

This is the final version of the manuscript sent to journal for publication after acceptance. Note the final printed version might be different from this one due to the editing process.

The full citation:

Fugazza, C., Petró, E., Miklósi, Á., Pogány, Á. 2018. Social learning of goal-directed actions in dogs (*Canis familiaris*): Imitation or emulation? *Journal of Comparative Psychology*, 133: 244–251. doi: 10.1037/com0000149

Title: Social learning of goal-directed actions in dogs (*Canis familiaris*): Imitation or emulation?

Authors: Claudia Fugazza*, Eszter Petro*#, Ádám Miklósi* and Ákos Pogány*

Affiliation:

*Department of Ethology, Eötvös Loránd University, Budapest

#Research Centre for Natural Sciences, Institute of Cognitive Neuroscience and Psychology, Hungarian Academy of Sciences, Budapest, Hungary

Author for correspondence: claudia.happydog@gmail.com

Abstract

A goal-directed action is composed of two main elements on which the observer may focus his attention: the movement performed (i.e. the action) and the outcome (i.e. the goal). In a social learning situation, consequently, the observer may imitate the action of the model or emulate the result of its action. In humans and primates, the tendency to selectively engage in any of these two processes is considered to be dependent upon the availability and saliency of information about the goal, implying the capacity to recognise the goals of others' actions. Dogs are skilful in learning socially from humans and, when trained with the Do as I Do method, they imitate human actions. Here we tested trained dogs for engaging in imitation or emulation based on information about the goal. We found that dogs observing the demonstration of an object-related action in the absence of a clear goal tended to solve the task by matching the body movement of the human demonstrator. In contrast, when they could observe the exact same movement, but the goal was apparent, they attempted to solve the task by their own means, i.e. by emulation, instead of imitating the demonstrated action. These results provide experimental evidence for dogs being able to recognize the goals of others and adjust their behaviour accordingly, relying flexibly on imitation or emulation.

Key words

Imitation; Emulation; Dog; Goal-directed action; Social learning

Introduction

The demonstration of goal-directed actions contains two main observable sources of information: a movement or motor part and a consequence or effect that is the goal of the action (Elsner 2007). A goal is defined as an observable, physical end-state or outcome (e.g. Wohlschläger et al. 2003; Leighton et al. 2010). Emulation is the process by which an observer, by watching a model, learns about the results of its actions - i.e. the goals - rather than the details of the behaviour involved (Tomasello et al. 1987; Horner and Whiten 2005). Therefore, in emulation only the end-state of what the model has done is copied (Tomasello and Call 1997; Wood 1989; Whiten et al. 2004; Whiten et al. 2009). By imitation, in contrast, the observer learns some specific aspects of the intrinsic form of the act from the observation of the model (Whiten and Ham 1992). Thus, apart from vocal imitation, it is the orientation and the shape of the action - i.e. the action in terms of movements performed - that is attended to and reproduced when imitating (Horner and Whiten 2005).

Whether human infants represent the goals and intentions of others has been the focus of many empirical studies (e.g. Meltzoff 1995; Olinek and Dubois 2009; see also Elsner 2007 for a review). Human infants' sensitivity to goal-directed actions is apparent already from the first year of their life (Thoermer et al. 2013; Hamlin et al. 2008) and they are generally considered to encode the object-related actions of others in terms of their goals from this early age (Robson and Kuhlmeier 2016; Gergely et al. 1995; Meltzoff 1995; Woodward 1998).

The evolution of the ability to recognise the goals of others and the imitation of others' actions have been intensely researched (e.g., Call et al. 2005). In case of primates, the most common opinion is that they acquire information socially about the goal to be reached, instead of imitating the actions that they have seen performed by the demonstrator (Call and Tomasello 1994; Myowa-Yamakoshi and Matsuzawa 1999; Nagell et al. 1993; Tomasello et al. 1987; Tomasello 1996; Visalberghi and Fragaszy 1990). Such a view questions primates' ability to learn socially features of the actions used by the model (i.e. imitation). Nevertheless, evidence for motoric imitation has been found in various taxa (e.g., chimpanzees: Whiten et al. 1996; marmosets: Bugnyar and Huber 1997; Voelkl and Huber 2000; 2007; orangutans: Stoinski and Whiten 2003) and remarkably, even in species that are more phylogenetically distant from humans, including birds (e.g., Dorrance and Zentall 2001), whales and dolphins (e.g., Rendell and Whitehead 2001). Studies applying the Do as I Do method, in which the subject is specifically trained to imitate on command, casted away any doubt that the ability to imitate evolved also in non-human species (e.g., chimpanzees: Custance et al. 1995; orangutans: Call 2001; dolphins: Herman 2001; parrots: Moore 1992 and dogs: Topál et al. 2006; Fugazza and Miklósi 2014a).

