

Hierarchical stimulus processing by dogs (*Canis familiaris*)

Elisa Pitteri · Paolo Mongillo ·
Paolo Carnier · Lieta Marinelli

Received: 16 July 2013 / Revised: 22 November 2013 / Accepted: 2 December 2013 / Published online: 13 December 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract The purpose of this study was to assess the visual processing of global and local levels of hierarchical stimuli in domestic dogs. Fourteen dogs were trained to recognise a compound stimulus in a simultaneous conditioned discrimination procedure and were then tested for their local/global preference in a discrimination test. As a group, dogs showed a non-significant trend for global precedence, although large inter-individual variability was observed. Choices in the test were not affected by either dogs' sex or the type of stimulus used for training. However, the less time a dog took to complete the discrimination training phase, the higher the probability that it chose the global level of test stimulus. Moreover, dogs that showed a clear preference for the global level in the test were significantly less likely to show positional responses during discrimination training. These differences in the speed of acquisition and response patterns may reflect individual differences in the cognitive requirements during discrimination training. The individual variability in global/local precedence suggests that experience in using visual information may be more important than predisposition in determining global/local processing in dogs.

Keywords Dog · Global precedence · Hierarchical stimulus · Learning · Visual cognition

Elisa Pitteri and Paolo Mongillo have contributed equally to this work.

E. Pitteri · P. Mongillo · P. Carnier · L. Marinelli (✉)
Laboratory of Applied Ethology, Department of Comparative Biomedicine and Food Science, University of Padova,
Viale dell'Università 16, 35020 Legnaro, PD, Italy
e-mail: lieta.marinelli@unipd.it

Introduction

In most natural situations, the task of visual processing is to respond to a given input, but it is also that to select which parts of such an input are to be perceived, attended to and processed. Since Navon's first experiments (Navon 1977), a central issue in humans' visual perception has been hierarchical processing of wholes and their component parts. Evidence supporting the hypothesis that humans tend to process first the global form of hierarchical visual patterns has been reported in several studies (Kinchal and Wolf 1979; Lamb et al. 1990; Kmichi 1992, 1998; see also Wagemans et al. 2012, for a recent review on conceptual and theoretical foundations). This global precedence in processing images is viewed as a flexible, economical mechanism, probably emerging in humans during the evolution of visual cognition. Accordingly, other conditions being constant, non-human primates show a greater tendency to local precedence: this is evident in monkeys (Fagot and Deruelle 1997; Deruelle and Fagot 1998; Hopkins and Washburn 2002; Spinozzi et al. 2003; De Lillo et al. 2005; Spinozzi et al. 2006) more than in apes (Fagot and Tomonaga 1999; Hopkins and Washburn 2002). Comparative studies in other species have been conducted in pigeons (Fremouw et al. 1998, 2002; Cavoto and Cook 2001; Goto et al. 2004) and fishes (Truppa et al. 2010) although, to the best of our knowledge, the phenomenon has never been studied in mammals other than primates.

Within the same species, the relative efficacy of global and local processing can be modulated by varying the experimental procedure (i.e., duration of stimulus presentation, size of global form, size and density of local element, primed allocation of attention at one particular level). The effect of individual characteristics on global/local precedence is also well documented in humans.

Greater local than global bias has been reported in women (Roalf et al. 2006), children and adolescents (e.g. Sherf et al. 2009), the elderly (e.g. Lux et al. 2008) and people with neurological disorders. However, the role of individual characteristics on global/local precedence has not yet been studied in animals. Notably, the domestic dog has been proposed as a valuable animal model for Alzheimer's disease (Adams et al. 2000) and attention-deficit hyperactivity disorder (ADHD; Hejjas et al. 2007), two conditions affecting global precedence in humans (Slavin et al. 2002; Song and Hakoda 2012). In this respect, analysis of the relative readiness to process global/local aspects in healthy adult dogs is necessary for future studies in dogs affected by such disorders.

Given its history of domestication, the dog is a good candidate for comparative studies on visual cognition. A substantial body of literature shows that dogs can use visual information to engage communicative processes with humans (e.g. Hare et al. 2002; Miklósi 2007; Topál et al. 2009; Horn et al. 2012; Buttelmann and Tomasello 2013). In this context, analysis of visual signals must prevail over other sensory modalities, since olfactory communication is limited in humans and human auditory signals are mainly semantic and need specific learning by dogs. The sophisticated inter-specific social skills of dogs are thought to be a case of convergent evolution with humans (see Miklósi and Topál 2013, for a recent review). If this is so, a global advantage in processing visual information may have emerged in dogs.

