excluded because they stopped responding before completing at least eight 8 trials during the first occasion. At the end, we had 41 subjects that completed all of the experimental trials.

Data extraction from the video footages
The synchronized videos were analyzed with Solomon Coder (17.03.22, copyright by András Péter). The following behavioral variables were coded: success of choice, latency of eye contact.
Success of choice ('Success'): whether or not the cat chose the indicated bowl. If it did, the trial was considered as successful, if it did not, then the trial was unsuccessful. We considered the cat as making a choice when it looked into a bowl or reached into it with its paw. We also coded trials that were considered as invalid. Within this, three sub-categories were distinguished, according to what caused the error. (1) No-choice – when the cat did not choose (cat does not leave the start position; comes to the experimenter in between the bowls; cat goes away and does not approach the bowls); (2) Human fault – the experimenter or the owner made a mistake; (3) Other – any other (rare) event that occurred only once, disturbing the experiment (e.g. sudden noise that distracted the cat). However, the invalid trials were repeated during the test, therefore each subject had 24 valid trials at the end (successful or unsuccessful).

Latency of eye contact ('Latency'): the time elapsed between the initiation of the attention eliciting by the experimenter until the cat looked at the experimenter. When the experimenter noticed the cat's eye contact she gave the gazing cue. As it was hard to see from the video recording whether the cat looked at the experimenter or not, we coded the time interval that elapsed between the start of attention getting and the end of the first phase of the gazing cue (i.e. when the experimenter finished the turning of her head towards the target) as the latency of eye contact.

The reliability of behavioral coding was verified with the help of an assistant, who coded 11 from the 41 video footages. Subsequently we performed a correlation analysis between the two sets of behavioral variables ('Success', 'Latency'). Because 'Success' was a nominal

variable, we used Cramer's association coefficient to determine the extent of its association. We found an excellent match between the two sets of 'Success' data (Cramer's V=0.978). After this we calculated the Cohen's Kappa values for testing the consistency of the two coders: 'Success' (κ=0,978). The association between the two sets of 'Latency' data was analyzed with the Pearson correlation method, which showed excellent agreement between the two coders (r(120)=0.875; p=0.000).

Statistical analyses

Success rate analyses (both on the group and individual level) were performed with SPSS (22). Further analyses on the associations among 'Success' and 'Latency' with independent factors were performed in R (3.3.2).

'Success'

On the group level overall success rate of cats along the 24 trials was compared to the chance level (12 correct choices) with one sample t-test. We compared the treatment groups whether they are different in terms of how many cats performed successfully above chance level. For pairwise comparisons Fisher's exact test was used, in case of four groups we used Pearson's chi-squared test. For determining whether a cat performed above chance level we used Binomial tests. In case of 24 trials cats had to choose successfully in at least 18 of the 24 trials (p=0.023). In case of 12 trials (treatment groups by gazing type and ostension type) cats were considered as performing above chance level if it chose successfully in at least ten trials from 12 (p=0.039). Finally, in case of six trials (combinations of the gazing type and ostension type treatments) cats had to perform successfully all six trials for being above chance level (p=0.031).

With paired t-test we analyzed whether the cats' performance was improving along the 24 trials. For this we compared the number of correct trials between the first and last 5 trials. To test for the effects of looking type, ostension and individual specific factors on the success of the cats we run a binomial Generalized Linear Mixed Model (lme4, glmer function) with the individuals added as random factor. Initial model included as fixed factors the looking type (momentary or dynamic), ostension type (ostensive or non-ostensive) and their interaction, cats' age ('young' = 1 year old or younger; 'adult' = 1 < x < 8 years old; 'old' = 8 years old or older), origin (where did the owner acquire the cat from) and their interactions, the order of indication (trial order 1 and 2) and whether one or two occasions was needed for the given cat to complete the 24 trials. Parsimonious model was identified using dredge (MuMin package) with AIC based model selection. The best model is reported in the results. For post-hoc testing Tukey corrected pairwise comparisons were used (emmeans package, pairs function).

