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Visual discrimination of species in dogs (*Canis familiaris*)

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Abstract In most social interactions, an animal has to determine whether the other animal belongs to its own species. This perception may be visual and may involve several cognitive processes such as discrimination and categorization. Perceptual categorization is likely to be involved in species characterized by a great phenotypic diversity. As a consequence of intensive artificial selection, domestic dogs, *Canis familiaris*, present the largest phenotypic diversity among domestic mammals. The goal of our study was to determine whether dogs can discriminate any type of dog from other species and can group all dogs whatever their phenotypes within the same category. Nine pet dogs were successfully trained through instrumental conditioning using a clicker and food rewards to choose a rewarded image, S+, out of two images displayed on computer screens. The generalization step consisted in the presentation of a large sample of paired images of heads of dogs from different breeds and cross-breeds with those of other mammal species, included humans. A reversal phase followed the generalization step. Each of the nine subjects was able to group all the images of dogs within the same category. Thus, the dogs have the capacity of species discrimination despite their great phenotypic variability, based only on visual images of heads.

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Introduction

Social life relates to associations of individuals from the same species (Campan and Scapini 2002; Tinbergen 1953). These associations require a recognition that can be at the level of a species, a specific group, a particular social category or a particular individual (Gheusi et al. 1994). The sensory modalities involved in recognition processes vary among species. In mammals, olfaction, audition and vision are involved to a greater or lesser extent depending of the species (Porter 1987). Nevertheless, the discrimination still seems to be possible using only one sense, when the animal is deprived of others as demonstrated in sheep (*Ovis aries*: Porter et al. 1997; Ligout and Porter 2004; Ligout et al. 2004). So, numerous studies have demonstrated the ability of animals to discriminate conspecifics from visual cues alone. Examples include rhesus macaques (*Macaca mulatta*):

Pascalis and Bachevalier (1998); Fujita (1987), and others macaques (*Macaca fuscata*, *M. radiata*, *M. nemestrina*): Fujita (1987), in sheep (*Ovis aries*): Kendrick et al. (1995, 1996), in heifers (*Bos Taurus*): Coulon et al. (2007), in dogs (*Canis familiaris*): Racca et al. (2010); Somppi et al. (2012), in birds (*Melopsittacus undulatus*): Brown and Dooling (1992), and in invertebrates, paper wasps (*Polistes fuscatus*): Tibbetts (2002).

In humans, faces seem to have a special informational value for individual recognition. In fact, face discrimination has been shown to be more efficient and specific compared to non-face object discrimination (Farah et al. 1998). This specific face processing has also been suggested by the results of brain studies using neuroimaging, single-cell and MEA experiments in temporal cortex (Kendrick et al. 2001a; Perrett and Mistlin 1990; Perrett et al. 1982, 1988; Pinsk et al. 2009; Tate et al. 2006; Tsao et al. 2006). Face discrimination is configurally sensitive, since the presentation of an upside-down face decreases discrimination performance. This so-called "inversion effect" has been shown in humans (Yin 1969), in chimpanzees (Parr et al. 1998) and in sheep (Kendrick et al. 1996; Peirce et al. 2000). The inversion effect seems less obvious in some others species such as dogs (Racca et al. 2010) or in macaques, where studies showed contrasting results (Bruce 1982; Parr and Heintz 2008; Perrett et al. 1988). For the investigation of face discrimination, 2D pictures seem to be appropriate stimuli (for review, see Leopold and Rhodes 2010; Tate et al. 2006).

In some species, individuals recognize more easily or are more attracted by images of individuals belonging to their own species, than those belonging to another species. This so-called "species-specific effect" has been shown in macaques (Fujita 1993; Fujita and Watanabe 1995; Pascalis and Bachevalier 1998; Dahl et al. 2009), chimpanzees (Hattori et al. 2010) and humans (Pascalis and Bachevalier 1998; Dahl et al. 2009; Hattori et al. 2010). Moreover, it has been demonstrated that below the species level, individuals showed less difficulty to discriminate individuals of their own breed (e.g., in heifers; Coulon et al. 2009) or of their own race (e.g., in humans; Malpass and Kravitz 1969; Meissner and Brigham 2001; Young et al. 2009) rather than of others. Those preferences (for the own species or own breed/race) may be linked with sex (Fujita and Watanabe 1995) or with cognitive development (Pascalis et al. 2002). Moreover, cross-fostering experiences in sheep and goat have pointed to the primacy of the species providing maternal care upon other social or interspecific interactions (Kendrick et al. 1998, 2001b).

Ultimately, these studies compared behavioral responses of subjects confronted to images of conspecifics compared to images of a limited number of species, and generally with a limited number of instances of each category. For example, in one of the most exhaustive studies in non-human primates (Dufour et al. 2006), subjects were tested with only four categories of faces (humans, own species and two species of the same genus), with 10 instances per face category. This is also the case in studies involving domestic animals. Species discrimination has been confirmed only for a few categories: in sheep, only with humans, dogs and unfamiliar sheep breeds (Kendrick et al. 1995); in heifers with sheep (5 pictures), horses (3 pictures), goat (1 picture) and dog (1 picture; Coulon et al. 2007). In dogs, the only two studies highlighting their ability to discriminate 2D images of their own species among other species used a procedure involving visual preferential looking between dogs and humans, with 24 pictures per category, humans and dogs, for the first study (Racca et al. 2010) and a similar number for the second one (Somppi et al. 2012).

Because of the small number of stimuli used, these studies could not take into account morphological species-specific diversity. In fact, there is more morphological diversity among breeds in domestic species compared to wild species (Hemmer 1990). The largest morphological variety among all animal species is found in domestic dogs, *Canis familiaris* (Wayne and Ostrander 2007). There are considerable variations between breeds in size, weight (from less than one kg -Chihuahua- to 100 kg—Mastiff-), color, hair length and texture (stiff or curly), form and position of ears (upright or drooping) and tail, independent profile, etc. (Denis 2007). According to the American Kennel Club and the International Cynologic Federation (FCI), 400–500 breeds of dogs are now registered, some of which are nearly identical morphologically, while others differ to a very large degree (cf. Miklósi 2007 pp 109). Diversity and changes in morphotypes are still increasing with hybridization and the proliferation of dogs associated with their short duration of gestation.

Considering this amazing morphological diversity among dogs, visual species recognition may represent a true cognitive challenge. Kerswell et al. (2010) showed that changes in morphological features could affect communication in young dogs. For example, a shorter snout seems to increase the frequencies with which some social signals are sent or elicited from other dogs; Relationships with eye cover and coat length were also found. Several studies have shown that visual cues are significant for domestic canids in interactions between conspecifics and heterospecifics (Gaunet and Deputte 2011; Hare and Tomasello 1999; Range et al. 2007a; Virányi et al. 2004, 2008). With the constraint of its large morphological diversity, companion dogs are an interesting model for studying visual species discrimination with 2D images of faces.

Behavioral responses of domestic dogs confronted to still 2D pictures have been investigated under various

procedures. On the one hand, procedures have explored preferential looking with black and white pictures of dogs, humans and objects (Racca et al. 2010) or with color pictures of dogs, humans, children's toys or alphabetic characters (Somppi et al. 2012). On the other hand, operant conditioning procedures have explored dogs' choices when confronted with color pictures of dogs and landscapes (Range et al. 2007b) or confronted with black and white images of humans faces, blank or smiling (Nagasawa et al. 2011). A further paper (Adachi et al. 2007) has examined whether dogs have a cross-modal (acoustic and visual) representation of human individuals. These studies have shown that the particularity of a dog's visual system does not prevent them being sensitive to still pictures. Compared with that of human beings (Kanwisher and Yovel 2006) or non-human primates (Tate et al. 2006; Tsao et al. 2006), for which an efficient system for the processing of its own species faces was demonstrated, the canine visual system could be considered inferior: in degree of binocular overlap (Sherman and Wilson 1975), in color perception (Jacobs et al. 1993), in brightness discrimination (Pretterer et al. 2004), in accommodative range and in visual acuity (Neuhaus and Regenfuss 1967; Miller 2008). In other ways, such as the capacity to be sensitive to rapid movements (Coile et al. 1989), the canine visual systems may outperform the human visual system.

In short, dogs display a very efficient visual communication system toward conspecifics and also to human beings. We assume that this communication could not work without efficient discrimination of conspecifics. Moreover, the dog is subjected to significant constraints such as a large morphologic diversity and the fact that some dog morphotypes may impair visual communication. Therefore, the present study aims at exploring whether dogs using only visual cues are able to discriminate various morphotypes of conspecifics not only from humans but also from other animal species. To address this issue, we used a great variety of pictures of faces from various dog breeds and cross-breeds, to be discriminated from a variety of pictures of faces from humans and other animal species, domestic and wild.