From the before-mentioned studies it seems apparent that both imitation and emulation can take place in various taxa, but the factors influencing whether one or the other learning process takes place in a social learning situation are not fully explored. For instance, it appears that most of the studies on primates in which some evidence of copying the means (i.e., imitation) was found, focused on reproduction of direct manipulation of objects (e.g., Whiten et al. 1996; Whiten 1998; 2002) or reproduction of arbitrary acts (e.g., Custance et al. 1995). In contrast, when tool use is involved, evidence of imitation does not typically emerge (e.g., Tomasello et al. 1987; Nagell et al. 1993; Call and Tomasello 1994). Horner and Whiten (2005) suggest that the perception of the information about the causal relationship between the means and the goal may be a factor influencing the type of social learning that takes place. In particular, when a critical causal relationship is apparent to the observer, emulation is preferred because it is more flexible and prone to generalization, allowing the individual to adjust the means to different situations. In contrast, imitation is preferred when such a causal relationship is difficult to infer. To address this assumption, Horner and Whiten (2005) experimentally varied the availability of information about causal relationship in a tool use task for observer chimpanzees. The subjects observed actions performed to obtain a reward with a tool inserted either into a transparent box, where the causal relationship between the actions performed and the outcome was visible, or into an opaque box, that did not allow observing that some actions were irrelevant to solve the task. The authors found that the animals flexibly switched from emulation

(carrying out only the necessary actions to reach the goal when using the transparent box) to imitation (copying also all unnecessary actions when using the opaque box), confirming that the causal relationship between the actions and the outcome influenced which of the two social learning processes was used.

Besides the causal link between the action and the outcome, studies on human infants (Gergely et al. 2002), chimpanzees (Buttelmann et al. 2007) and dogs (Range et al. 2007) revealed that they tend to imitate the actions of others when these actions are unusual means to reach a goal, but only if the model does not have an apparent situational constraint to perform the strange action. In these experiments, the demonstrated actions included such unusual tasks as using the forehead instead of the hand to turn on a light (in case of human infants) or using the paw, instead of the mouth, to pull a handle (in case of dogs). The same (unusual) actions were demonstrated in different conditions; the subjects observed these unusual actions either when freely performed, or when the model was constrained to perform the less common or less efficient action (e.g. the model could not use his hand/mouth to operate the apparatus, because that given body part was occupied). In all these three studies, the subjects (humans, chimpanzees and dogs) that observed a model performing the unusual action because of situational constraints, tended to reach the same goal by different means (emulation), while those that observed the model performing the unusual actions for no apparent reason tended to imitate its behaviour. Consequently, Gergely et al. (2002) and Buttelmann et al. (2007) concluded that both infants and chimpanzees have some representation of the rationality of others' intentional actions and rely on this when learning socially. Range et al. (2007) concluded that dogs copy in an inferential selective manner. An alternative explanation to the above findings is provided by perceptual distraction; Beisert et al. (2012) and Kaminski et al. (2011) suggested that perceptual factors may affect the likelihood of imitation of these unusual acts by perceptually distracting the observer from some relevant parts of the demonstration. Accordingly, the rationale behind behaviours that seemingly indicate the representation of others' goals would be differences in perception or attention rather than inference (see also Leighton 2010). Therefore, in experiments aimed at testing the mechanisms underlying imitation and emulation, it seems important to control for any potential perceptual distractors.

The aim of the present study is twofold; first, we investigate whether dogs trained with the Do as I Do method can represent the demonstrator's goal. Second, we investigate whether the dogs' social learning strategy depends on information about the goal or whether they blindly copy the action. Dogs are considered not only being able, but also being predisposed, to learn socially from humans (Pongrácz et al. 2003). Dogs trained with the Do as I Do method become especially skilful imitators (e.g., Topál et al. 2006; Fugazza and Miklósi 2014a; Fugazza et al. 2016a; Huber et al. 2009). By this training the individuals specifically learn that they are required to match the demonstrated action in terms of body movements performed. Dogs' ability to imitate has been experimentally supported by combining the Do as I Do paradigm with the two-action method, in which different actions (i.e. movements) are demonstrated on one object (for more details, see Fugazza and Miklósi 2014a). Here we tested dogs trained with the Do as I Do method and this training ensures that dogs learn to copy the demonstrated action also in terms of body movement performed. Therefore, imitation, rather than other forms of social learning, was their expected response and by manipulating the presence of a relevant goal in the demonstration, we could test whether they revert to emulation. Dogs were tested in conditions that were considered to facilitate using one of the two main sources of information of a goal-directed action differently, namely the action (i.e. body movement) and the goal. A human demonstrator performed an object-related action (opening an apparatus) using her hand. This action was identical in all conditions, but in one condition the demonstrator opened the apparatus to take an object (i.e. had a goal), whereas in the other condition the demonstrator performed the exact same opening action but without any apparent reason (i.e. she did not take anything from the apparatus). In the latter condition, the object was already outside of the apparatus, visibly lying on the ground close to it, to ensure that the presence of the object (as a perceptual factor) would not distract the dogs in some, while not in other conditions (Beisert et al. 2012; Kaminski et al. 2011). After the