'Latency'

To test whether ostension and individual specific factors did have an effect on eye contact latency we run Mixed effects Cox regression model (coxme package) with the individuals added as random factor. Initial model included as fixed factors cat age, origin and their interaction, whether one or two occasions were needed for the given cat to complete the 24 trials and ostension type. Type of gazing was not included to the analysis as the gazing cue was always provided after the experimenter established eye contact with the cat. Backwards elimination was used to find the parsimonious model which is reported in the results.

Results

'Success'

The overall success rate of cats on the group level was 70.42%, which is significantly above the chance level (one-sample t-test: t(40)=7.819; p=0.001). On the individual level 18 cats

performed above chance level based on the full set of trials (at least 18 correct choices from the 24, Binomial test). The number of individually successful cats was as follows in the case of the different treatment groups: dynamic gazing: 14; momentary gazing: 15; ostensive cue: 16; non-ostensive cue: 12; dynamic-ostensive: 8; dynamic-non-ostensive: 7; momentary-ostensive: 7; momentary-non-ostensive: 10. We did not find significant differences between the number of individually successful cats either in the pairwise comparisons (Fisher's exact test, type of gazing: p=1.000; ostension: p=0.485), or in the case of the complex treatment groups (type of gazing x type of ostension, $\chi^2(3)=0.932$; p=0.818). Cats' performance did not change along the course of the 24 trials (based on the comparison of success rates in the first and last five trials, paired t-test: t(40)=-1.138; p=0.262; M=3.51; SD=1.19 vs. M=3.73; SD=1.14).

According to the binomial GzLMM the rate of successful choices did not show significant association with either the type of gazing or ostension. From the additionally tested factors in the final model we found only a significant trend effect of cats' age on the successful choices ($\chi2(4) = 8.8637$ p = 0.0646, see Table 1 and Table 2 for further details). According to the post hoc test cats in the youngest age group were somewhat more successful than the adult cats; with the oldest age group's success rate in between (Figure 1).

	χ^2	df	Pr ($>\chi^2$)
testing occasions	2.1396	**1**	0.14354
cat's age	4.9298	**2**	0.08502
gazing order	2.5180	**1**	0.11255

Table 1 – Wald test for fixed effects in case of the association between cats' success and factors describing the testing conditions and cats' age.

cat's age contrast	odds ratio	SE	df	z.ratio	p.value
1 vs. 2	2.0402909	0.6562197	Inf	2.217	0.0683
1 vs. 3	1.6498030	0.5731883	Inf	1.441	0.3198
2 vs. 3	0.8086116	0.2142340	Inf	-0.802	0.7019