Methods

Animals

Nine adult domestic dogs (*Canis familiaris*), five females and four males, were used as subjects (Fig. 1). Two dogs were pure-bred (one Labrador, one Border collie), seven were cross-breeds (Fig. 1). None had the same morphotype in terms of form, color, marking, hair length, type of ears, that is, upright or drooping (Fig. 1). At the beginning of the experiment, the dogs were between 2 and 5 years old (means 2.4), and their height at eye level was approximately the same as that of the stimuli. Our dog subjects were pets owned by students at the National Veterinary School of Lyon, France, VetAgro Sup. They were fed twice a day on a normal diet. They all had extensive experience of visual interspecific and intraspecific interactions before the study. They all stayed in Vet School kennels during the day and were at their owner's home by evening. Before the beginning of our study, all the dogs had acquired basic obedience training. Moreover, prior to the study, all the subjects were submitted to an ophthalmological examination and to a behavioral evaluation in the clinics of VetAgro-Sup, to make sure that they had no visual or behavioral disorders.

Visual stimuli

Stimuli were presented as pairs of a positive stimulus (S+) and a negative stimulus (S−). Two sets of colored digital head pictures were used as stimuli: one set of unfamiliar dogs and one set of unfamiliar "non-dog" animals. The set of dog pictures consisted of 3,000 pictures from cross-breed and pure breed dogs illustrating the unique variability of dog morphotypes (Clutton-Brock 1996; Denis 2007; Megnin 1897; Regodon et al. 1991) with respect to the four major morphotypes, wolf type, hound type, mastiff type or greyhound type (Megnin 1897). This variability included for instance different features of head shape, hair length and color, position of ears (upright or drooping). The set of "non-dog species" included 3000 pictures of domestic and wild species (e.g., cows, cats, rabbits, and birds, reptilians, wild felines and humans; cf. Fig. 2). No faces of wolves or foxes were included within the "non-dog" species sample. Stimuli were front, right and left profile and ¾ views of both dog and "non-dog" heads (Fig. 2) distributed in equal proportions within each session. The original background of all pictures was replaced by a uniform blue color (R17G97B168: Adobe Photoshop CS3 2007®). The blue color was chosen in light of the dichromatic vision of the dog (Jacobs et al. 1993) and provided the best contrast with the fur and feathers of all stimuli (Fig. 2). The size of the different stimuli was adjusted to cover about 70 % of the overall screen. All the stimuli were controlled for brightness. Stimuli were presented on two 19'' screens by DELL Intel Core 2 Duo® computer (Fig. 3), using Microsoft PowerPoint 2007® software. They produced a 36.9 cm × 23.2 cm picture on the screens. A summary of the stimuli is shown in Table 1. Throughout the experiment, all the sessions, whatever the task, were comprised of 12 pairs of stimuli. The position (left/right) of S+ and S− varied randomly from trial to trial. During all the training tasks, the same single pair of

Fig. 1 Dog subjects. The subject's name, its breed (*Bc* border collie, *L* labrador) or cross-breed (Cb) its sex and age (*2 y* 2 years) are specified below each portrait. These *portraits highlight* the variety of the subject's phenotype

Babel (Cb,♀, 2 y) Bag (Cb,♀, 2 y) Bahia (L,♂, 2 y)

Bounty (Bc,♀, 2 y) Canail (Cb,♂, 3 y) Cusco (Cb,♂, 2 y)

Cyane (Cb,♀, 2 y) Sweet (Cb,♂, 2 y) Vodka (Cb,♀, 5 y)
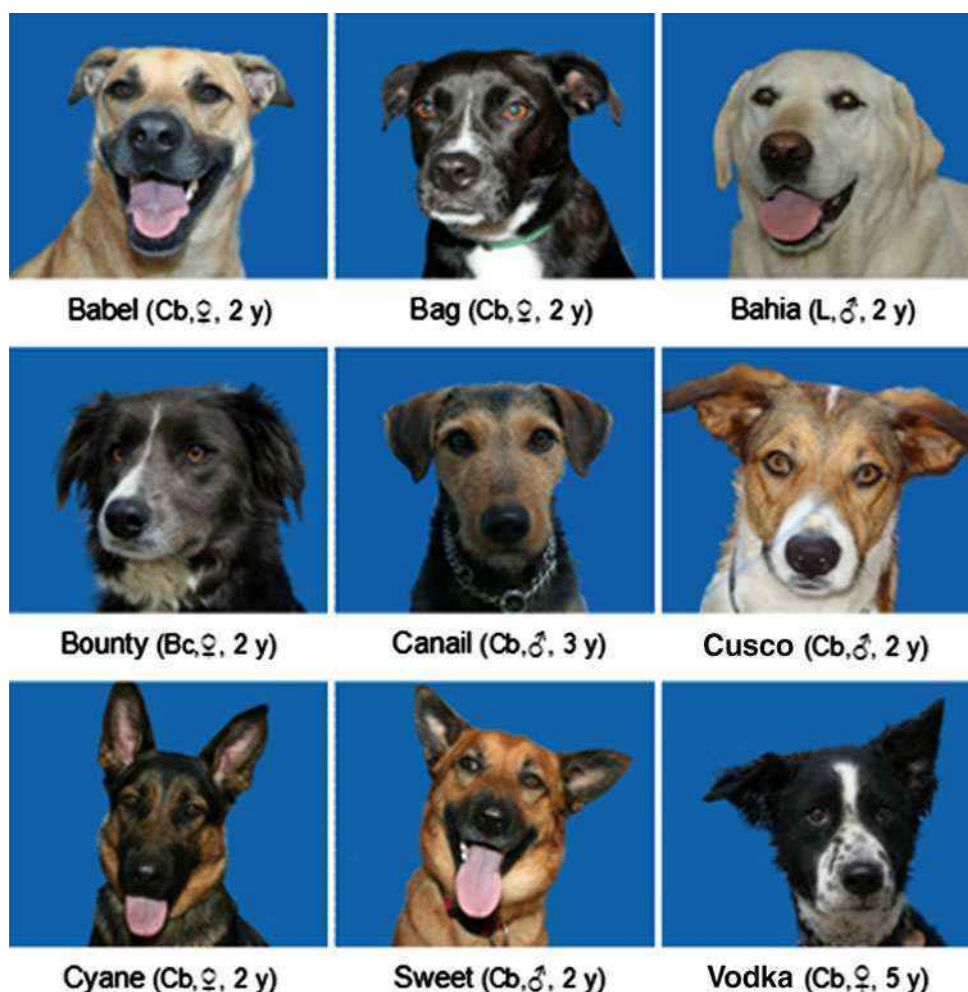

Facial Profile ¾ Frontal

(a)

(b)

Fig. 2 Examples of stimuli used. **a** Dog heads displaying the variety of dog breeds (shape of head, hair length, ears and coat color). **b** "Other species" stimuli including humans, and domestic and wild vertebrates

pictures was presented repeatedly to the nine subjects (Table 1; Fig. 4). During the generalization tasks, each stimulus, dog or "non-dog", was presented only once (Table 1; Fig. 4): therefore, a subject never saw the same stimulus twice. Stimuli were randomly drawn from the sets of dog and "non-dog" pictures.
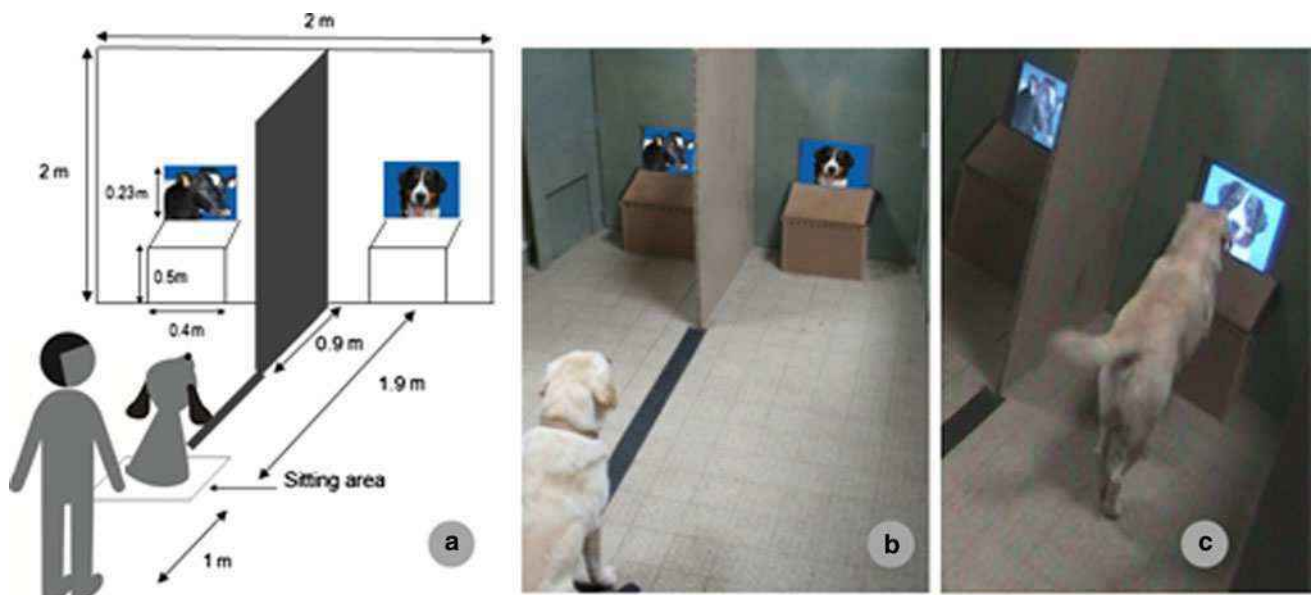
Fig. 3 Apparatus. **a**, **b** The dog sits in front of the experimenter, on a line between the 2 screens. **c** When hearing an order, the dog expressed his choice by going to a given screen and putting his paw in front of the chosen image