demonstration, the dog was required to imitate. While humans typically perform such opening actions using their hands, dogs may do so either by pushing with their nose or by using their front paw. By testing Do as I Do trained dogs, our prediction was that they would match the demonstrated action in terms of body movements, i.e. they would imitate (e.g., Fugazza and Miklósi 2014a; Fugazza et al. 2016a; 2016b) when no clear goal is apparent. However, if dogs can represent the goal-directed actions of others in terms of their consequences, this representation may trigger the performance of the action that is mostly connected with that consequence (Brass et al. 2001; Prinz 1997), instead of performing the demonstrated action. We predicted, therefore, dogs to be less likely to match the human body movement and perform other actions than those demonstrated, when observing the demonstrator interacting with the apparatus to take an object (i.e., the demonstrator's apparent goal).

Methods

Subjects

20 adult pet dogs that were previously trained by their owners with the Do as I Do method (Topál et al. 2006; Fugazza and Miklósi 2014b) were included in the study. The age of the dogs ranged from 3 to 11 years old (mean \pm SD: 5.8 \pm 2.5 years), 16 of them were females and 4 were males. The dogs belonged to various breeds (mixed breed N=4; Shetland sheepdog N=2; German shepherd N=1; poodle N=2; Springer spaniel N=1; Schnauzer N=1; border collie N=6; grey hound N=1; Australian shepherd N=1; Czechoslovakian wolf dog N=1).

Do as I Do preliminary training

Before the study began, all subjects had been trained by their owners with the Do as I Do method to match their behavior to demonstrated actions (based on Topál et al. 2006 and Fugazza and Miklósi 2014b). Successful training was assessed by the Do as I Do exam (Fugazza and Miklósi 2014b). The training method first uses operant conditioning to train dogs to match their behavior to a small set of familiar actions on command 'Do it!'. In the next phase, the training continues until dogs are able to generalize this rule to novel actions and different demonstrators (for more details on the training protocol, see Fugazza and Miklósi 2014a and 2014b). For this preliminary training every owner selected the actions for his/her dog by choosing actions that were already familiar to them. Examples of commonly used actions include: spin, lay down, jump over a hurdle and climb onto a chair or table. The actions used during the training were not related to those used in this study.

Experimental protocol

Pre-exposure to the object

Before the test trials, all subjects underwent a pre-exposure phase. The aim was to provide all subjects with the same experience about the object that was used as a 'goal' during the tests, by showing them that this object was relevant for the experimenter. We used an object that was unfamiliar for the dogs (a small lilac cloth wallet, size: 14 x 8 x 2 cm). Pre-training was carried out in presence of the owner, while the dog was free in the testing area. The experimenter held the wallet and showed it to the dog, expressing positive emotions (e.g.: "look at this, how nice!") for 5 seconds. Then the experimenter tossed it on the floor and asked the dog to fetch it. If the dog took it in its mouth, it was rewarded socially, by verbal praise and petting. This procedure was repeated twice; all dogs took the object in the first two trials.

Test trials

Dogs were tested with the Do as I Do method on their reproduction of two actions, each performed on one of two different apparatuses. Specifically, the two tasks/apparatuses were to open a sliding door (always from right to left) of a cabinet (size: 110 x 85 x 47 cm) and to push the dump lid of a litterbin (size: 41 x 41 x 30 cm). Neither of the apparatuses were transparent. All dogs were repeatedly tested in both conditions (object condition and no-object condition), with each apparatus (cabinet and bin). Furthermore, for each condition/apparatus combination, dogs were

tested in two trials, so that every dog was repeatedly tested in a total of 8 trials. Trial order was semi-randomized, so that for the first two trials both apparatus and condition were randomized and in the following trials they were counterbalanced - e.g., if the object was present in the first pair of trials with the cabinet, it was absent in the second pair of trials with the litter bin; also, in the third pair of trials the same apparatus was used as in the first pair of trials, counterbalanced for object presence (i.e. no object and cabinet, in this specific example). Likewise, in the fourth pair of trials the same apparatus was used as in the second pair of trials, balanced for object presence (i.e. with object and litterbin).