To date, our knowledge about canine vision mainly concerns dogs' ability to detect light, colours and motion (Miller and Murphy 1995; Murphy et al. 1997; Pretterer et al. 2004); very little is known about their higher-order processing of visual information. Most data on visual cognition in dogs come from behavioural experiments on two-dimensional images. Although little is known about dogs' ability to perceive elementary shapes (Miller and Murphy 1995), there is an increasing number of studies on their use/inspection of two-dimensional images representing social stimuli, in particular faces. Dogs extract important features from such images, since they can associate visual and auditory information (i.e., the picture and the voice of their owner; Adachi et al. 2007), differentiate individual facial cues of dogs and humans (Racca et al. 2010; Huber et al. 2013), identify various emotional states of the same person (Nagasawa et al. 2011) and use life-sized images of pointing humans to solve simple communication tasks (Pongrácz et al. 2003). More impressively, Range et al. (2008) trained dogs to classify natural visual stimuli (dog/landscape pictures) according to a perceptual response rule. The spontaneous two-dimensional image discrimination ability of dogs has been tested with a novelty preference paradigm (Racca et al. 2010) and contact-

Table 1 Characteristics of dogs and S+ assigned to each dog

Name	Sex	Age (years)	Breed	Size (cm)	S+
Amy	F	2	Golden retriever	55	X
Kim	F	3	Crossbreed	60	O
Lana	F	2	Crossbreed	56	X
Molly	F	3	Crossbreed	42	X
Stasi	F	6	Crossbreed	40	O
Unca	F	2	German Shepherd	55	O
Spigola	F	8	Crossbreed	40	O
Ares	M	2	Crossbreed	62	X
Charlie	M	6	West Highland White Terrier	38	O
Cuzco	M	3	Border Collie	60	X
Kobe	M	7	Beagle	41	O
Oliver	M	5	Crossbreed	45	X
Rey	M	6	Border Collie	57	X
Rino	M	7	Cocker spaniel	43	O

F female, M male; size is expressed as height at the withers; X S+ presented in Fig. 2a, O S+ presented in Fig. 2b

free eye movement tracking (Somppi et al. 2012). Dogs inspect images by focusing on the informative regions of a figure (Somppi et al. 2012), and their gaze behaviour vary according to the type of image (Guo et al. 2009; Racca et al. 2010, 2012; Somppi et al. 2012). It has also recently been observed that reducing the informational richness of visual stimuli decreases dogs' discriminative ability when they are presented with pictures of human heads (Huber et al. 2013). Interestingly, in that study, only 20 % of the dogs were able to discriminate between a picture of their owner and that of another familiar person, when the internal parts of the face were presented instead of the full head. The above authors argued either that dogs use global features to discriminate human faces or that they receive little help from internal facial features. Overall, these findings indicate that parts of an image or their position may be important factors in dogs' spontaneous allocation of visual-spatial attention and visual discriminative ability. Although other mechanisms may be involved, the spontaneous allocation of attention to a particular level of a stimulus seems to be a key factor in explaining differences in global/local processing (De Lillo et al. 2011).

The purpose of the present study was to assess the visual processing of global and local dimensions of hierarchical stimuli in domestic dogs. In the absence of previous studies on dogs, our experimental procedure was adapted from that of studies on other non-human animals. Since comparative studies typically use stimuli with global shapes formed by the spatial arrangement of small local shapes, similar Navon-type stimuli were used in our experiments. We first trained dogs to discriminate a compound stimulus



Fig. 1 Video stills: **a** front part of apparatus during presentation of two stimuli in discrimination phase; dog is gently restrained by operator in starting position; **b** back of apparatus during inter-trial interval, with operator preparing stimuli for next trial

characterised by a clear-cut two-level hierarchy and then tested them for their local/global preference in a visual discrimination test. As a further control on dogs' ability to extract information from local shapes, in the last phase of the procedure, the dogs were retrained to discriminate between two stimuli differing only at local level.

Materials and method

Subjects

Dogs' characteristics that are known to affect global/local precedence in humans (i.e., age, sex and health status) were

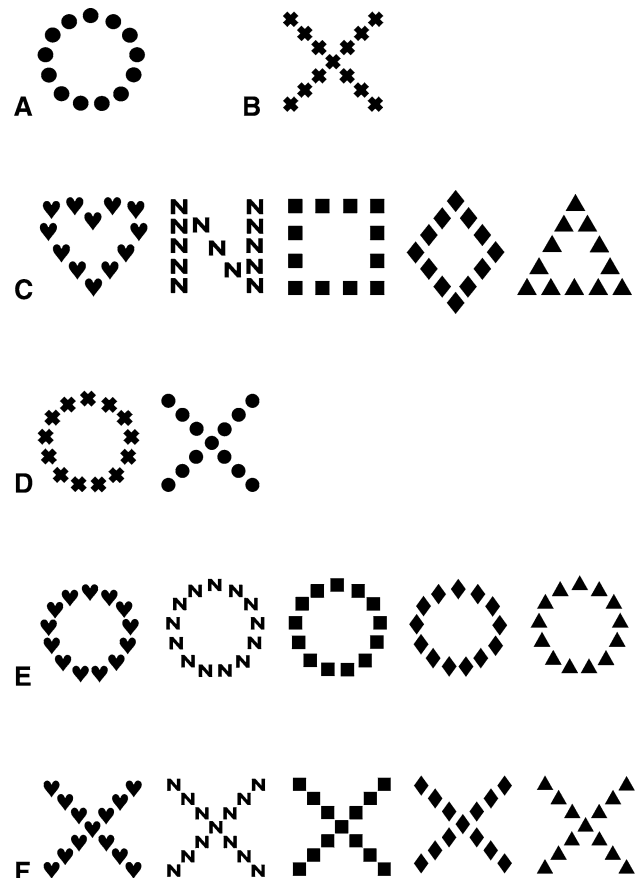


Fig. 2 Representations of stimuli used in various training and test phases. **a** or **b** = S+ used throughout study; **c** = set of S− used in consistent training; **d** = stimuli used in test trials; **e** = set of S− used in local training for dogs trained with **a**; **F** = set of S− used in local training for dogs trained with **b**

carefully checked for the present study. The sample was composed of 14 adult family dogs 4.4 ± 2.2 years old and balanced for gender; Table 1 lists their characteristics. All dogs were recruited from University of Padova students and employees, who took part in this study on a voluntary basis. Prior to inclusion, the dogs underwent physical and behavioural veterinary examinations, to exclude overt medical conditions that might have influenced the study.