Table 1 Experimental procedure and presentation stimuli

Type of task	Task	Stimulus pictures in each session (12 trials/session)
Training	0	A single pair of a bowl (S+) versus a black screen (S−)
Training	1	A single pair of the dog D1 (S+) versus a black screen (S−)
Training	2	A single pair of the dog D1 (S+) versus a blue screen (S−)
Training	3	A single pair of the dog D1 (S+) versus the cow C1 (S−)
Generalization	4	A set of 12 dogs (S+) versus 12 cows (S−)
Generalization	5	A set of 12 dogs (S+) versus 6 cows and 6 others species (S−)
Generalization	6	A set of 12 dogs (S+) versus 12 others species (S−)
Reversal reward contingencies		
Training	7	A single pair of the cow C2 (S+) versus the dog D2 (S−)
Training	8	A single pair of the cow C2 (S+) versus the dog D2 (S−)
Generalization	9	A set of 12 cows (S+) versus 12 dogs (S−)
Generalization	10	A set of 12 others species (S+) versus 12 dogs (S−)

In training tasks, a same single pair of pictures was used in a different random side -left or right- each trial. In generalization tasks, 12 different pairs of pictures were used in each session of 12 trials. In generalization tasks, a given picture was never used twice as a stimulus, so the subjects never saw twice a same stimulus, dog or "non-dog"

First training task with "S+ = a bowl of kibble" (Task 0)

In the first training task, called Task 0, the pair of pictures included a picture of a bowl of kibble as S+ and a black screen as S− (Table 1; Fig. 4).

Training tasks with "S+ = dog" (Task 1–3)

In the second training task, called Task 1, the pair of pictures included the picture of the dog D1 as S+ and a black screen as S− (Table 1; Fig. 4). Then in Task 2, the pair of pictures included the picture of the same dog D1 as S+ and a blue screen as S− (The same blue as the backgrounds of the animal pictures; Table 1; Fig. 4) and in Task 3, the picture of the same dog D1 as S+ and that of the cow C1 as S− (Table 1; Fig. 4).

Generalization tasks with "S+ = dog" (Task 4–6)

In the generalization tasks, we used dog pictures that were as varied as possible. Within each session, the 12 dog pictures included 3 pictures of each of the four major morphotypes of dog (wolf, hound, mastiff and greyhound types). In Task 4, pairs of dog pictures as S+ and cow pictures as S− were presented to the subjects (Table 1; Fig. 4). Then in Task 5, we introduced species other than cows in the pairs "dog/non-dog". A session of 12 trials was then constituted with 12 dog pictures as S+ versus 12 "non-dog" pictures as S−, divided into 6 cows and 6 species different than dogs and cows (Table 1; Fig. 4). In Task 6, the diversity in "non-dog" stimuli was even larger,
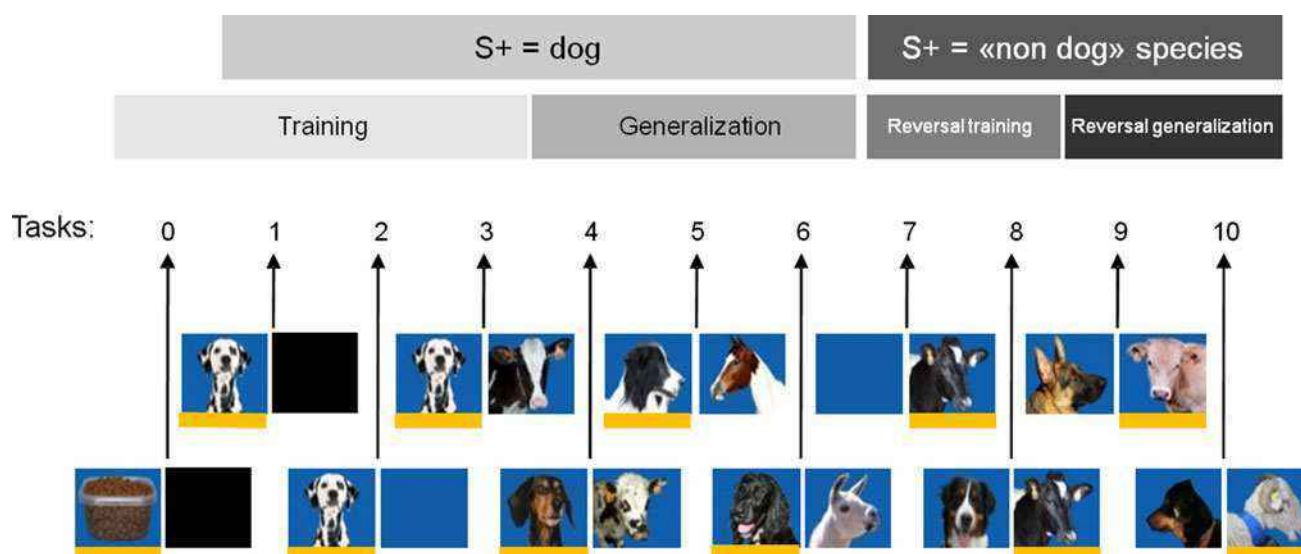
Fig. 4 Procedure with the 11 discrimination tasks from 0 to 10. Examples of pair of stimuli used during trials are presented in pictures below. From Task 1 to 6, the stimulus rewarded S+ is a dog. From Task 7 to 10, which corresponds to the reversal learning of phase 1, the stimulus rewarded is another species than dog, that is, "not a dog". The stimulus rewarded S+ is highlighted with a line below the pictures. Tasks are divided into training and generalization. Training tasks 0, 1, 2, 3, 7, 8: subjects discriminate between the same single pair of stimuli as showed in the pictures. Generalization tasks 4, 5, 6, 9, 10: subjects discriminate between pairs of unknown stimuli

as sessions included 12 dog pictures as S+ versus 12 "non-dog" pictures as S− including different species other than dogs, all different from each other (Table 1; Fig. 4).

Training tasks in reversal reward contingencies with "S+ = non-dog species" (Task 7–8)

After Task 6, the stimulus-reward contingency was reversed, so that S+ was a "non-dog" picture and S− was a dog picture. As in the previous training tasks, in Task 7, the same single pair was used as stimuli, that is, the picture of the cow C2 as S+ and the blue screen as S− (Table 1; Fig. 4). Then in Task 8, the single pair used was the picture of the same cow C2 as S+ and the picture of the dog D2 as S− (Table 1; Fig. 4).

Generalization tasks in reversal reward contingencies with "S+ = non-dog species" (Task 9–10)

In Task 9, sessions included 12 different pairs of different stimuli, 12 cow pictures as S+ versus 12 dog pictures as S− (Table 1; Fig. 4). In Task 10, sessions included 12 different pairs, 12 pictures of "non-dog" species as S+, all species being different from each other, and 12 dog pictures as S− (Table 1; Fig. 4).

Apparatus

The apparatus was installed in a windowless room of 3 m × 5 m. The two computer screens presenting stimuli were inserted in a wooden panel (Fig. 3). The dog could see the two pictures placed at its eye level when assuming a relaxed posture with its neck in the horizontal position. The stimuli were presented at a distance of 1.9 m from the sitting area where subjects made their choice. This distance of 1.9 m was chosen in light of data on the visual acuity of dogs (Neuhaus and Regenfuss 1967) and was validated by preliminary testing. A partition of 0.9 m length was set perpendicularly to the panel between the two screens (Fig. 3a, b); when the dog was in front of one screen, it was unable to see the other screen (Fig. 3c).

Procedure

Subjects were tested using a simultaneous discrimination paradigm. The experimental protocol was adapted from previous experiments in cows (Rybarczyk et al. 2001; Coulon et al. 2007, 2009, 2010), sheep (Ferreira et al. 2004) and dogs (Pretterer et al. 2004). Each trial consisted of a choice between two stimuli, one of them (S+) being rewarded while the other (S−) was not. Prior to conducting the experiments (3–5 weeks), the dogs were trained using an operant positive conditioning method with a clicker followed by a food reward. The experimenter first taught them to sit and stay motionless on the "sitting area" (Fig. 3); then to move toward one of the stimuli after hearing a verbal order (namely "image") given by the experimenter; then to put the paw on the tablet in front of the stimulus chosen (Fig. 3c). The pair of stimuli used during this initial shaping was a bowl full of kibble (S+)

versus a uniformly black screen (S−). The position (left/right) of the picture with the bowl of kibble varied randomly from trial to trial. The criterion for passing this shaping period was that the dog without any assistance immediately returned to the "sitting area" and retook the sitting position after the order "place!/here!" was given by the experimenter behind him, sitting motionless before hearing the order "image!" given by the same experimenter, and then in a delay of less than 10 s gets up to put his paw in front of the chosen stimulus.