Previous studies (e.g., Fugazza and Miklósi 2014b) showed that dogs need several demonstrations and attempts to learn to complete this type of complex actions (e.g. opening doors and drawers). In the present study, we focused only on the subjects' first interaction with the apparatus, immediately after the "Do it!" command because we were only interested in how they attempted to approach the problem after the observation of the demonstration. By rewarding the dog after its first physical contact with the apparatus, we also excluded the possibility for motor practicing and trial and error learning of the most effective action to open the cabinet.

Test procedure

1. At the beginning of each trial, the experimenter stood next to the apparatus (cabinet or litterbin) facing the dog;
2. The owner was present and standing at the other side of the apparatus. S/he did not look at nor interacted with the dog;
3. The experimenter requested the dog to stay ca. 2 m from the apparatus and to pay attention, using cues known by the dog;
4. The experimenter demonstrated the given action (opening the bin or the cabinet) using her hand to push the door/lid of the apparatus;
5. In the object condition only: the experimenter took the object from inside the apparatus with her hand, held it for ca. 2 seconds and replaced it into the apparatus;
6. The door of the cabinet was then immediately moved to its original position by the owner, always without looking at or interacting with the dog (the lid of the bin returned automatically to its starting position);
7. The experimenter gave the 'Do it!' command while looking straightforward;
8. The dog typically approached and interacted with the apparatus;
9. After the dog's first physical interaction with it (i.e. first touch on the apparatus), the experimenter praised and rewarded it with food;
10. Immediately after the dog consumed the food reward, the subsequent trial started with the above steps being repeated (Figure 1).



Figure 1: *a1 and a2: No object condition.* The experimenter opens the bin using her hand (a1); The dog interacts with the apparatus using its paw (a2); The wallet is visible on the ground, close to the apparatus (a1 and a2, indicated by the arrow); *b1, b2, b3: Object condition.* The experimenter opens the bin using her hand. The wallet is inside the apparatus (b1); the experimenter takes the wallet out of the bin (b2); the dog interacts with the apparatus using its nose (b3). In this condition the wallet is visible for the dog during the demonstration, when the experimenter takes it in her hand (b2).

Behavioural variables and data analysis

The tests were video recorded for behavioural coding. An observer that did not witness the demonstration (i.e., only observed the dog's behaviour after the 'Do it!' command was given) coded the body part that the dog used when interacting with the apparatus: none (i.e. no interaction), paw, nose or both paw and nose. Using the paw, that is a matching behaviour between human demonstrator and dog, was expected if dogs imitated the demonstrated actions (i.e., performed the action using a body part that corresponded to the one used by the demonstrator). Thus, we scored the dog's performance (i.e. the body part they used) based on behavioural similarity between demonstrator's action and subject's action according to the below definitions:

Action (body part)	Description	Score	Interpretation
Paw	A front paw of the dog is in physical contact with any part of the apparatus	3	Maximum degree of similarity between the action of the demonstrator and that of the

			dog: they interact with the apparatus using their functionally same body part
Paw and nose	Both a front paw and the nose of the dog are in physical contact with any part of the apparatus	2	Medium degree of similarity between the action of the demonstrator and that of the dog: the dog uses the same body part as well as a different one compared to that used by the demonstrator
Nose	The nose of the dog is in physical contact with any part of the apparatus	1	The dog performs an action that differs from the one performed by the demonstrator: the dog interacts with the apparatus using a different body part
None	The dog does not get in physical contact with the apparatus	0	The dog does not perform any action on the apparatus that can be related in any ways to the demonstrated action

Statistical analyses were carried out using R statistical environment (v. 3.2.3, RCoreTeam, 2015). Action scores (response variables) were analysed in Mixed Effects Ordinal Regression Models (MEORMs; R package ‘ordinal’; Christensen 2015). The full model included object presence (factor with two levels: not present or present), apparatus (factor with two levels: litter bin or cabinet), trial (factor with eight levels) and all possible two-way interactions between these variables as fixed effects, and dog ID as a random term. Stepwise model selection was based on AIC values, and we selected the new model whenever delta AIC was above 2. The effects of explanatory variables were analysed by likelihood ratio tests (LRT): we provide χ^2 and p -values of likelihood ratio tests of models with and without the explanatory variable. In addition, odds ratios ($\exp[\beta]$) with 95% confidence intervals are provided between levels of a given significant fixed effect.

Ethics committee approval

The authors confirm that the experiments reported in this paper are in accordance with the current Hungarian laws regarding animal protection. The study was approved by the ethical committee of Eötvös Loránd University (PE/EA284-4/2016).

Results

The odds of paw use were influenced by condition (MEORM of action score, LRT of models with and without object presence: $\chi^2_1 = 9.370$, $p = 0.002$). Dogs less likely used their paws and more likely used their nose in the object conditions compared to the no object conditions (no object \rightarrow object: $\exp(\beta) = 0.384$ [0.206; 0.716], Figure 2).