Experimental setting

The test apparatus (Fig. 1) consisted of a rectangular wooden panel (140×150 cm) with two symmetrical vertical metallic tracks mounted on it at 14 cm from the side edges. Rectangular frames (35×23 cm) made of two overlapping transparent acrylic panels and containing the visual stimuli were made to slide along the tracks. To allow the dogs to see and touch the stimuli properly, the height of presentation was adjusted for each animal, so that the centre of the stimulus was level with the dog's eyes.

A dog mattress was placed at a distance of 130 cm from the apparatus, a chair for the experimenter was placed beside the mattress, and a plastic bowl, used as a reward zone, was placed 100 cm behind the mattress.

The experimental stimuli were two-dimensional hierarchical compound images (Fig. 2), composed of 13 identical figures (local elements), spatially arranged to form one larger figure (global element). The density of local shapes within a stimulus was similar to that used for primates (Fagot and Tomonaga 1999; Spinozzi et al. 2003). The size of the shapes was established according to current knowledge of canine visual acuity (Miller and Murphy 1995; Murphy et al. 1997). Depending on the experimental phase (see below), the stimuli could be either consistent (Fig. 2a–c) or inconsistent (Fig. 2d–f) between their global and local elements. The stimuli were printed in black ink on white A4 sheets of paper, the total black area being identical across all stimuli (87.50 cm²). Stimuli were created with Adobe® Illustrator® CS4 (14.0.0, © Adobe Systems Inc. 1987–2008).

Experimental procedure

The experiment consisted of a pre-training phase, a consistent training phase, the test and a local training phase. The dogs underwent sessions of 20 (pre-training and training phases) or 25 (test) trials for a maximum of four sessions per day with inter-session intervals of at least 30 min. On average, the dogs were involved in the experiment for 4.2 ± 0.9 days a week.

One operator sat behind the apparatus, unseen by the dog, and controlled the presentation of the stimuli. The experimenter sat on the chair and handled the dog. At the beginning of each trial, the dog was told to sit on the mattress and was gently restrained by its collar by the experimenter. When the dog was sitting and visually oriented towards the apparatus, the experimenter said “Ok!” and the two stimuli were presented. To avoid any unintentional influence on the dog’s choice, the experimenter closed his eyes, waited for 3 s, and then told the dog to “Go!” and released it. If the dog approached and touched the positive stimulus (S+), the experimenter actuated a click and rewarded the dog, while the stimuli were removed. If the dog touched the negative (S–) stimulus (or the empty frame in the pre-training phase), the experimenter said “Up!” and the stimuli were removed, and the dog was called back to the starting position for the next trial. If the dog did not approach the stimuli within 60 s, or moved away from the apparatus, the stimuli were removed, the dog was called back to the starting position (if it had moved), and the trial was repeated.

The learning criterion to complete one phase successfully and proceed to the next one was set at 85 % correct

choices in three consecutive sessions (i.e., 51 correct trials out of the last 60).

In each training session, the side of presentation of S+ was semi-randomised, with the constraint that it could not be presented on the same side for more than three consecutive trials and that right/left presentations were balanced within the session.

Pre-training

The dogs were first conditioned to approach and touch with the snout a single stimulus which was leaning on a wall after hearing the “Go!” signal. One out of two possible positive stimuli was chosen (Fig. 2a, b; Table 1). The literature shows that global or local information bias can be altered by varying the features of the stimulus, such as the spatial arrangement pattern of its elements (e.g. Kmichi 1992). To reduce the possibility of biased results due to the particular aspect of a given pattern, two positive stimuli were used, with very distinctive distribution of local elements around the centre of the image, i.e., a cross and a circle. Once the dogs had learnt to touch the stimulus reliably and without hesitation when the “Go!” signal was given, standardised sessions of 20 trials were begun, as described in the general procedure. Only S+ was presented in these trials; the frame on the opposite side was empty. When the dogs had achieved the learning criterion, they were admitted to the next phase.

Consistent training

The dogs were trained to recognise a consistent stimulus (S+) in a simultaneous conditioned discrimination procedure. Sessions involved 20 trials, during which the consistent S+ and one of the five consistent S– were presented, as described above. For any given dog, the S+ was the same as that used in the pre-training phase; the set of S– was the same for all dogs (Fig. 2c), and each S– of the set was presented four times within the session. Upon reaching the learning criterion, the dogs moved on to the next phase.