The experimenter wore dark glasses and stood motionless, arms by his sides, 1 m behind the dog. The experimenter gave the order "place" to the dog. The experimenter looked at his feet and changed the stimuli with a remote control. He then gave the order "image" in a neutral tone. The experimenter raised his eyes only when the dog ran toward a picture and made his response. Then, the experimenter activated the clicker if the dog's choice was correct and dropped a food reward behind him. After making an incorrect choice, the dog simply returned to the "sitting area" where he resumed his sitting position, facing the screens (Fig. 3). Thus, great care was taken to avoid visual, tactile, or acoustical cues that could inform the subject about the location of the rewarded stimulus. Before the experiment, the experimenter was trained to stay motionless by means of a video under observation by two other experimenters. The whole experiment was video recorded and then checked for possible cueing of the dogs.

All sessions were the same for the nine dog subjects. The criterion for a subject to pass from a given task to the following one was set at 10 correct trials out of 12, for two consecutive sessions. These thresholds were chosen to considerably decrease the probability of passing a session by chance. The probability of getting at least 10 successful trials out of 12 trials by chance, when the probability for one trial is 0.5, was $P = 0.019$. The probability of obtaining two consecutive successful sessions was $0.019^2 = 0.00037$. When the subject succeeded with a task, it was moved on to the next one.

The training and generalization tasks included discrimination tasks of increasing complexity (Table 1). Without this progressive complexity, the subjects lost their motivation for the experiments (personal observation in pilot studies). They laid in front of the screens showing distress (moaning, intention to leave the room, yawns, scrapings, e.g., Beerda et al. 1997).

One to four consecutive sessions of 12 trials were given in the morning, depending on the dog's motivation. There were at least 24 h between daily blocks of sessions. At the beginning of the test, a dog was taken from the kennel and led to the experiment room after a relaxing walk. The owner was not present in the experimental room unlike other studies using dogs (Range et al. 2007b; Racca et al. 2010; Nagasawa et al. 2011; Somppi et al. 2012); the attention of the dogs was considerably reduced in all preliminary tests when the owner was present, even if he or she was hidden from the dog's view.

Data analysis and statistical tests

For each trial, we recorded the success or the failure of the dog to choose S+. For each task, we recorded the number of sessions that each subject needed to reach the criterion. The number of sessions constituted the main variable. The data analysis was carried out using R 2.13.1 (R Development Core Team 2010).

Since the same dogs were tested repeatedly in different tasks, data were not independent, so we took into account the individual dog as a "random effect" in the analysis. The comparison of the number of sessions to reach the criterion between tasks for all subjects was analyzed by means of a generalized linear mixed model using lme4 package version 0.999375-35 for R (Bates and Maechler 2010). This model aimed at explaining the variation of the number of sessions that the dogs required for a given task. Using this model, it was possible to predict the expected mean value of the number of sessions for each task. Task 3 was chosen as a reference because it was the first task where the subject had to discriminate between two pictures of animals. Since the number of sessions to criterion was a count, we used a Poisson regression; since the observations were made on the same dogs, the effect of individual was taken into account as a random effect (Ogura 2011). In order to find the most relevant model for describing the average number of sessions required for a task, we used the minimal Akaike Information Criterion (AIC) method (Akaike 1973; Ogura 2011). The most relevant model was obtained for the Poisson regression model with dogs as random effect on the intercept and "tasks as a factor" for a fixed effect. The normality of the distribution of the residuals was assessed by graphic representation and the Shapiro test. We considered that a difference was significant when P value (P) was lower than 0.05.

In order to complete the analysis, using the same method with a generalized linear mixed model (Bates and Maechler 2010), with the dog as a "random-effect", and the task as a "fixed-effect", a comparison of the numbers of sessions with the same dogs was carried out for successive periods (A, B, C, D and E). The successive periods were defined as periods of monotonic increase or decrease periods in the number of sessions. This procedure establishes the best way to explain the task effect as a factor, or as an ordinal value, for each period. A significant task effect as ordinal value highlighted whether response tendencies are significantly increasing or decreasing.

Ethical note

The protocol (schedules and duration of the session blocks of our experiment) was approved by the Ethical Committee of VetAgro-Sup (Lyon, France) registered as number 1058, complying with French law.

Results

Task 0

All nine dogs met the criterion of success for Task 0 (a single pair: a bowl of kibble S+ vs. a black screen S−; Figs. 5, 6). Dogs needed from 6 to 29 sessions (Median = 11; Fig. 6) to complete the training Task 0.

Training tasks with "S+ = dog" (Task 1–3)

For the training tasks with "dog as S+", the nine dogs reached the criterion of success for all the tasks (Figs. 5, 6). Dogs needed 2–13 sessions in training Task 1 (a single pair: the dog D1, S+, vs. a black screen S−: Median = 5; Fig. 6), 2–3 sessions in training Task 2 (a single pair: the dog D1, S+, vs. a blue screen S−: Median = 2; Fig. 6) and 2–12 sessions in training Task 3 (a single pair: the dog D1, S+, vs. the cow C1, S−: Median = 3; Fig. 6).

The generalized linear mixed model showed that the number of sessions needed to reach criterion on Task 0 (a single pair: a bowl of kibble vs. a black screen) was significantly (P < 0.001) higher than for the reference Task 3 (a single pair: the dog D1 vs. the cow C1; Table 2; Fig. 6). In contrast, Task 2 (a single pair: the dog D1 vs. a blue screen) seemed less difficult (P ≈ 0.05) than Task 3 (Table 2; Fig. 6).

Generalization tasks with "S+ = dog" (Task 4–6)

For the generalization tasks with dog as S+, all nine dogs reached the criterion of success for all the tasks (Figs. 5, 6). Dogs needed 2–13 sessions in generalization Task 4 (12 dogs S+ vs. 12 cows S−: Median = 4; Fig. 6), 2–10 sessions in generalization Task 5 (12 dogs S+ vs. 6 cows + 6 other species, S−: Median = 6; Fig. 6) and 2–6 sessions