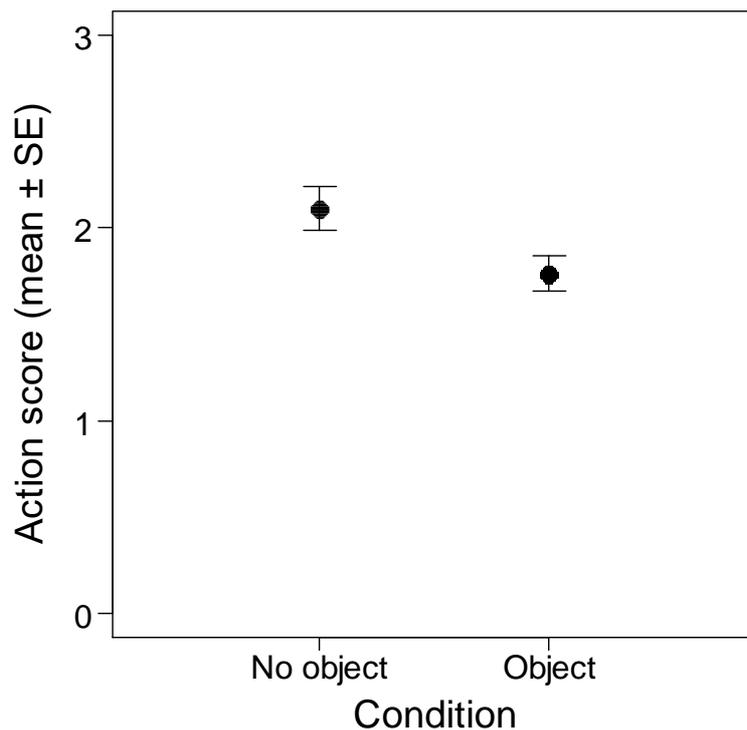


Figure 2. Behavioural responses of dogs in Do as I Do tasks with or without an apparent goal being involved in the demonstration. Action scores (i.e., body part of the dog used when interacting with the experimental apparatus: 0 – none; 1 – nose; 2 – both paw and nose; 3 – paw) were averaged over repeated trials of the same 20 dogs when using different apparatuses.

Apparatus and trial had no effect and were therefore excluded from the final model (both $p < 0.364$).

Discussion

This study revealed that dogs flexibly engage in imitation or emulation in a social learning situation based on the availability of the information about the goal to be achieved. This implies that dogs, similarly to primates, can recognize the goal of others' actions. As expected, dogs trained with the Do as I Do method interacted with the apparatus using a body part that matched the one used by the demonstrator, when she operated on the apparatus without an apparent goal. However, when the demonstrator opened the apparatus to take the object that was inside, the dogs' behaviour varied and they tended to perform a different action, using a non-matching body part. Thus, when the information about the goal was provided, dogs tended to use their own means to solve the task (emulation), instead of copying the demonstrator's body movement, despite being specifically trained for the latter (i.e. to imitate). In contrast, when the information about the goal was not provided, dogs matched the action of the demonstrator more closely (imitation).

We interpret these findings as follows; when the dogs could observe the goal, this became more

important in their representation of the demonstrated act than the exact actions performed and, when attempting to reproduce it, they focused on the goal but not on the means. This is consistent with the view that understanding others' goals does not facilitate imitation but actually hinders it because such direct insight overshadows the precise means (Froese and Leavens 2014).

Different mechanisms have been proposed to explain the capacity to understand and reproduce the goals of an action and how this affects the social learning process used by the observer. According to Froese and Leavens (2014), imitation requires the observer to change its attention from the goal of the action to how exactly the action was realized, while emulation is possible without this extra-effort. The authors suggest that saliency of the observed goals and saliency of the observed means (i.e., action performed) influence fidelity of copying. Similarly, according to Call and Carpenter (2002) and Call et al. (2005), when information about the goal is perceived and recognized, it may trigger in the observer the action that is mostly connected to reaching that goal, without the need of relying on the demonstrator's movements. In our no object condition the information about the goal was not intelligible, thus the dogs could only focus on the actions of the model to try to solve the task, making it more likely that they would attend to the body movements that were performed. According to Leighton (2010), the perceived action is composed from various aspects, of which only few are selected and hierarchically ordered; for instance, the means are usefully interpreted only after the goal is recognized. This implies that, if the goal is apparent, then it is more important than the means (i.e., the actions) to reach it. Similarly, according to the so-called 'ideomotor theory' (Brass et al. 2001; Prinz 1997; 2002), goal-directed actions are represented in terms of their sensory consequences (i.e. the goal) and this representation elicits the performance of the action that is mostly connected with that consequence. Accordingly, our results suggest that the dogs recognized that the goal was to take the object in the object condition. This in turn may have elicited the action that, in their experience, was mostly connected to reaching this goal, without the need of further focusing on the actions performed by the demonstrator.