Table 2 – Results of the Tukey post hoc test in case of the trend-like association between cats' age and cats' successful choices. Cats' age is marked with 1-3, where 1= young cats (1 year old or younger); 2= adult cats (1<x<8 years old); 3= old cats (8 years old, or older).
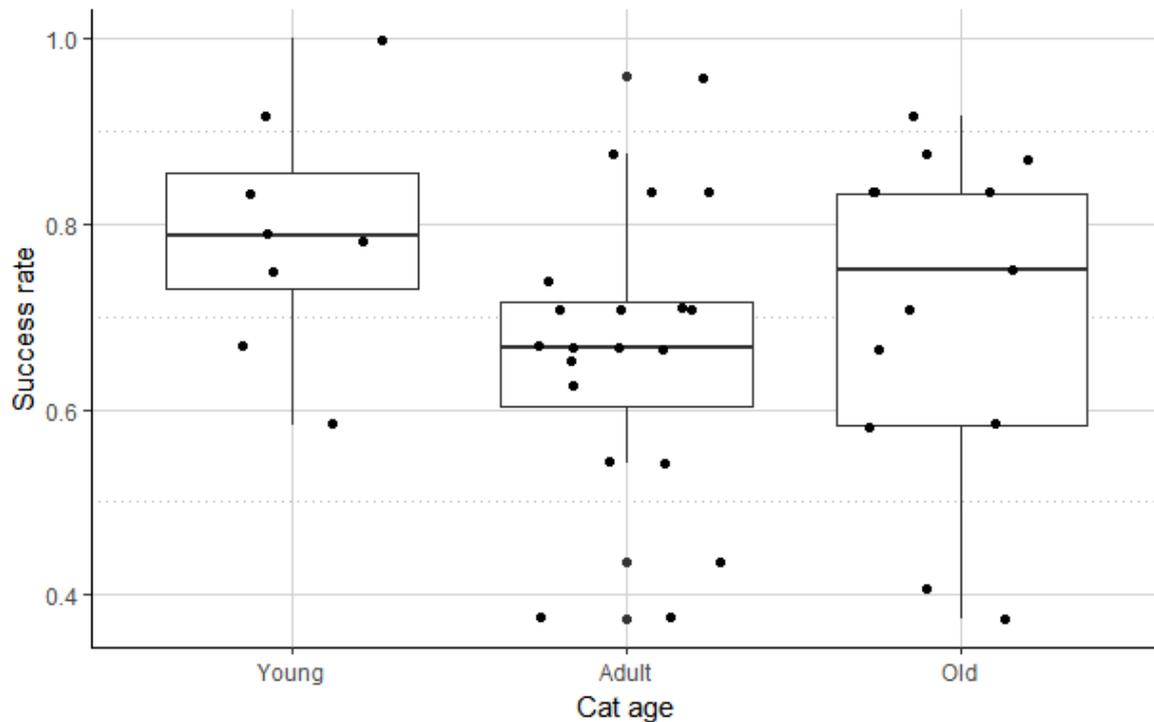

Figure 1 – Trend-like association between cats' age and cats' success. Young cats tended to be more successful than adult subjects in the two-way choice test by following human gazing signals. Tukey post hoc test (p=0.0683). Cats' age is marked with 1-3, where 1= max. 1 year old; 2= 1<x<8 years old; 3= at least 8 years old cats.

'Latency of eye contact'