Fig. 5 Individual changes in the number of sessions to reach the criterion, according to the type of the task, arranged sequentially along increasing difficulty (11 tasks from 0 to 10), for each of the 9 subjects
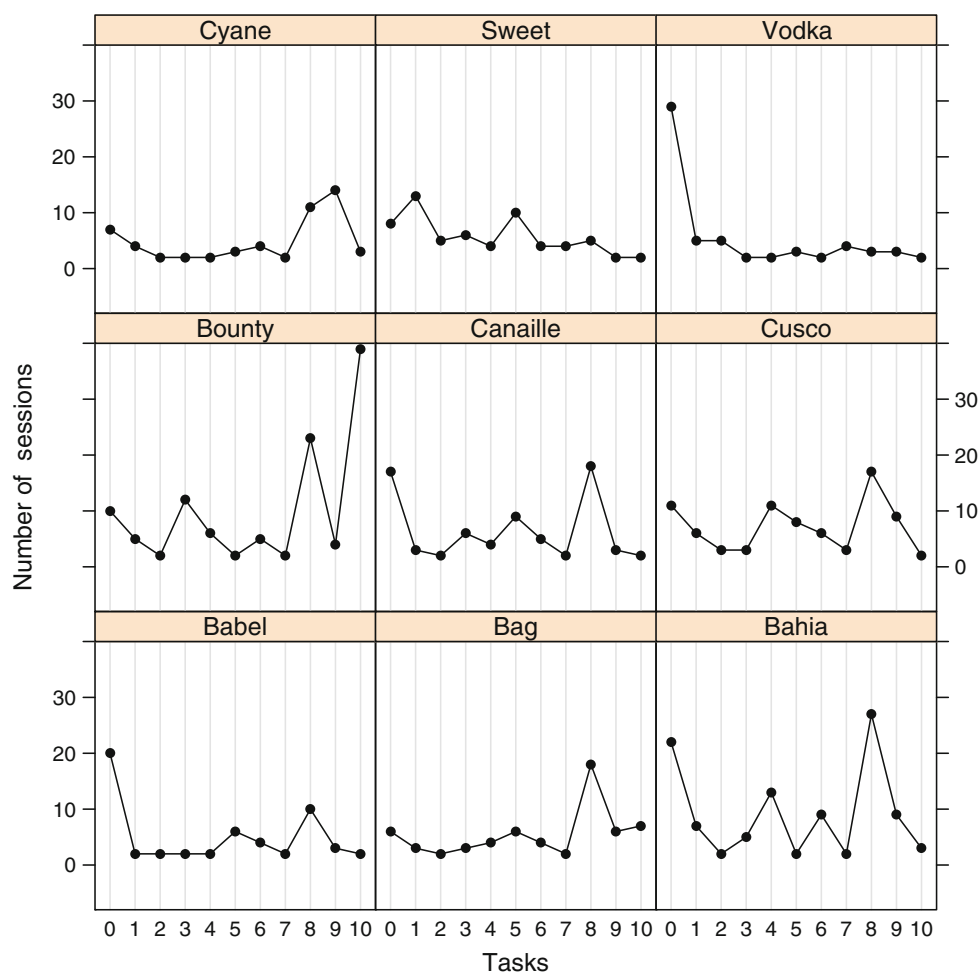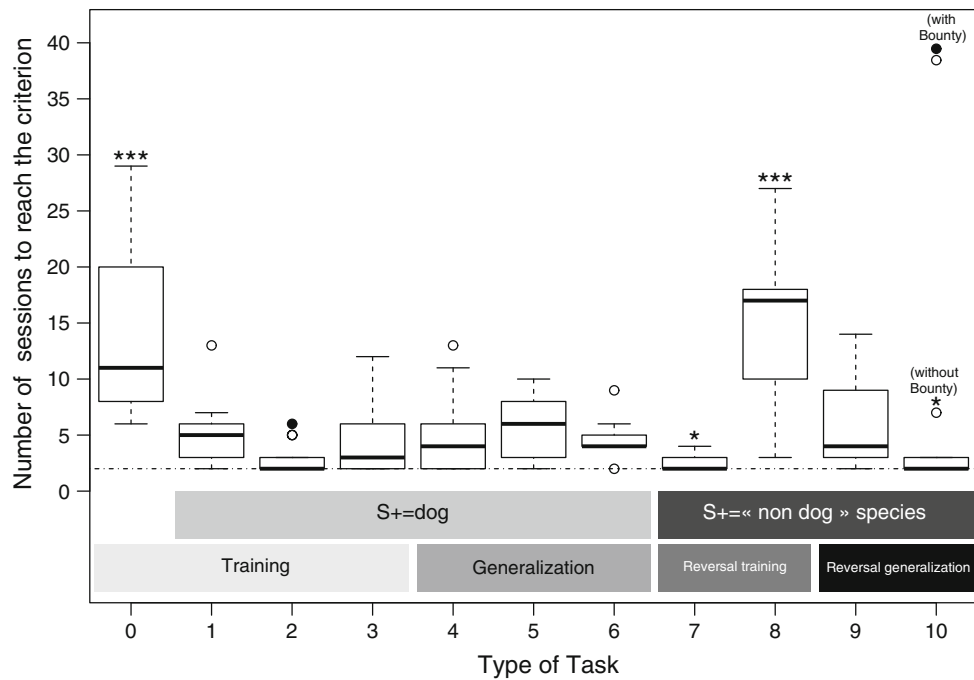
Fig. 6 Influence of the type of task on the overall performances of the dog subjects ($N = 9$). The 11 tasks are arranged sequentially, in a chronological order also corresponding to an increasing complexity. The variable is the number of sessions to reach the criterion. The box plots present the median (the *bold line within the box*), the bottom of the box represents the first quartile, the top of the box the third quartile, the *dotted lines* with horizontal segments figure the overall range of the variable (Minimum and Maximum). The different types of tasks are mentioned below *the box plots*. The *horizontal dotted line* indicates the minimum number of sessions to reach the criterion, that is, 2. Out values are represented by a small circle. The *P* value for the test related to Table 1 is represented with ***($P \leq 0.001$), **($0.001 < P \leq 0.01$), *($0.01 < P \leq 0.05$), (0.05 < P \leq 0.1$) and NS ($0.1 < P$); in task 10, results of *P* value are represented with and without the dog Bounty, cf. Table 2. For more information about the type of tasks, please see the text and Table 1

Table 2 Estimate of parameters

$Task_i$	Parameter	Estimate	Standard error	Expected value	P	Comments
–	α (Intercept)	1.490	0.173		<2e−16	***
0	β_0	1.150	0.179	14	1.21e−10	***
1	β_1	0.158	0.213	5.2	0.459	NS
2	β_2	-0.495	0.254	2.7	0.051	·
3	β_3	–	–	–	–	Reference task
4	β_4	0.158	0.213	5.2	0.459	NS
5	β_5	0.178	0.212	10.8	0.400	NS
6	β_6	0.048	0.226	4.6	0.827	NS
7	β_7	-0.578	0.261	2.5	0.027	*
8	β_8	1.169	0.124	14.3	6.33e−11	***
9	β_9	0.257	0.208	5.7	0.214	NS
10	β_{10}	0.413	0.201	6.7	0.040	*With bounty at task 10
		-0.454	0.261	2.82	0.082	·Without bounty at task 10

The *P* value for the test for comparison of the parameters estimate to 0 is represented with *** ($P \leq 0.001$), ** ($P \leq 0.01$), * ($P \leq 0.05$), · ($P \leq 0.1$) and NS ($0.1 < P$)

for generalization Task 6 (12 dogs S+ vs. 12 "non-dog" species S−: Median = 4; Fig. 6).

The generalized linear mixed model showed that the number of sessions needed for Tasks 4, 5 and 6 were not significantly different than for Task 3 (Table 2; Fig. 6).

Training tasks in reversal reward contingencies with "S+ = non-dog species" (Task 7–8)

For the training tasks, when the stimulus-reward contingency was reversed, the nine dogs met the success criterion

for all the tasks (Figs. 5, 6). Dogs needed 2–4 sessions in reversal training Task 7 (a single pair: the cow C2, S+ vs. a blue screen S−: Median = 2; Fig. 6) and 3–27 sessions in reversal training Task 8 (a single pair: the cow C2, S+ vs. the dog D2, S−: Median = 17; Fig. 6).

The generalized linear mixed model showed that the number of sessions needed for Task 8 (a single pair: the cow C2 vs. the dog D2) was significantly ($P < 0.001$) greater than that for Task 3 (a single pair: the cow C1 vs. the dog D1; Table 2). In contrast, the number of sessions needed for Task 7 (a single pair: the cow C2 vs. a blue screen) was significantly ($P < 0.05$) lower than for Task 3 (Table 2; Fig. 6).

Generalization tasks in reversal reward contingencies with "S+ = non-dog species" (Task 9–10)

For the generalization tasks in reversal reward contingencies, the nine dogs met the success criterion for all the tasks (Figs. 5, 6). Dogs needed 2–14 sessions in the reversal generalization Task 9 (12 cows S+ vs. 12 dogs S−: Median = 4; Fig. 6), and 2–3 sessions in the reversal generalization Task 10 (12 "non-dog" species S+ vs. 12 dogs S−: Median = 3; Fig. 6).

The generalized linear mixed model showed that the number of sessions needed for Task 9 was not significantly different from Task 3 (Table 2). With respect to Task 10, the results were different depending on whether the dog Bounty was taken into account or not. Bounty needed a considerable number of sessions to reach criterion on Task 10 (39 sessions). With Bounty included, median performance in Task 10 was significantly more difficult than in Task 3 ($P < 0.05$; Table 2; Fig. 6). Without Bounty's data, Task 10 was marginally less difficult than the reference Task 3 ($P < 0.1$; Table 2; Fig. 6).

The minimal AIC method was used to analyze the increasing and decreasing trends in the number of sessions needed by the subjects to succeed in the subsequent tasks (Fig. 6; Table 3). The models demonstrated that there were significant increases or decreases in the number of sessions according to the rank of the task ($P < 0.001$ except for period B ($P < 0.01$); Table 2). For decreasing periods,

tasks 0–2 (A), tasks 5–7 (C) and tasks 8–10 (E), the trend was a decrease in the number of sessions for each successive task. For increasing periods, tasks 2–5 (B) and tasks 7–8 (D), the trend was an increasing number of sessions for each successive task (Table 2; Fig. 6).

Progression across the tasks differed between individual dogs (Fig. 5). One dog (Vodka) presented an extreme pattern. This dog took more time for the learning Task 0 (with 29 sessions), but then, it succeeded rapidly with all of the following tasks, needing only 5 sessions for Tasks 1 and 2, and after that, no more than 3 sessions for each task. This dog needed fewer and fewer sessions to meet the criterion for the subsequent tasks. Ultimately, this dog was among those which needed the lowest number of generalization sessions (i.e., 12 sessions = 144 trials). On the contrary, Bounty needed increasing numbers of sessions to reach the criterion for the later tasks, with a peak at 39 sessions for the final generalization Task 10. Bounty was among those needing the greatest number of generalization sessions (i.e., 56 sessions = 672 trials).

Discussion

Our results explore the dog's ability to visually discriminate 2D pictures of the faces of various species depending on whether they represent dogs or not. Behavioral studies investigating the capacities of dogs to use visual cues for face identification are still relatively sparse compared with humans and other animals such as non-human primates, sheep and heifers (Leopold and Rhodes 2010). Compared to previous studies investigating such abilities in domestic dogs (Range et al. 2007b; Racca et al. 2010; Somppi et al. 2012), our study is the only one using as stimuli species other than dogs and humans, that is, domestic species (cats, cows, sheep, horses, etc.) and wild species (tigers, birds, rodents, etc.).