Our results also add to the study of Range et al. (2007) by showing that in social learning situations dogs are sensitive to various aspects of the demonstration they observe. Range et al. (2007) showed that dogs modified their behaviour based on the situational constraints of the model, while in our study dogs did so depending on the information about the goal of the action. Moreover, in our study, the tendency to imitate or emulate cannot be explained by the presence of the object in terms of a potential perceptual distractor, because the object was present and well visible also in the no object condition.

The key information that made dogs switch from imitation to emulation was the information about the final goal of the demonstrated act, rather than causal relationship between the means and the result, as in the Horner and Whiten (2005) study with chimpanzees. The extent to which dogs can recognize causal relationships of this type is unexplored, however, dogs' understanding of means-end connection is considered to be rather limited (e.g. Osthaus et al. 2005; Range et al. 2012). Consequently, their social learning strategies likely rely on recognition of the goals and the actions of the demonstrator, rather than on the causal relationship between the physical elements of the means and their outcome.

Similar to the dogs in our study, human infants that observed a model moving a mouse on a table were more likely to match the action of the demonstrator (sliding or hopping the mouse) when there was no final destination for the mouse (i.e. a goal), than when it was moved to a house (Carpenter et al. 2005). Moreover, in human infants there is a relationship between the ability to produce an action and the ability to predict the outcome of that action (e.g. Falk-Ytter et al. 2006; Kanakogi and Itakura 2011). Specifically, infants' experience with objects can impact the expectations they have for the actions to be done with those objects (Robson and Kuhlmeier 2016). The dogs tested in our study were pre-exposed to the object that represented a goal in the experiment and the importance of the object for the experimenter became apparent. It is likely that such previous experiences made the goal particularly relevant and recognizable for them. Future studies are needed to support this assumption by focusing on how the role of experience with the goal may affect flexible social learning strategies.

In this study, we made use of the Do as I Do training method by which subjects were specifically trained to imitate on command, thus imitation can be considered as their default response in a Do as I Do task. This may explain the rather small difference between the conditions with and without goal. The results of this study, at least regarding the tendency to imitate human actions when requested, should not be automatically generalized to dogs that did not undergo this training. We call for future studies that may investigate the role of information (and lack of it) about the goal in social learning situations of dogs that are not trained to imitate on command.

Conclusions

Our study provides experimental evidence for dogs flexibly engaging in imitation or emulation based on the availability of the information about the goal to be reached, implying that they are able to recognize the goals of others' actions. When the goal is present and recognizable, even dogs trained specifically for imitation with the Do as I Do method tend to attempt to reach the goal by their own means, instead of reproducing the details of the action. However, when the goal is not intelligible, they imitate the movement of the human demonstrator. We conclude, therefore, that dogs' social learning strategies (imitation or emulation) are driven by the perception and recognition of the goal of the action.

Acknowledgements

This study was supported by the National Brain Research Program (2017-1.2.1-NKP-2017-00002). CF also received a grant from APDT (Association of Professional Dog Trainers). A.P. was supported by the ÚNKP-17-4 New National Excellence Program of the Ministry of Human Capacities, Hungary and by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. A.M. received funding from MTA-ELTE Comparative Ethology Research Group (MTA01 031). We are grateful to the dog owners that participated with their dogs in this study.

References

- Beisert, M., Zmyj, N., Liepelt, R., Jung, F., Prinz, W. et al. (2012). Rethinking 'Rational Imitation' in 14-Month-Old Infants: A Perceptual Distraction Approach. *PLoS ONE* 7(3): e32563. doi:10.1371/journal.pone.0032563.
- Brass, M., Bekkering, H. & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, 106, 3–22.
- Bugnyar, T. & Huber, L. (1997). Push or pull: an experimental study on imitation in marmosets. *Animal Behaviour*, 54, 817–831.
- Buttelmann, D., Carpenter, M., Call, J. & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science*, 10, F31eF38.
- Call, J. & Tomasello, M. (1994). The social learning of tool use by orangutans (*Pongo pygmaeus*). *Human Evolution*, 9, 297–313.
- Call, J. (2001). Body imitation in an enculturated orangutan (*Pongo pygmaeus*). *Cybernetics and Systems*, 32, 97–119.
- Call, J. & Carpenter, M. (2002). Three sources of information in social learning. In: Dautenhahn K, Nehaniv C (eds) *Imitation in animals and artifacts*. MIT Press, Cambridge, Mass., pp 211–228
- Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*) *Animal Cognition*, 8, 151–163, doi: 10.1007/s10071-004-0237-8
- Carpenter, M., Call, J., & Tomasello, M. (2005). Twelve- and 18-month-olds copy actions in terms of goals. *Developmental Science*, 8, F13–F20.
- Custance, D.M., Whiten, A., & Bard, K. A. (1995). Can young chimpanzees (*Pan troglodytes*) imitate arbitrary actions? Hayes & Hayes (1952) revisited. *Behaviour*, 132, 837–859. <http://dx.doi.org/10.1163/156853995X00036>
- Dorrance, B.R. & Zentall, T.R. (2001). Imitative learning in Japanese quail (*Coturnix japonica*)