Type of ostension had the only significant effect on eye-contact latency ($\chi 2(1) = 7.5564$; p = 0.00598; expB = 0.832) showing that ostensive signals grabbed the cats attention quicker than the non-ostensive ones (Figure 2).
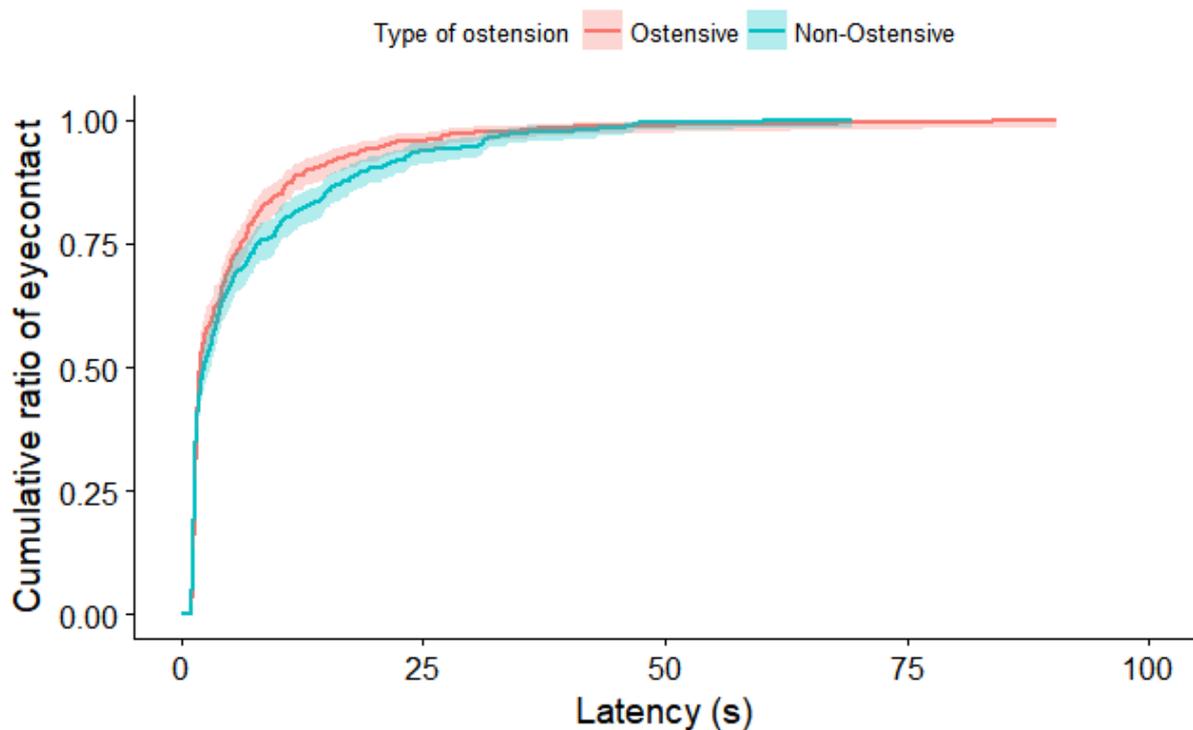
Figure 2 – The association between latency of eye contact with the cat and the type of attention grabbing signal (ostensive vs. non-ostensive). In case of ostensive calls cats established eye contact with the experimenter sooner. Mixed effect Cox regression model (p=0.006).

Discussion

Based on a relatively large sample of privately owned companion cats (N=41), our experiment showed that cats can find a hidden treat with success rates significantly above chance level by following human gazing in a two-way object choice situation. Cats were equally successful regardless of the type of gazing (momentary vs. dynamic) and whether the experimenter called the cats' attention with ostensive or non-ostensive acoustic signals before gazing. From the various modifying factors, such as demographic features of the cat (age, origin) and technical details of the experimental conditions (number of testing occasions, trial order) only cats' age had a trend-like effect, showing that young cats performed slightly better than the adult subjects. The ostensive manner of calling the cats' attention before the gazing cue was provided had a strong effect on how quickly the cat established eye contact with the experimenter. Cats established eye contact sooner in the case of ostensive signals compared to the effect of non-ostensive vocalizations of the experimenter.

Considering the main goal of this study, our results provided first time evidence that domestic cats that were kept as companions can follow human gazing cues high above chance level. Their group-level success rate (slightly above 70%) is similar to the results of Miklósi et al. (2005), where cats followed distal momentary pointing (with extended arm and pointing finger) with an approximately 70% success rate. However, gazing signals are considered more difficult to follow in nonhuman animal species (e.g. Itakura, 1996) than pointing with arm, therefore our present results show a remarkable performance in cats. Although Miklósi et al. (2005) did not report the number of successful subjects on the individual level, our results can be compared to the data reported about dogs in other publications on two-way choice tests. Pongrácz et al. (2013a, b) found that 30 to 60 % of dogs performed above chance level in case of relatively complex ('momentary cross-pointing') and more conventional ('distal momentary

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pointing') types of arm signals. In this present study we found that 43% of the cats performed above the individual chance level in the case of the whole set of trials – a result that again underlines the successfulness of cats in following interspecific referential signals. The reliance on human visual cues is obviously an adaptive strategy for companion cats that belong to a species which predatory success mainly relies on its visual capacity once it localized the prey based on auditory cues (Fitzgerald and Turner, 2000). In nature, the individual cats' hunting success can be largely variable, depending on whether the cat attacks its preferred prey type or not (Dickman and Newsome, 2015); or whether it hunts among more or less favorable environmental conditions (McGregor et al., 2015). In our sample more than 40% of the subjects reached the 75% individual success rate that is comparable with the highest observed hunting success rates reported by the aforementioned studies. If we consider that cats may often pursue high success rates during foraging, it could explain why we mostly encountered subjects that 'gave up' (i.e. refused to continue choosing) when they made consecutively incorrect choices 3-4 times beforehand.