Moreover, in our study, the dogs were confronted by a large diversity of stimuli: for the images of dog faces, the four morphological types of dogs were used in balanced proportions, from the smallest such as Chihuahua (1 kg) to the largest such as mastiff (100 kg). Also images of

Table 3 Estimate of parameter with the standard error in brackets

Parameter	Period A			Period B				Period C			Period D		Period E[a]		
α	2.60 (0.133)***			0.775 (0.289)**				3.48 (0.686)***			−11.4 (1.79)***		8.77 (0.916)***		
β	−0.870 (0.102)***			0.196 (0.0715)**				−0.346 (0.118)***			−1.75 (0.227)***		−0.784 (0.105)***		
Task	0	1	2	2	3	4	5	5	6	7	7	8	8	9	10
Expected value	13.5	5.6	2.4	3.2	3.9	4.7	5.8	5.7	4.1	2.9	2.3	13.5	12.1	5.52	2.53

The P value for the test for comparison of the parameter estimate to 0 is represented with *** for $P < 0.001$ and ** for $0.001 < P < 0.01$

[a] Poisson regression done without "Bounty" dog

"non-dog" species included about forty different species in roughly equal proportions. As a result, our subjects were confronted by more than 144 pictures of morphologically different dogs versus others species (144 being the number of trials performed by the dog which was the fastest to complete the successive tasks), whereas the number of stimuli in "non-dog" category was less than 30 in previous studies (Racca et al. 2010, Somppi et al. 2012).

Thus, our study may suggest that dogs can form a visual category of "dog pattern", as assumed in rhesus macaques (Yoshikubo 1985). We may then hypothesize that there may exist some invariants in dog morphotypes that allow the nine subjects to group pictures of very different dogs into a single category despite the great diversity in canid species. The rapid generalization from a single training instance (a single pair: a dog picture versus a cow picture in Task 3) to multiple new instances in Task 4 goes against the "category size effect", which has been thoroughly explored in pigeons (cf. Soto and Wasserman 2010): in general, when animals are trained on category discriminations, generalization is quite poor when only a few instances are used in training, let alone only one. There is one well-known exception, where training pigeons to respond to a single oak leaf silhouette image led to instant generalization to all oak leaf silhouettes (Cerella 1979). Cerella interprets this unexpected result by saying that the oak leaf pattern is "transparent" to the pigeons, that is, they do not have to learn its extension. Could this hypothesis apply with the "dog pattern"? This might be possible in light of the performances in the first sessions of generalization (Task 4), and especially in the first trials of the first session of that task: the performances of the dogs were generally above chance for the majority of them.

But there might be another explanation for this very rapid generalization: the performance could be the consequence of (1) progressive training with the same picture of the dog D1 versus a black screen (Task 1), and then versus a blue screen (Task 2) and further a single cow C1 (Task 3); (2) the fact that the instances in Task 4 included only cows as S− (not other species) against dogs as S+. When in Task 5 a greater diversity appeared in the trials with other species than cows presented against dogs, the subjects had more trouble in reaching the criterion, although this difference was not significant. Dogs' morphology varies more than that of cows (Wayne and Ostrander 2007). In Task 4, the dogs may have developed a strategy "not to choose the cow picture" in order to choose the picture of a dog. But this strategy was no longer possible in Task 5 with various species (not only cows) pitted against various dogs. It may be that ultimately it was only in Task 5 that the subjects understood the "dog categorization" required by the experimenter. The "dog category" is an insight which has been especially explored in various species. For human babies, cats are treated as a kind of dog, but dogs are not treated as a kind of cat (Eimas et al. 1994; Quinn and Eimas 1996). Experiments conducted on humans and pigeons confronted by pictures of dogs and cats showed that pigeons and humans do not form categories using the same features (Ghosh et al. 2004; Goto et al. 2011). We assume that such differences may exist between dogs and humans, and further investigations are needed to support the idea and the nature of "a dog species pattern" in dogs as Cerella (1979) suggested with the oak leaf pattern for pigeons. According to the five levels of categorization of Herrnstein (1990), from simple discrimination based on perceptual cues to categorization based on complex concepts, we cannot conclude more than that dogs based on their categorization of dog faces on perceptual cues.

Another unusual feature of our study was the use of a reversal of the stimulus-reward contingency. This procedure has not often been used in category discrimination studies, particularly in dog studies. However, reversal learning in categorization studies can be used to strengthen the demonstration of categorization abilities. Spence's theory (1960) predicts that the more the initial discrimination is learned, the more difficult it will be to learn the reversed stimulus-reward contingency. This theory has been supported by numerous studies (e.g., in pigeons: Vaughan 1988; heifers: Coulon et al. 2007). In contrast, our dogs succeeded easily in the first reversal task (Task 7). This could be explained by the "overtraining reversal effect ORE" (Sperling 1965; Sweller 1973), where under some conditions, and contrary to Spence's theory, overtrained subjects (as our dogs could be considered by numerous successive training) acquire the reversal discrimination more easily than those trained only to criterion. On the other hand, the ORE effect may not be the only explanation of the small number of sessions required for the first reversal task. We may suppose, as observed in the individual performances in the first session of Task 7, dogs rapidly learned to choose the screen containing an image, not just a dog, versus a blue uniform screen. This explanation seems consistent with the peak in the following task 8 (a same single pair: the cow C2 as S+ versus the dog D2 as S−), showing the persistence of the initial habit as described by Spence (1960).

Each procedure that can be used to investigate categorization abilities has methodological advantages and disadvantages. With preferential looking procedures, some factors, such as attractiveness and interest in certain categories of stimuli which carry more informative value, can affect the preferences for a category (Buswell 1935; Faragó et al. 2010). This interest could be the result of the diversity within a category: for instance, as between photographs of dogs and those of humans, dogs could be attracted by the diversity of dog stimuli while human faces belonging to a

single human race (Caucasian) presented less diversity to them (Somppi et al. 2012). Category-dependent gazing behavior could indeed be a consequence of differences in the physical complexity of the stimuli. As a matter of fact, even though they used sophisticated eye tracking procedures, the authors conclude that they "cannot draw any conclusions as to whether the attention of dogs was directed mainly by stimulus features or semantic information, or both" (Somppi et al. 2012). This bias could also explain contrasting results in different studies using the same paradigm: Somppi et al.'s dogs fixated on a familiar image longer than on novel stimuli regardless of the category (dogs or humans), whereas it was not the case in the study of Racca et al. (2010). The use of an operant positive conditioning method has the advantage of allowing the subjects to make an unambiguous choice. To the best of our knowledge, our study is the first one using such a procedure to demonstrate species discrimination in dogs.

It remains true, however, that the conditioning procedure also has some disadvantages, because reinforced (or not) choices may affect the motivation of the dog, and ultimately the outcome of the trials. However, this motivation effect may influence the number of sessions needed to reach the criterion more than the final outcome of the trials. The repetition of tasks may lead to "learning set" formation (Harlow 1949). Learning set formation refers "to the learning of visual and other types of discrimination problems more quickly as a function of training on repeated series of such problems" (Schrier 1984). Due to the succession of the tasks, dogs had greater discrimination experience when it came to reversal Task 9 than in the equivalent Task 4.

Our results do not allow us to determine which dog morphotypes or which species were easier to discriminate by our dogs because 1) we used crossbreed dogs as stimuli, whose morphological types were not always well defined 2) the number and diversity of stimuli presented to the dogs was high and was not similar because they depended on the dog's facility to reach the criterion. In our study, the "Category size effect" (Soto and Wasserman 2010), instead of reducing the learning speed of our dog subjects, may in fact have facilitated their extraction of the "Common elements" (Soto and Wasserman 2010) in dog faces, despite the large phenotypic diversity. "Error-driven learning" (Soto and Wasserman 2010) may have played a role in the rapid generalization shown in the difficult reversal task. This "error-driven" learning is probably based on the analysis of the stimuli themselves rather than on a strategy based on choosing a side. In the latter case, this would have not led to the rapid improvement observed. Thus by considering the stimuli, the dogs may have learned to reverse their responses based on "error-driven" learning. This kind of learning, in relation to the "Common

elements" theory (Soto and Wasserman 2010), leads us to assume that our dog subjects only formed a "dog category" rather than a "dog category" and a "non-dog category". It is likely that having already formed a "dog category" based on a reward contingency in the generalization tasks, the subjects may have shifted their strategy in relation to the two stimuli, and in recognizing the "dog category", chose the "non-dog" stimuli based on the reward associated to it. While dog faces were likely categorized, the "non-dog" stimuli were only "identified" (Soto and Wasserman 2010). It is then likely that the reversal learning task has helped the dogs to strengthen their categorization of the dog species.