- depends on the motivational state of the observer quail at the time of observation. *Journal of Comparative Psychology*, 115, 62-67.
- Elsner, B. (2007). Infants' imitation of goal-directed actions: The role of movements and action effects. *Acta Psychologica*, 124, 44-59
- Falck-Ytter, T., Gredebäck, G., & von Hofsten, C. (2006). Infants predict other people's action goals. *Nature Neuroscience*, 9, 878–879. doi: 10.1038/nn1729
- Froese, T. & Leavens, D.A. (2014). The direct perception hypothesis: perceiving the intention of another's action hinders its precise imitation. *Frontiers in Psychology*, 65, 1-15, doi: 10.3389/fpsyg.2014.00065.
- Fugazza, C. & Miklósi, Á. (2014a). Deferred imitation and declarative memory in dogs. *Animal Cognition*, 17, 237-247, doi: 10.1007/s10071-013-0656-5.
- Fugazza, C. & Miklósi Á. (2014b). Should old dog trainers learn new tricks? The efficiency of the Do as I do method and shaping / clicker training method to train dogs. *Applied Animal Behaviour Science*, 153, 53-61, doi: 10.1016/j.applanim.2014.01.009.
- Fugazza, C., Pogány Á. & Miklósi Á. (2016a). Spatial generalization of imitation in dogs. *Journal of Comparative Psychology*, 130, 249–258.
- Fugazza, C., Pogány Á. & Miklósi Á. (2016b). Recall of others' actions after incidental encoding reveals episodic-like memory in dogs. *Current Biology*, 26, 3209-3213.
- Gergely, G., Nádasdy, Z., Csibra, G., & Biró, S. (1995). Taking the intentional stance at 12 months of age. *Cognition*, 56, 165–193. doi:10.1016/0010-0277(95)00661-H.
- Gergely, G., Bekkering, H., & Király, I. (2002). Rational imitation in preverbal infants. *Nature*, 415, 755.
- Hamlin, K.J., Hallinan, E.V., & Woodward, A.L. (2008). Do as I do: seven-month-old infants selectively reproduce others' goals. *Developmental Science*, 11, 487–494.
- Herman, L. M. (2001). Vocal, social, self-imitation by bottlenosed dolphins. In K. Dautenhahn & C. L. Nahaniv (Eds.), *Imitation in animals and artifacts* (pp. 63–108). Cambridge, MA: MIT Press.
- Horner, V. & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*) *Animal Cognition*, 8, 164–181 doi: 10.1007/s10071-004-0239-6
- Huber, L., Range, F., Voelkl, B., Szucsich, A., Virányi, Z., & Miklósi, A. (2009). The evolution of imitation: What do the capacities of non-human animals tell us about the mechanisms of imitation? *Philosophical Transactions of the Royal Society of London: Series B. Biological Sciences*, 364, 2299–2309.
- Kaminski, J., Nitschner, M., Wobber, V., Tennie, C., Brauer, J., Call, J. & Tomasello, M. (2011). Do dogs distinguish rational from irrational acts? *Animal Behaviour*, 81, 195-203, doi:10.1016/j.anbehav.2010.10.001
- Kanakogi, Y. & Itakura, S. (2011). Developmental correspondence between action prediction and motor ability in early infancy. *Nature Communications* 2, 341. doi: 10.1038/ncomms1342.
- Leighton, J., Bird, G. & Heyes, C. (2010). 'Goals' are not an integral component of imitation. *Cognition*, 114, 423-435.
- Meltzoff, A.M. (1995). Understanding the intentions of others: re-enactments of intended acts by 18-month-old children. *Developmental Psychology*, 31, 838–850. doi: 10.1037/0012-1649.31.5.838.
- Moore, B.R. (1992). Avian movement imitation and a new form of mimicry: Tracing the evolution of complex learning behaviour. *Behaviour*, 122, 231–263.
<http://dx.doi.org/10.1163/156853992X00525>
- Myowa-Yamakoshi, M. & Matsuzawa, T. (1999). Factors influencing imitation of manipulatory actions in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 113, 128–136.
- Nagell, K., Olguin, R., Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, 107, 174-186.
- Olinek, K.M. & Dubois. D.P. (2009). Infants' understanding of intention from 10 to 14 months:

- Interrelations among violation of expectancy and imitation tasks. *Infant Behavior & Development*, 32, 404–415.
- Osthaus, B., Lea, S.E.G. & Slater, A.M. (2005). Dogs (*Canis lupus familiaris*) fail to show understanding of means-end connection in a string-pulling task. *Animal Cognition*, 8, 37–47.
- Pongrácz, P., Miklósi, A., Kubinyi, E. Topál, J., Csanyi, V. (2003). Interaction between individual experience and social learning in dogs. *Animal Behaviour*, 65, 595–603. doi:10.1006/anbe.2003.2079
- Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, 9, 129–154.
- Prinz, W. (2002). Experimental approaches to imitation. In A. N. Meltzoff & W. Prinz (Eds.), *Imitative mind: Development, evolution, and brain bases* (pp. 143–162). New York: Cambridge University Press.
- Range, F., Viranyi, Z. & Huber, L. (2007). Selective imitation in domestic dogs. *Current Biology*, 17, 868e872.
- Range, F., Moslinger, H. & Viranyi, Z. (2012). Domestication has not affected the understanding of means-end connection in dogs. *Animal Cognition*, 15, 597–607.
- Rendell, L. & Whitehead, H. (2001) Culture in whales and dolphins. *Behavioural and Brain Sciences*, 24, 309–382.
- Robson, S.J. & Kuhlmeier, V.A. (2016). Infants’ Understanding of Object-Directed Action: An Interdisciplinary Synthesis. *Frontiers in Psychology*, 7, 111. doi: 10.3389/fpsyg.2016.00111
- Stoinski, T.S. & Whiten, A. (2003). Social learning by orangutans (*Pongo abelii* and *Pongo pygmaeus*) in a simulated food-processing task. *Journal of Comparative Psychology*, 117, 272–282.
- Thoermer, C., Woodward, A., Sodian, B., Perst, H. & Kristen, S. (2013). To get the grasp: Seven-month-olds encode and selectively reproduce goal-directed grasping. *Journal of Experimental Child Psychology*, 116, 499–509.
- Topál, J., Byrne, R.W., Miklósi, A. & Csanyi, V. (2006). Reproducing human actions and action sequences: ‘Do as I do!’ in a dog. *Animal Cognition*, 9, 355–367, doi: 10.1007/s10071-006-0051-6.
- Tomasello, M., Davis-Dasilva, M., Camak, L. & Bard, K. (1987). Observational learning of tool use by young chimpanzees and enculturated chimpanzees. *Human Evolution*, 2, 175–183.
- Tomasello, M. (1996). Do apes ape? In: Heyes CM, Galef BG Jr (eds) *Social learning in animals: the roots of culture*. Academic Press, New York, pp 319–346.
- Tomasello, M. & Call, J. (1997). *Primate cognition*. Oxford, UK: Oxford University Press.
- Visalberghi, E., Frigaszy, D.M. (1990). Do monkeys ape? In: Parker ST, Gibson KR (eds) “Language” and intelligence in mon- keys and apes. Cambridge University Press, Cambridge, pp 247–273.
- Voelkl, B. & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, 60, 195 – 202, doi:10.1006/anbe.2000.1457
- Voelkl, B. & Huber, L. (2007). Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS ONE* 2, e611. doi:10.1371/journal.pone.0000611.
- Whiten, A. & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. In: Slater PJB, Rosenblatt JS, Beer C, Milinski M (eds) *On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research*. Academic, New York, pp 239–283.
- Whiten, A., Custance, D.M., Gomez, J.C., Teixidor, P. & Bard, K.A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110, 3–14.
- Whiten, A (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 112, 270–281.
- Whiten, A. (2002). Imitation of sequential and hierarchical structure in action: experimental studies

- with children and chimpanzees. In: Dautenham K, Nehaniv C (eds) *Imitation in animals and artifacts*. MIT Press, Cambridge, pp 191–209.
- Whiten, A., Horner, V., Litchfield, C. A. & Marshall-Pescini, S. (2004). How do apes ape? *Learning and Behavior*, 32, 36–52.
- Whiten, A., McGuigan, N., Marshall-Pescini, S. & Hopper L.M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society of London B*, 364, 2417–2428 doi:10.1098/rstb.2009.0069.
- Wohlschläger, A., Gattis, M., & Bekkering, H. (2003). Action generation and action perception in imitation: An instance of the ideomotor principle. *Philosophical Transactions of the Royal Society of London B*, 358, 501–515.
- Wood, D. (1989). Social interaction as tutoring. In *Interaction in human development* (eds M. H. Bornstein & J. S. Bruner), pp. 59–80. Hillsdale, NJ: Lawrence Erlbaum Associates, Publishers.
- Woodward, A.L. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition*, 69, 1–34. doi: 10.1016/S0010-0277(98)00058-4.