Test

The dogs underwent sessions of 25 trials each, 20 of which were identical to those described in the consistent training phase. They had to maintain the 85 % correct responses criterion in these trials; otherwise, they had to repeat the previous training phase. The remaining five trials were tests, presented once every five trials, starting from trial nine. In the test trials, the dogs were presented with two inconsistent test stimuli (Fig. 2d), of which one (G) showed the same global element as S+ and local elements never

seen before. Conversely, the other stimulus (L) was composed of the same local elements as S+, forming a global element never seen before. The dogs were always rewarded in the test trials, regardless of their choice. Four test sessions were performed, for a total of 20 trials. Right/left presentations of G and L were balanced within session.

Local training

This phase was performed after the test phase, to ascertain that the dogs were able to use the local elements of the compound forms to discriminate between stimuli and ensuring that their choices in the test trials were not affected by any inability to perceive the local elements.

The procedure was identical to that of the consistent training phase, with the exception that S− (Fig. 2e or f) differed from S+ only at local level.

Data collection and statistical analysis

All experimental phases were video-recorded by CCTV (WV-GP250, Panasonic, Osaka, Japan) for subsequent data collection.

Data on the duration of sessions and response latency (time between the dog's release and its choice of stimulus) were extracted from videos with The Observer^{®XT} software (Noldus Information Technology, the Netherlands). In each training session, mean latency was calculated as the mean of data of trials 1, 10 and 20, and the number of S+, S− and left and right choices was collected. For the test phase, mean latency was measured as the mean of all 20 test trials, and the side and type (G or L) of the test stimulus chosen in each trial were recorded.

To assess whether the use of different positive stimuli affected the speed of learning in the consistent training, an independent-samples Student's *t* test was used to compare the number of sessions needed to reach the learning criterion between the two groups of dogs that used different positive stimuli.

To assess whether an overall prevalence for G or L was present in our sample, we performed a right-tailed Student's *t* test on the dogs means for the type of choice (0 = L, 1 = G) expressed in the 20 test trials, testing the null hypothesis H0 that the mean was equal to or lower than 0.5. Also, we computed the probability that the true mean for the type of choice was in the range between 0.501 and +∞. A binary logistic regression model (Allison 2001) was then used to analyse whether the logit of choices for G in the test phase was significantly affected by factors such as dogs' sex, side of presentation of G, type of S+ used and speed of learning in consistent training. The dependent variable was a dichotomous categorical variable (1 = choice of G; 0 = choice of L); explanatory variables

were dogs' sex (female/male), side of presentation of G in each test trial (left/right), type of S+ used (X/O) and number of sessions required to reach the learning criterion in the training phase. The dog's identification number was added to the model as a random effect.

All statistical analyses were performed with Statistical Analysis System software (SAS Institute Inc. SAS/STAT[®] 9.2 User's Guide, Cary, NC: SAS Institute Inc., 2008). Statistical significance was set at 5 % for all tests.

Results

Sessions lasted on average 7.6 ± 2.4 min in the training phases and 8.4 ± 1.9 min in the test phase.

The dogs showed a great degree of variability in the speed of acquisition of the task in the consistent training phase. The number of sessions needed to reach the learning criterion in this phase ranged from 5 to 36, average 16.7 ± 10.4 . No difference was detected in the number of sessions needed to reach the learning criterion between the two groups of dogs that used different S+ ($t_{12} = -0.977$, $P = 0.348$). The average response latency in the trials of this phase was 4.0 ± 2.8 s.

In the test phase, all the dogs maintained the learning criterion of 85 % correct responses. The average response latency of test trials was 9.9 ± 22.2 s. As a group, dogs chose the G test stimulus 164 times versus 116 choices for the L test stimulus; a right-tailed *t*-test could not reject, at a level of significance $P < 0.05$, the null hypothesis that the mean of choices expressed by dogs in the 20 test trials was less than or equal to 0.5 ($t_{13} = 1.25$, $P = 0.11$). The probability that the true mean for the type of choice was greater than 0.5 was 81 %, suggesting that a tendency towards a global precedence may exist. The binary logistic regression model indicated that choices in the test phase were not affected by dogs' sex, side of presentation of G or type of S+ used for consistent training. A significant effect was detected for the speed of acquisition of the consistent training; specifically, a lower number of sessions to reach the learning criterion were associated with a higher probability of choosing G in the test trials (Table 2).

Considered individually, six dogs chose G significantly above chance level (i.e., 15 or more global choices, two-tailed $P < 0.05$, binomial test), four chose L significantly above chance (15 or more local choices), and the remaining four did not show any significant preference. Accordingly, they were classified as 'global', 'local' or 'uncertain' dogs, respectively. A binary logistic model was then used to examine whether global, local and uncertain dogs had used a positional response modality in the training phase. The dependent variable of the model was a dichotomous categorical variable which identified each consistent training

Table 2 Results of the binary logistic regression model showing the effect of dogs' sex, side of presentation of G, type of S+ used and number of sessions to reach the criterion in the consistent training on G choices in test trials

Effect	Levels	G choices (mean \pm SD)	OR	90 % CI	P
Sex	Male	12.7 \pm 5.2	0.606	0.178–2.067	0.501
	Female	10.7 \pm 5.9			
Side of G presentation	Right	5.8 \pm 3.0	0.927	0.588–1.461	0.783
	Left	5.9 \pm 3.3			
Type of S+	O	11.7 \pm 4.6	0.580	0.169–1.995	0.468
	X	11.7 \pm 6.7			
Number of sessions to criterion	None (continuous predictor)		0.924	0.876–0.976	0.017