Whereas paradigms using spontaneous responses have to deal with subjects' motivation and attention, requiring a reduction in the duration of the session and likely the number of stimuli used, paradigms that use operant conditioning also have to deal with frustration. Failing to respond correctly leads to no reward. The effect of this frustration may have varied consequences depending on the subject's temperament (Svartberg and Forkman 2002). Differences in temperament and emotional stability may explain some differences in the dogs' performance. Another temperament trait, perseverance, might be useful in interpreting individual differences in performance. We have observed that often errors came in bouts, thus making the session unsuccessful (only 2 errors were accepted if the session was to reach the criterion for success). This trait could explain both the rapid success of some individuals (Babel, Bag, Cyane, Vodka) when they applied the right rule and stuck to it, and difficulties in reaching the criterion when perseveration was applied to errors, especially when dogs persistently stuck to their preferred side ("Laterality effect": Bahia, Bounty). Perseveration is likely an important temperament trait in dogs, as it has "doggedness" as a synonym. Another important aspect for interpreting dogs' differences in performances, and one which is quite specific to dogs, is their degree of obedience training. On the one hand, a very obedient dog may have initial difficulties in adapting to the experimenter and the new commands used in the procedures. This "smart obedient" dog will then become a "slow learner" (e.g., Vodka). On the other hand, a less obedient dog might have difficulties in adapting to the constraints of the experiment and fail to be attentive to the screens, and then be a "slow learner" throughout the experiments (e.g., Bahia). Another aspect that was mentioned by Morgan (1898) is the fact that an initially "slow learner" might become the "fastest learner" when the stimulus-reward contingency is reversed as he might be more flexible once he has understood a rule (such as Vodka). A perseverant dog might have difficulties in reversing the rule (such as Bounty).

Moreover, our study also shows that dogs are able to discriminate unfamiliar dog faces (and likely "non-dog" faces) in pictures from different viewpoints (front, profile, etc.). This capacity has already been shown in domestic species, in sheep (Kendrick et al. 2001a; Ferreira et al. 2004) and heifers (Coulon et al. 2007, 2009, 2010). As we were using a large variety of "non-dog" species, we had to reduce or increase the size of natural stimuli to adjust it to a standard surface. We did that in order to prevent the dogs making their discrimination on the size of the surface of colored pixels different from the uniform blue background. Although some authors suggested that still images as they may change the natural size of the stimuli reduce their informational content (Bovet 1999; Van der Velden et al. 2008), our dogs succeeded in spite of this drawback. This recalls the performances of pigeons which were not impaired when the size of stimuli was modified (Lombardi and Delius 1990).

In our study, we presented stimuli against a standardized background even though dogs seem able to discriminate a dog picture with heterogeneous background such as landscape (cf Range et al. 2007b). This ensured that our dog subjects' performances were based on elements found within the pictures, or the contour of them, rather than on features present in the background with no relation to the categories tested.

In conclusion, we have demonstrated that dogs are able to discriminate their own species in 2D pictures of faces alone, from different viewpoints, as shown previously in several other species (for a review Leopold and Rhodes 2010). The species discrimination demonstrated in our study might be considered as an "open class" categorization (Herrnstein 1990), as the dog faces presented covered the great variability in dog breed. This phenotypical diversity includes both contour and intrafigural features of dog faces. A natural further step would be to determine the salient features of dog faces, both common and stimulus specific elements (Soto and Wasserman 2010) on which the subjects relied to make their discrimination and their categorization. It might also be possible that the species "open class" categorization that we proposed might be of a higher level such as a conceptual one (Herrnstein 1990). This would be the case if dogs were also able to group in the same category familiar conspecifics and in other category non-familiar ones.

The fact that dogs are able to recognize their own species visually and that they have great olfactory discriminative capacities insures that social behavior and mating between highly morphologically different breeds is still potentially possible and therefore that, although humans have stretched *Canis familiaris* to its morphological limits, its biological entity has been preserved.

References

Adachi I, Kuwahata H, Fujita K (2007) Dogs recall their owner's face upon hearing the owner's voice. Anim Cogn 10(1):17–21

Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Second international symposium on information theory. Akademiai Kiado, Budapest, pp 267–281

Bates D, Maechler M (2010) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-35

Beerda B, Schilder MBH, van Hooff JARAM, de Vries HW (1997) Manifestations of chronic and acute stress in dogs. Appl Anim Behav Sci 52(3):307–319

Bovet D (1999) Capacités d'abstraction et de catégorisation: etude comparative chez le babouin et l'enfant. Dissertation. University of Aix-marseille, France

Brown SD, Dooling RJ (1992) Perception of conspecific faces by budgerigars (Melopsittacus undulatus) I. Natural faces. J Comp Psychol 106:203–216

Bruce C (1982) Face recognition by monkeys: absence of an inversion effect. Neuropsychology 20:515–521

Buswell GT (1935) How people look at pictures: a study of the psychology of perception in art. University of Chicago Press, Chicago

Campan R, Scapini F (2002) Ethologie: approche systémique du comportement. De Boeck Université, Bruxelles

Cerella J (1979) Visual classes and natural categories in the pigeon. J Exp Psychol Hum Percept Perform 5(1):68–77

Clutton-Brock J (1996) Origin of the dog: domestication and early history. In: Serpell J (ed) The domestic dog: its evolution, behaviour and interaction with people. Cambridge University Press, New York, pp 6–20

Coile DC, Pollitz CH, Smith JC (1989) Behavioral determination of critical flicker fusion in dogs. Physiol Behav 45(6):1087–1092

Coulon M, Deputte BL, Heyman Y, Delatouche L, Richard C, Baudoin C (2007) Visual discrimination by heifers (*Bos taurus*) of their own species. J Comp Psychol 121(2):198–204

Coulon M, Deputte BL, Heyman Y, Baudoin C (2009) Individual recognition in domestic cattle (*Bos taurus*): evidence from 2D-images of heads from different breeds. PLoS ONE 4(2):e4441

Coulon M, Baudoin C, Heyman Y, Deputte BL (2010) Cattle discriminate between familiar and unfamiliar conspecifics by using only head visual cues. Anim Cogn 14(2):279–290

Dahl CD, Wallraven C, Bülthoff HH, Logothetis NK (2009) Humans and macaques employ similar face-processing strategies. Curr Biol 19(6):509–513

Denis B (2007) Génétique et sélection chez le chien, vol 2ème édition. PMCAC et SCC, Paris

Dufour V, Pascalis O, Petit O (2006) Face processing limitation to own species in primates: a comparative study in brown capuchins, Tonkean macaques and humans. Behav Process 73:107–113

Eimas PD, Quinn PC, Cowan P (1994) Development of exclusivity in perceptually based categories of young infants. J Exp Child Psychol 58(3):418–431

Faragó T, Pongrácz P, Miklósi Á, Huber L, Virányi Z, Range F (2010) Dogs' expectation about signalers' body size by virtue of their growls. PLoS ONE 5(12):e15175

Farah MJ, Wilson KD, Drain M, Tanaka JN (1998) What is "special" about face perception? Psychol Rev 105(3):482–498

Ferreira G, Keller M, Saint-Dizier H, Perrin G, Lévy F (2004) Transfer between views of conspecific faces at different ages or in different orientations by sheep. Behav Process 67:491–499

Fujita K (1987) Species recognition by five macaques monkeys. Primates 28(3):353–366

Fujita K (1993) Development of visual preference for closely related species by infant and juvenile macaques with restricted social experience. Primates 34(2):141–150

Fujita K, Watanabe K (1995) Visual preference for closely related species by Sulawesi macaques. Am J Primatol 37(3):253–261

Gaunet F, Deputte B (2011) Functionally referential and intentional communication in the domestic dog: effects of spatial and social contexts. Anim Cogn 14(6):849–860

Gheusi G, Bluthé R-M, Goodall G, Dantzer R (1994) Social and individual recognition in rodents: methodological aspects and neurobiological bases. Behav Process 33(1–2):59–87

Ghosh N, Lea SEG, Noury M (2004) Transfer to intermediate forms following concept discrimination by pigeons: chimeras and morphs. J Exp Anal Behav 82(2):125–141

Goto K, Lea SEG, Wills AJ, Milton F (2011) Interpreting the effects of image manipulation on picture perception in pigeons (*Columba livia*) and humans (*Homo sapiens*). J Comp Psychol 125(1):48–60

Hare B, Tomasello M (1999) Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. J Comp Psychol 113:173–177

Harlow HF (1949) The formation of learning sets. Psychol Rev 56:51–65

Hattori Y, Kano F, Tomonaga M (2010) Differential sensitivity to conspecific and allospecific cues in chimpanzees and humans: a comparative eye-tracking study. Biol Lett 6:610–613

Hemmer H (1990) Domestication: the decline of environmental appreciation. Cambridge University Press, Cambridge

Herrnstein RJ (1990) Levels of stimulus control: a functional approach. Cogn 37(1–2):133–166

Jacobs GH, Deegan JF, Crognale MA, Fenwick JA (1993) Photopigments of dogs and foxes and their implications for canid vision. Vis Neurosci 10:173–180

Kanwisher N, Yovel G (2006) The fusiform face area: a cortical region specialized for the perception of faces. Phil Trans R Soc B 361:2109–2128

Kendrick KM, Atkins K, Hinton MR, Broad KD, Fabre-Nys C, Keverne B (1995) Facial and vocal discrimination in sheep. Anim Behav 49(6):1665–1676

Kendrick KM, Atkins K, Hinton MR, Heavens P, Keverne B (1996) Are faces special for sheep? Evidence from facial and object discrimination learning tests showing effects of inversion and social familiarity. Behav Process 38(1):19–35

Kendrick KM, Hinton MR, Atkins K, Haupt MA, Skinner JD (1998) Mothers determine sexual preferences. Nature 395:229–230