We found a trend, indicating that the young cats (maximum one year old) had somewhat higher success rate than the adults. Although there are indications that cats' sociocognitive abilities decline with aging (Pan et al., 2013), in our sample the difference between the success rates of adult and old cats was not significant. Although there are papers dealing with the early ontogeny of cognitive functions in cats (e.g. Villablanca and Olmstead, 1979; object permanence - Dumas and Doré, 1989; motoric asymmetry Wells and Millsopp, 2012), so far there has been no investigation on the development of interspecific communicative abilities of young cats. Based on the results, we can assume that different amounts of exposure to human signaling between the adult and young cats did not affect their ability to follow human gazing, as adults performed somewhat weaker than the youngest age class. Perhaps the tendency in younger cats to be more curious and more social than older animals (Lee et al., 2007) resulted in a more effective reaction to the visual cues of the unfamiliar experimenter. Similarly to cats, in companion dogs it was also found that even very young subjects perform with remarkable success in two-way choice experiments based on following human visual cues (Gácsi et al., 2009b). In comparative experiments it was also shown that young dogs do not require excessive training (repeated testing) for being successful in point-following, while intensively socialized young wolves reached the success level of dogs only when they were 11 months old (Virányi et al., 2008). It is also worth to mention that adult socialized wolves were shown to be capable of outperforming shelter dogs in following human pointing where the latter were of unknown level of socialization (Udell et al., 2008). In the case of making eye contact with humans, young dogs develop this skill seemingly spontaneously compared to socialized wolves, which require a lengthy and frequently repeated exposure to communicative tasks with humans to reaching the level of dogs (Miklósi et al., 2003; Gácsi et al., 2005; Virányi et al., 2008). Based on our results showing the high performance of young cats in the gaze following task, we can assume that the development of this skill starts early and may only require a relatively short learning period in cats.

Although the ostensive vocal cues did not affect the success rate of cats, however, ostension had an effect on the latency of eye contact. Cats responded faster when the experimenter addressed them with ostensive cues. This finding is in parallel with the results of many studies done on dogs, where researchers found that dogs exclusively pay attention to the social addressing from humans when ostensive signals are provided (e.g. Pongrácz et al., 2004; Topál et al. 2009). In the case of cats, ostensive signals may facilitate the easy recall of such contexts where they learned that some sort of reward (e.g. food) follows particular attention elicitors. However, surprisingly cats did not perform with higher success rate in case of ostensive signaling. With the exception of a few papers (Tauzin et al. 2015; Téglás et al. 2012) we do not know of any published results on the effect of ostensive cues on gaze or point

following behavior of dogs, however in the case of object permanence tasks, dogs tended to commit perseverative errors in a two-way object choice situation when the experimenter used ostensive signals (Topál et al., 2009; Péter et al., 2015; Péter et al., 2016). This means that instead of choosing the location where the experimenter visibly placed the reward, dogs kept choosing the previously rewarded location – but only if the experimenter addressed the subject in an ostensive manner during the placement of the reward to its location. Comparing these results with the new findings with cats, we can conclude that ostensive signals may serve as effective attention grabbers for both cats and dogs, informing them about the communicative intention of humans. However, in case of ostensive signals the subject may easily miss what is actually going on by reverting some kind of behavioral routine from the recent or more distant past – as the studies on perseverative errors showed. At the same time, cats' obvious sensitivity to ostensive cueing is definitely remarkable, because apart from companion dogs there is no known exemplar of non-human animals being specifically responsive to human ostension.