G test stimulus featuring the same global element as S+, OR odds ratio, CI confidence interval, X S+ presented in Fig. 2a, O S+ presented in Fig. 2b

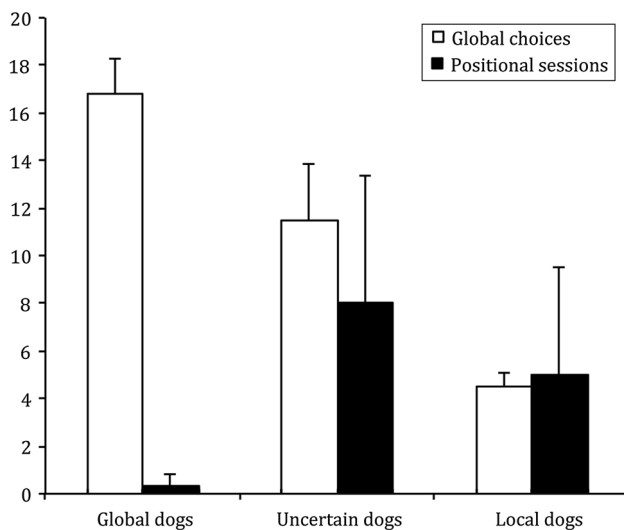


Fig. 3 Mean number (\pm SD) of global choices in test and positional sessions (15 or more same-side responses during 20 trials) in consistent training performed by dogs which showed 15 or more global choices in test trials (global dogs), 15 or more local choices in test trials (local dogs) or fewer than 15 global or local choices (uncertain dogs)

session as positional (i.e., the dog showed 15 or more same-side responses in the 20 trials) or non-positional. The predictor was the dog's classification based on test choices (global, local and uncertain).

The analysis revealed the significant effect of the predictor in the dogs' likelihood of showing positional sessions in consistent training ($F_{2,234} = 9.25$, $P < 0.001$). Specifically, global dogs were less likely to show positional sessions than both uncertain dogs (odds ratio 9.12, 95 % confidence interval 2.0–42.7) and local dogs (odds ratio 20.4, 95 % confidence interval 4.5–91.5) (Fig. 3).

Lastly, all dogs reached the learning criterion in local training (average 5.7 ± 3.0 sessions), demonstrating that choices in the test phase were not influenced by their incapacity to perceive or discriminate stimuli that differed

only at local level. Response latency in this phase was on average 3.7 ± 2.7 s.

Discussion

We studied global or local precedence in processing hierarchical visual stimuli in dogs. The dogs were initially trained in a simultaneous conditioned discrimination procedure to recognise a stimulus made of several local elements arranged to form a larger global figure. In a subsequent test, they showed inter-individual variability in responses, although a non-significant trend to prefer the stimulus containing the reinforced global element emerged. All the animals could then easily rely on local elements, when required to do so in local discrimination training, indicating that the results of the global/local test were not due to their inability to perceive local elements.

In this study, we found no effect of type of training stimulus on the likelihood that our subjects would choose the global or local stimulus in the test phase. In a similar study, Truppa et al. (2010) found no evidence that stimuli like those we used had an effect on global/local precedence in redtail splitfin fish (*Xenotoca eiseni*).

We found no evidence of an effect of sex on the likelihood of choosing the global or local level of a learnt stimulus. To the best of our knowledge, the effect of sex on global/local precedence has not been investigated in non-human animals, and even in humans, there are few direct examinations of gender differences (Roalf et al. 2006; Müller-Oehring et al. 2007; Kimchi et al. 2009). Although it is suggested that gender differences may arise depending on the nature of the task and its visual context, Kimchi et al. (2009) showed that, generally, men and women do not differ in global and local processing. Our results indicate that this may also be the case in dogs.

Despite a trend towards a general global advantage in processing hierarchical visual stimuli, our results were

characterised by wide inter-individual variability. It is difficult to examine this finding from a comparative standpoint, since individual variability in global/local processing is seldom discussed in non-human animals. However, limits to inter-specific comparisons may also derive from substantial procedural differences. Primate and pigeon studies often rely on visual matching to sample (MTS) tasks. We initially tried to use such a procedure with dogs, but found various difficulties in training them on MTS, an obstacle also reported by others (e.g. Milgram et al. 1994). We therefore opted for a procedure similar to that used on redbait splitfin fish by Truppa et al. (2010), which relies on the initial discrimination learning of a given probe stimulus and subsequent presentation of test stimuli. One implication of this procedure is that the dogs' choices in the test were the result of previous learning and perception, rather than of a purely perceptual process. However, this allows us to formulate hypotheses on the neuropsychological mechanisms associated with acquiring global/local information and may help to explain the variability we observed.