Kendrick KM, Leigh A, Peirce J (2001a) Behavioural and neural correlates of mental imagery in sheep using face recognition paradigms. Anim Welf 10:89–101

Kendrick KM, Haupt MA, Hinton MR, Broad KD, Skinner JD (2001b) Sex differences in the influence of mothers on the sociosexual preferences of their offspring. Hormon Behav 40(2):322–338

Kerswell KJ, Butler KL, Bennett P, Hemsworth PH (2010) The relationships between morphological features and social signalling behaviours in juvenile dogs: the effect of early experience with dogs of different morphotypes. Behav Process 85(1):1–7

Leopold DA, Rhodes G (2010) A comparative view of face perception. J Comp Psychol 124(3):233–251

Ligout S, Porter RH (2004) The role of visual cues in lambs' discrimination between individual agemates. Behaviour 141(5):617–632

Ligout S, Keller M, Porter RH (2004) The role of olfactory cues in the discrimination of agemates by lambs. Anim Behav 68:785–792

Lombardi CM, Delius JD (1990) Size invariance of pattern recognition in pigeons. Behavioral approaches to pattern recognition and concept formation. In: Commons ML, Herrnstein RJ, Kosslyn SM, Mumford DB (eds) Behavioral approaches to pattern recognition and concept formation. Quantitative analyses of behavior, vol 8. Lawrence Erlbaum Associates, Hillsdale, NJ, pp 41–65

Malpass RS, Kravitz J (1969) Recognition for faces of own and other race. J Personal Soc Psychol 13(4):330–334

Megnin P (1897) Le chien et ses races. Tome I: Histoire du chien depuis les temps les plus reculés, Origine des races et classification. Bibliothèque de l'Eleveur, Vincennes

Meissner CA, Brigham JC (2001) Thirty years of investigating the own-race bias in memory for faces: a meta-analytic review. Psychol Public Policy Law 7(1):3–35

Miklósi A (2007) Dog: behaviour, evolution, and cognition. Oxford University Press, Oxford

Miller PE (2008) Structure and function of the eye. In: Maggs DJ, Miller PE, Ofri R (eds) Slatter's fundamentals of veterinary opthalmology. Saunders Elsevier, St Louis, Missouri, pp 1–19

Morgan CL (1898) An introduction to comparative psychology. Walter Scott Ltd, London

Nagasawa M, Murai K, Mogi K, Kikusui T (2011) Dogs can discriminate human smiling faces from blank expressions. Anim Cogn 14(4):525–533

Neuhaus W, Regenfuss E (1967) Über die Sehschärfe des Haushundes bei verschiedenen Helligkeiten. Z Vgl Physiol 57(2):137–146

Ogura T (2011) Contrafreeloading and the value of control over visual stimuli in Japanese macaques (Macaca fuscata). Anim Cogn 14:427–431

Parr LA, Heintz M (2008) Discrimination of faces and houses by Rhesus monkeys: the role of stimulus expertise and rotation angle. Anim Cogn 11:467–474

Parr LA, Dove T, Hopkins WD (1998) Why faces may be special: evidence of the inversion effect in chimpanzees. J Cogn Neurosci 10:615–622

Pascalis O, Bachevalier J (1998) Face recognition in primates: a cross-species study. Behav Process 43:87–96

Pascalis O, de Haan M, Nelson CA (2002) Is face processing species-specific during the first year of life? Science 296:1321–1323

Peirce JW, Leigh AE, Kendrick KM (2000) Configurational coding, familiarity and the right hemisphere advantage for face recognition in sheep. Neuropsychol 38(4):475–483

Perrett DI, Mistlin AJ (1990) Perception of facial characteristics by monkeys. In: Stebbins WC, Berkley MA (eds) Comparative perception: complex signals, vol 2. Wiley, New York, pp 187–215

Perrett DI, Rolls ET, Caan W (1982) Visual neurones responsive to faces in the monkey temporal cortex. Exp Brain Res 47:329–342

Perrett DI, Mistlin AJ, Chitty A, Smith PAJ, Potter DD, Broennimann R, Harries M (1988) Specialized face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction time studies. Behav Process 29:245–258

Pinsk MA, Arcaro M, Weiner KS, Kalkus JF, Inati SJ, Gross CG, Kastner S (2009) Neural representations of faces and body parts in macaque and human cortex: a comparative fMRI study. J Neurophysiol 101(5):2581–2600

Porter RH (1987) Kin recognition: functions and mediating mechanisms. In: Crawford C, Smith M, Krebs D (eds) Sociobiology

and psychobiology: ideas, issues and applications. Lawrence Erlbaum Associates, Mahwah, NJ, pp 175–203

Porter RH, Nowak R, Orgeur P, Lévy F, Schaal B (1997) Twin/non-twin discrimination by lambs: an investigation of salient stimulus characteristics. Behaviour 134:463–475

Pretterer G, Bubna-Littitz H, Windischbauer G, Gabler C, Griebel U (2004) Brightness discrimination in the dog. J Vis 4:241–249

Quinn PC, Eimas PD (1996) Perceptual cues that permit categorical differentiation of animal species by infants. J Exp Child Psychol 63(1):189–211

R Development Core Team (2010) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Racca A, Amadei E, Ligout S, Guo K, Meints K, Mills D (2010) Discrimination of human and dog faces and inversion responses in domestic dogs (Canis familiaris). Anim Cogn 13(3):525–533

Range F, Viranyi Z, Huber L (2007a) Selective imitation in domestic dogs. Curr Biol 17:868–872

Range F, Aust U, Steurer M, Huber L (2007b) Visual categorization of natural stimuli by domestic dogs. Anim Cogn 11(2):339–347

Regodon S, Robina A, Franco A, Vivo JM, Lignereux Y (1991) Détermination radiologique et statistique des types morphologiques Crâniens chez le Chien: dolichocéphalic. Mésocéphalie et Brachycéphalie. Anat Histol Embryol 20(2):129–138

Rybarczyk P, Koba Y, Rushen J, Tanida H, de Passillé AM (2001) Can cows discriminate people by their faces? Appl Anim Behav Sci 74(3):175–189

Schrier AM (1984) Learning how to learn: the significance and current status of learning set formation. Primates 25(1):95–102

Sherman SM, Wilson JR (1975) Behavioral and morphological evidence for binocular competition in the postnatal development of the dog's visual system. J Comp Neurol 161(2):183–195

Somppi S, Törnqvist H, Hänninen L, Krause C, Vainio O (2012) Dogs do look at images: eye tracking in canine cognition research. Anim Cogn 15(2):163–174

Soto FA, Wasserman EA (2010) Error-driven learning in visual categorization and object recognition: a common-elements model. Psychol Rev 117:349–381

Spence KW (1960) Behavior theory and Learning. Prentice Hall, Englewood Cliffs, NJ

Sperling SE (1965) Reversal learning and resistance to extinction: a supplementary report. Psychol Bull 64(4):310–312

Svartberg K, Forkman B (2002) Personality traits in the domestic dog (Canis familiaris). Appl Anim Behav Sci 79(2):133–155

Sweller J (1973) The effect of task difficulty and criteria of learning on a subsequent reversal. Q J Exp Psychol 25(2):223–228

Tate AJ, Fischer H, Leigh AE, Kendrick KM (2006) Behavioural and neurophysiological evidence for face identity and face emotion processing in animals. Phil Trans R Soc B 361:2155–2172

Tibbetts EA (2002) Visual signals of individual identity in the wasp Polistes fuscatus. Proc R Soc Lond B 269:1423–1428

Tinbergen N (1953) Social behaviour in animals with special references to vertebrates. Methuen & Co. Ltd, London

Tsao DY, Freiwald WA, Tootell RBH, Livingstone MS (2006) A cortical region consisting entirely of face-selective cells. Science 311:670–674

Van der Velden J, Zheng Y, Patullo BW, Macmillan DL (2008) Crayfish recognize the faces of fight opponents. PLoS ONE 3(2):e1695

Vaughan W (1988) Formation of equivalence sets in pigeons. J Exp Psychol Anim Behav Process 14(1):36–42

Virányi Z, Topál J, Gácsi M, Miklósi Á, Csányi V (2004) Dogs respond appropriately to cues of humans' attentional focus. Behav Process 66(2):161–172

Virányi Z, Gácsi M, Kubinyi E, Topál J, Belényi B, Ujfalussy D, Miklósi Á (2008) Comprehension of human pointing gestures in young human-reared wolves (Canis lupus) and dogs (Canis familiaris). Anim Cogn 11(3):373–387

Wayne RK, Ostrander EA (2007) Lessons learned from the dog genome. Trends Genet 23(11):557–567

Yin RK (1969) Looking at upside-down faces. J Exp Psychol 81(1):141–145

Yoshikubo S (1985) Species discrimination and concept formation by rhesus monkeys (Macaca mulatta). Primates 26:285–299

Young SG, Hugenberg K, Bernstein MJ, Sacco DF (2009) Interracial contexts debilitate same-race face recognition. J Exp Soc Psychol 45(5):1123–1126