Conclusions

Our experiment showed that companion cats follow the gazing cues of a previously unknown human experimenter with a remarkable success rate. Their performance is comparable with other non-human species (e.g. Primates – Itakura, 2004; dogs – Téglás et al., 2012) that were proven to be capable of inter-specific gaze following. Cats' performance was stable across conditions where more or less 'difficult' types of gazing signals were provided. More static cues (i.e. dynamic gazing in our experiment) are considered to be easier to follow, however, in the case of cats, the more subtle momentary gazing was also proven to be highly effective.

Contrary to our initial hypothesis, ostensive vocal utterances by the experimenter did not enhance the success rate of cats throughout the test, which was seemingly a large difference compared to results with dogs (Tauzin et al., 2015; Téglás et al., 2012). There are several explanations for this result: (1) the generally high success rate of cats may create a plateau effect where no further improvement was possible; (2) cats do not possess a similarly strong affinity for human ostension as dogs do, due to their shorter and different evolutionary common past with humans (Galvan and Vonk, 2016); (3) cats may also respond to the visual ostensive cues (i.e. eye contact, Topál et al., 2014), therefore the ostensive or non-ostensive manner of vocal cues bears less importance for them.

Regarding the possible origins of cats' remarkable performance in following heterospecific referential signaling, it is worth considering the theory of Wilkinson et al. (2010) who proposed that even solitary and 'asocial' species such as tortoises, can possess the basal forms of such social skills that earlier were thought to be evolved only among the nurturing conditions of social species. This theory highlights the modularity of evolution, where for example, the capacity of gaze following may have appeared much earlier than it actually could have manifested itself in gaze following situations. Solitary species might have benefited from these skills on other (non-social) ways, or these capacities might remain unused and 'neutral' until new evolutionary challenges emerged. In the case of the domestic cat, besides the evolutionary changes during domestication, we should also not underestimate the role of individual experience that turned to be an important factor in case of the socio-cognitive competences of dogs (D'Aniello et al., 2017).

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Appendix

trial	trial order 1	trial order 2
1	momentary, ostensive, right	dynamic, ostensive, left
2	dynamic, ostensive, left	momentary, ostensive, right
3	dynamic, ostensive, right	momentary, non-ostensive, right
4	dynamic, non-ostensive, left	dynamic, ostensive, left
5	momentary, ostensive, right	dynamic, non-ostensive, right
6	dynamic, non-ostensive, right	momentary, non-ostensive, right
7	momentary, non-ostensive, left	dynamic, non-ostensive, left
8	dynamic, ostensive, right	momentary, ostensive, left
9	momentary, non-ostensive, left	momentary, ostensive, right
10	dynamic, non-ostensive, right	dynamic, non-ostensive, left
11	momentary, non-ostensive, left	momentary, ostensive, left
12	dynamic, ostensive, right	momentary, non-ostensive, right
13	momentary, ostensive, left	dynamic, ostensive, left
14	momentary, non-ostensive, right	dynamic, ostensive, right
15	dynamic, ostensive, left	dynamic, non-ostensive, left
16	dynamic, non-ostensive, right	momentary, ostensive, right
17	momentary, non-ostensive, right	dynamic, non-ostensive, right
18	dynamic, non-ostensive, left	momentary, non-ostensive, left
19	momentary, ostensive, left	dynamic, ostensive, right
20	momentary, ostensive, right	momentary, non-ostensive, left
21	dynamic, non-ostensive, left	dynamic, non-ostensive, right
22	momentary, ostensive, left	momentary, non-ostensive, left
23	momentary, non-ostensive, right	dynamic, ostensive, right
24	dynamic, ostensive, left	momentary, ostensive, left

Appendix 1 Trial orders 1 and 2. Twenty subjects were tested with trial order 1, twenty-one subjects were tested with trial order 2.