The variability in our results was not limited to global/local choices in the test, but also characterised the speed of acquisition of the initial discrimination training. Slower learners were also more likely to show persistent responses to the same presentation side within a given session. One explanation is that some dogs quickly learnt to execute a motor response upon presentation of a stimulus, as described by Guthrie and Horton (1946) in cats, and were more resilient in abandoning such ineffective responses. However, it is hard to explain how an ineffective motor response *per se* could lead to a different precedence in processing hierarchical visual stimuli. The variable performance in discrimination training may thus reflect individual differences in the cognitive requirements of the task. Hoar and Linnell (2013) showed that in humans, increasing the cognitive load of a global/local task results in disruption or inversion of the global advantage. Moreover, the recruitment of different attentional processes has been indicated as one of the main determinants of global/local bias (Deruelle and Fagot 1998), and individual differences in attentional control can predict the speed of learning even in simple visual discrimination tasks (Schmittmann et al. 2012). In the present study, non-global dogs were more resilient towards inhibiting motor responses, but eventually had to attend to task-relevant visual information about the stimuli in order to obtain food rewards. Therefore, completing the task may have imposed a higher attentional demand on some of the dogs, which in turn led to the absence of global advantage in the test. Notably, a relationship between individual differences in subjective cognitive demand and the likelihood of using a positional response modality in a visual discrimination task has been

reported in both laboratory (Milgram et al. 1994) and pet dogs (Huber et al. 2013). Lastly, we have previously shown that a slight reduction in the attention paid by a dog to a human partner, stemming from the impossibility of perceiving details about the person's head, resulted in the dogs being unable to acquire or use information about that person's movements (Mongillo et al. 2010), further supporting the role of attention in processing global/local information in dogs.

Our results also warrant an ecological consideration. It is often claimed that dogs are visual generalists, i.e., they lack specialisation for particular visual niches, reflecting the ability of the species to exploit its sight in a variety of conditions (Pretterer et al. 2004). The response patterns shown by our dogs in discrimination training and the associated variability in the test suggest that experience in using visual information may be more important than predisposition in determining global/local processing, although this would also allow better adaptability to varying environmental conditions.

In conclusion, the present study suggests that dogs may show a tendency for global advantage when looking at hierarchical visual stimuli. However, the large variability observed indicates the relevance of factors acting at individual level on the phenomenon. Among such factors, we are currently investigating the role of attention in the processing of hierarchical images by dogs. Beyond its importance for our understanding of canine visual cognition, the importance of this topic extends to the veterinary and human medical fields. Specifically, the recent description of a canine equivalent of human ADHD and interest in dogs as models for this disorder prompts studies aimed at better characterisation of deficits in attention and related processes in dogs.

Acknowledgments We are very grateful to Francesco Valentini for assistance with experiments. Dr. Elisa Pitteri received a Ph.D. Grant from the University of Padova, Italy.

References

- Adachi I, Kuwahata H, Fujita K (2007) Dogs recall their owner's face upon hearing the owner's voice. *Anim Cogn* 10:17–21. doi:10.1007/s10071-006-0025-8
- Adams B, Chan A, Callahan H, Milgram NW (2000) The canine as a model of human cognitive ageing: recent developments. *Prog Neuro-Psychopharmacol* 24:675–692. doi:10.1016/S0278-5846(00)00101-9
- Allison PD (2001) Logistic regression using SAS system: theory and application. Wiley-SAS, WA
- Buttelmann D, Tomasello M (2013) Can domestic dogs (*Canis familiaris*) use referential emotional expressions to locate hidden food? *Anim Cogn* 16:137–145. doi:10.1007/s10071-012-0560-4
- Cavoto KK, Cook RG (2001) Cognitive precedence for local information in hierarchical stimulus processing by pigeons.

- J Exp Psychol Anim Behav Process 27:3–16. doi:[10.1037/0097-7403.27.1.3](https://doi.org/10.1037/0097-7403.27.1.3)
- De Lillo C, Spinuzzi G, Truppa V, Naylor DM (2005) A Comparative analysis of global and local processing of hierarchical visual stimuli in young children (*Homo sapiens*) and monkeys (*Cebus apella*). J Comp Psychol 119:155–165. doi:[10.1037/0735-7036.119.2.155](https://doi.org/10.1037/0735-7036.119.2.155)
- De Lillo C, Spinuzzi G, Palumbo M, Giustino G (2011) Attention allocation modulates the processing of hierarchical visual patterns: a comparative analysis of capuchin monkeys (*Cebus apella*) and humans. J Exp Psychol Anim Behav Process 37:341–352. doi:[10.1037/a0022989](https://doi.org/10.1037/a0022989)
- Deruelle C, Fagot J (1998) Visual search for global/local stimulus features in humans and baboons. Psychon Bull Rev 5:476–481
- Fagot J, Deruelle C (1997) Processing of global and local visual information and hemispheric specialization in humans (*Homo sapiens*) and baboons (*Papio papio*). J Exp Psychol Hum Percept Perform 23:429–442
- Fagot J, Tomonaga M (1999) Global and local processing in humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*): use of a visual search task with compound stimuli. J Comp Psychol 113:3–12
- Fremouw T, Herbranson WT, Shimp CP (1998) Priming of attention to local or global levels of visual analysis. J Exp Psychol Anim Behav Process 24:278–290
- Fremouw T, Herbranson WT, Shimp CP (2002) Dynamic shift of pigeon local/global attention. Anim Cogn 5:233–243
- Goto K, Wills AJ, Lea SEG (2004) Global-feature classification can be acquired more rapidly than local-feature classification in both humans and pigeons. Anim Cogn 7:109–113. doi:[10.1007/s10071-003-0193-8](https://doi.org/10.1007/s10071-003-0193-8)
- Guo K, Meints K, Hall C, Hall S, Mills D (2009) Left gaze bias in humans, rhesus monkeys and domestic dogs. Anim Cogn 12:409–418. doi:[10.1007/s10071-008-0199-3](https://doi.org/10.1007/s10071-008-0199-3)
- Guthrie ER, Horton GP (1946) Cats in a puzzle box. Rinehart & Company, New York
- Hare B, Brown M, Williamson C, Tomasello M (2002) The domestication of social cognition in dogs. Science 298:1634–1636. doi:[10.1126/science.1072702](https://doi.org/10.1126/science.1072702)
- Hejjas K, Vas J, Kubinyi E, Sasvari-Szekely M, Miklósi Á, Ronai Z (2007) Novel repeat polymorphisms of the dopaminergic neurotransmitter genes among dogs and wolves. Mamm Genome 18:871–879. doi:[10.1007/s00335-007-9070-0](https://doi.org/10.1007/s00335-007-9070-0)
- Hoar S, Linnell KJ (2013) Cognitive load eliminates the global perceptual bias for unlimited exposure durations. Atten Percept Psychophys 75:210–215. doi:[10.3758/s13414-012-0421-x](https://doi.org/10.3758/s13414-012-0421-x)
- Hopkins WD, Washburn DA (2002) Matching visual stimuli on the basis of global and local features by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). Anim Cogn 5:27–31. doi:[10.1007/s10071-001-0121-8](https://doi.org/10.1007/s10071-001-0121-8)
- Horn L, Virányi Z, Miklósi Á, Huber L, Range F (2012) Domestic dogs (*Canis familiaris*) flexibly adjust their human-directed behavior to the actions of their human partners in a problem situation. Anim Cogn 15:57–71. doi:[10.1007/s10071-011-0432-3](https://doi.org/10.1007/s10071-011-0432-3)
- Huber L, Racca A, Scaf B, Virányi Z, Range F (2013) Discrimination of familiar human faces in dogs (*Canis familiaris*). Learn Motiv. doi:[10.1016/j.lmot.2013.04.005](https://doi.org/10.1016/j.lmot.2013.04.005)
- Kimchi R (1998) Uniform connectedness and grouping in the perceptual organization of hierarchical patterns. J Exp Psychol Hum Percept Perform 24:1105–1118
- Kimchi R, Amishav R, Sulitzeanu-Kenan A (2009) Gender differences in global-local perception? Evidence from orientation and shape judgments. Acta Psychol 130:64–71. doi:[10.1016/j.actpsy.2008.10.002](https://doi.org/10.1016/j.actpsy.2008.10.002)
- Kinchal RA, Wolf JM (1979) The order of visual processing: “top-down”, “bottom-up”, or “middle-out”. Percept Psychophys 25:225–231
- Kimchi R (1992) Primacy of wholistic processing and global/local paradigm: a critical review. Psychol Bull 112:24–38
- Lamb MR, Robertson LC, Knight RT (1990) Component mechanisms underlying the processing of hierarchically organized patterns: interferences from patients with unilateral cortical lesions. J Exp Psychol Learn Mem Cogn 16:471–483
- Lux S, Marshall JC, Thimm M, Fink GR (2008) Differential processing of hierarchical visual stimuli in young and older healthy adults: implications for pathology. Cortex 44:21–28. doi:[10.1016/j.cortex.2005.08.001](https://doi.org/10.1016/j.cortex.2005.08.001)
- Miklósi Á (2007) Social cognition. In: Miklósi Á (ed) Dog behaviour, evolution, and cognition. Oxford University Press Inc., New York, pp 165–200
- Miklósi Á, Topál J (2013) What does it take to become ‘best friend’? Evolutionary changes in canine social competence. Trends Cogn Sci 17:287–294. doi:[10.1016/j.tics.2013.04.005](https://doi.org/10.1016/j.tics.2013.04.005)
- Milgram NW, Head E, Weiner E, Thomas E (1994) Cognitive functions and aging in the dog: acquisition of nonspatial visual tasks. Behav Neurosci 108:57–68. doi:[10.1037/0735-7044.108.1.57](https://doi.org/10.1037/0735-7044.108.1.57)
- Miller PE, Murphy CJ (1995) Vision in dogs. J Am Vet Med Assoc 207:1623–1634
- Mongillo P, Bono G, Regolin L, Marinelli L (2010) Selective attention to humans in companion dogs, *Canis familiaris*. Anim Behav 80:1057–1063. doi:[10.1016/j.anbehav.2010.09.014](https://doi.org/10.1016/j.anbehav.2010.09.014)
- Müller-Oehring EM, Schulte T, Raassi C, Pfefferbaum A, Sullivan EV (2007) Local-global interference is modulated by age, sex and anterior corpus callosum size. Brain Res 1142:189–205. doi:[10.1016/j.brainres.2007.01.062](https://doi.org/10.1016/j.brainres.2007.01.062)
- Murphy CJ, Mutti DO, Zadnik K, Ver Hoeve J (1997) Effect of optical defocus on visual acuity in dogs. Am J Vet Res 58:414–418
- Nagasawa M, Murai K, Mogi K, Kikusui T (2011) Dogs can discriminate human smiling faces from blank expressions. Anim Cogn 14:525–533. doi:[10.1007/s10071-011-0386-5](https://doi.org/10.1007/s10071-011-0386-5)
- Navon D (1977) Forest before trees: the precedence of global features in visual perception. Cogn Psychol 9:353–383
- Pongrácz P, Miklósi Á, Dóka A, Csányi V (2003) Successful application of video-projected human images for signalling to dogs. Ethology 109:809–821. doi:[10.1046/j.0179-1613.2003.00923.x](https://doi.org/10.1046/j.0179-1613.2003.00923.x)
- Pretterer G, Bubna-Littitz H, Windischbauer G, Gabler C, Griebel U (2004) Brightness discrimination in the dog. J Vision 4:241–249. doi:[10.1167/4.3.10](https://doi.org/10.1167/4.3.10)
- 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 13:525–533. doi:[10.1007/s10071-009-0303-3](https://doi.org/10.1007/s10071-009-0303-3)
- Racca A, Guo K, Meints K, Mills DS (2012) Reading faces: differential lateral gaze bias in processing canine and human facial expressions in dogs and 4-year-old children. Public Library of Science One 7:e36076. doi:[10.1371/journal.pone.0036076](https://doi.org/10.1371/journal.pone.0036076)
- Range F, Aust U, Steurer M, Huber L (2008) Visual categorization of natural stimuli by domestic dogs. Anim Cogn 11:339–347. doi:[10.1007/s10071-007-0123-2](https://doi.org/10.1007/s10071-007-0123-2)
- Roalf D, Lowery N, Turetsky BI (2006) Behavioral and physiological findings of gender differences in global-local visual processing. Brain Cogn 60:32–42. doi:[10.1016/j.bandc.2005.09.008](https://doi.org/10.1016/j.bandc.2005.09.008)
- Schmittmann VD, van der Maas HLJ, Raijmakers MEJ (2012) Distinct discrimination learning strategies and their relation with spatial memory and attentional control in 4- to 14-year-olds. J Exp Child Psychol 111:644–662. doi:[10.1016/j.jecp.2011.10.010](https://doi.org/10.1016/j.jecp.2011.10.010)
- Sherf KS, Behrmann M, Kimchi R, Luna B (2009) Emergence of global shape processing continues through adolescence. Child Dev 80:162–177. doi:[10.1111/j.1467-8624.2008.01252.x](https://doi.org/10.1111/j.1467-8624.2008.01252.x)

- Slavin MJ, Mattingley JB, Bradshaw JL, Storey E (2002) Local-global processing in Alzheimer's disease: an examination of interference, inhibition and priming. *Neuropsychologia* 40:1173–1186. doi:[10.1016/S0028-3932\(01\)00225-1](https://doi.org/10.1016/S0028-3932(01)00225-1)
- Somppi S, Törnqvist H, Hänninen H, Krause C, Vainio O (2012) Dogs do look at images: eye tracking in canine cognition research. *Anim Cogn* 15:163–174
- Song Y, Hakoda Y (2012) The interference of local over global information processing in children with attention deficit hyperactivity disorder of the inattentive type. *Brain Dev-JPN* 34:308–317. doi:[10.1016/j.braindev.2011.07.010](https://doi.org/10.1016/j.braindev.2011.07.010)
- Spinozzi G, De Lillo C, Truppa V (2003) Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *J Comp Psychol* 117:15–23. doi:[10.1037/0735-7036.117.1.15](https://doi.org/10.1037/0735-7036.117.1.15)
- Spinozzi G, De Lillo C, Salvi V (2006) Local advantage in the visual processing of hierarchical stimuli following manipulations of stimulus size and element numerosity in monkeys (*Cebus apella*). *Behav Brain Res* 166:45–54. doi:[10.1016/j.bbr.2005.06.043](https://doi.org/10.1016/j.bbr.2005.06.043)
- Topál J, Gergely G, Erdőhegyi Á, Csibra G, Miklósi Á (2009) Differential sensitivity to human communication in dogs, wolves, and human infants. *Science* 325:1269–1272. doi:[10.1126/science.1176960](https://doi.org/10.1126/science.1176960)
- Truppa V, Sovrano VA, Spinozzi G, Bisazza A (2010) Processing of visual hierarchical stimuli by fish (*Xenotoca eiseni*). *Behav Brain Res* 207:51–60. doi:[10.1016/j.bbr.2009.09.039](https://doi.org/10.1016/j.bbr.2009.09.039)
- Wagemans J, Feldman J, Gepshtein S, Kimchi R, Pomerantz JR, van der Helm PA, van Leeuwen C (2012) A century of gestalt psychology in visual perception: II. Conceptual and theoretical foundations. *Psychol Bull* 138:1218–1252. doi:[10.1037/a0029334](https://doi.org/10.1037/a0029334)

Copyright of Animal Cognition is the property of Springer Science & Business Media B.V. and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.