

Strategy planning in dogs (*Canis familiaris*) in a progressive elimination task

Claude Dumas*, Dominique Dorais Pagé

Université du Québec à Montréal, Canada

Received 25 January 2006; accepted 29 January 2006

Abstract

Domestic dogs (*Canis familiaris*) were administered a progressive elimination task in which they had to visit and deplete three baited sites. Dogs were brought back to the starting point after each visit to any site whether they had made a correct or an incorrect choice. In Experiment 1 ($n = 10$) the results revealed that the dogs randomly selected among the sites when they were equidistant from the starting point whereas they relied on the least distance rule when one of sites was closer to the starting point than were the other sites. In Experiment 2 ($n = 12$), the dogs first chose the left target when angular deviation between adjacent targets varied whether the least angular deviation was on the right of the left. Results are interpreted in terms of Gibson's hypothesis about cooperative hunters. The discussion also emphasizes comparisons with cats (i.e., solitary hunters).

© 2006 Elsevier B.V. All rights reserved.

Keywords: *Canis familiaris*; Strategy planning; Search behavior; Decision making

In order to survive animals must search for all sorts of items (e.g., food, mate, nest location and so on) whose availability varies in time and space. As such, search behavior appears to be of great adaptive value to animals. But search behavior often requires many decisions to be made as to what, when and where to search for. Hence it appears relevant to address the issue of the nature of the decision making process underlying search behavior in animals both in terms of short and long term causation (see Dukas, 1998; Shettleworth, 2001).

In the last few years, there has been a renewed interest in the use of the progressive elimination task to study decision making in animals (see De Lillo et al., 1997, 1998; Dorais Pagé and Dumas, 2003; Valsecchi et al., 2000). In the progressive elimination task animals are usually (although there are some variants) first trained to eat from a single site and they are introduced to the multi-site setting in the test phase only. Then animals are let free to visit the baited sites in any order as long as they empty all sites. According to De Lillo et al. (1997) and De Lillo et al. (1998) the progressive elimination task proved to be a heuristic tool to study search strategy and search efficiency as well.

Valsecchi et al. (2000) also underlined that the progressive elimination task can be a valuable tool to address the issue of interspecies comparisons. On one hand, De Lillo et al. (1997) showed that capuchin monkeys performed better when the baited sites were spatially clustered than when they were arranged in a matrix. On the other hand, Valsecchi et al. (2000) using the same task as that used by De Lillo et al. (1997) showed that mice were more efficient when the sites were arranged in a matrix than when they were spatially clustered. Valsecchi et al. (2000) interpreted these interspecies differences as reflecting different food distribution in the natural environment and different natural history as well. According to Valsecchi et al. (2000), mice which are granivorous evolved in habitats with scattered and unpredictable food resources where switching from one cluster to another may be interpreted as an antipredator strategy. Capuchin monkeys are mostly frugivorous, they forage in groups (and accordingly are less subject to predation) and they exploit spatially and temporally predictable food items (Valsecchi et al., 2000). Admittedly, procedural differences could also account for the differences observed between capuchins and mice when administered the progressive elimination task (De Lillo et al., 1997, 1998; Valsecchi et al., 2000). Whereas capuchins had to walk on a perch located above the ground so that they could reach the containers that were suspended from the ceiling, mice could walk on the floor of the experimental room to reach each container. Hence it remains to be seen how monkeys would

* Corresponding author at: Département de psychologie, Université du Québec à Montréal, C.P. 8888 Succ. C.V., Montréal, Que., Canada H3C 3P8.

Tel.: +1 514 9873000x4097; fax: +1 514 9877953.

E-mail address: dumas.claude@uqam.ca (C. Dumas).

perform with containers located on the ground where the risk of predation is higher than up in the trees.

Although food distribution and risk predation can influence search strategy and efficiency, Gibson (1990) suggested that the fact that a prey can move by itself (i.e., an autonomous prey) in space can also influence the predator's search strategy. (Both mice and monkeys feed on non-autonomous preys (i.e., seeds, fruits, etc.) in space.) According to Gibson (1990), the events involved in the pursuit of a prey create high demands on information processing skills. Pursuing a prey create contexts which favor quick moves in space. Hence, it is quite unlikely that the predator will be allowed to freely exhibit the behavioral sequence of actions that was initially set to reach for the prey. Gibson (1990) stated that such demands on information processing skills should be especially high in cooperative hunters as the predator must not only take into account and anticipate the movements of the prey, but it must also monitor the movements of the conspecifics participating in the hunt. It is then assumed that information processing demands must be different in cooperative hunters (e.g., canids) than in solitary hunters (e.g., felids). Hence, one can expect to observe differences in search behavior between cooperative hunters and solitary hunters. However, that hypothesis has largely been ignored so far (but see Gagnon and Doré, 1992).

Indeed both cats (i.e., felid) and dogs (i.e., canid) have been administered progressive elimination tasks. The data (Dorais Pagé and Dumas, 2003) revealed that the cats relied on the least distance rule to solve the task. That is the cats first chose the closest target and so on. If all targets were equidistant from the starting point but the distance between the adjacent targets varied, the cats first chose the targets separated by the least distance. Finally, when both the distance between the starting point and the targets and the distance between the adjacent targets were constant, the cats selected the targets in a random order. In dogs the results were contradictory. When being tested with a semi-circular array (Fabrigoule, 1974) the dogs relied on divergence (i.e., first choose the targets separated by the greatest distance), whereas when they were tested with a circular spatial array (Fabrigoule and Sagave, 1992) they relied on the least distance rule. Fabrigoule and Sagave (1992) did not provide any explanation for such discrepant results. But dogs and cats' performance can hardly be compared because they were not tested with the same procedure and the same spatial arrays. In Dorais Pagé and Dumas' study (2003) the cats were brought back to the starting point after each choice whether they were successful (i.e., visiting a baited site) or not (i.e., visiting an already visited site). In Fabrigoule's study (1974) the dogs were also brought back to the starting point when they were successful, but not when they made an error so that they were allowed to visit a baited site before being brought back to the starting point. In addition, in Fabrigoule's study (1974) the distance between the starting point and the targets was twice than that in Dorais Pagé and Dumas' study (2003) (see Discussion in Experiment 1 on that point). Finally, in Fabrigoule and Sagave's study (1992) the baited sites were located at the periphery of a circular spatial array and the dogs were brought back to the starting point only once all sites had been visited. Hence there is a need to reassess

dogs' performance in a progressive elimination task using the same procedure and the same spatial arrays used with cats.

Accordingly, the present research aimed at verifying Gibson's hypothesis by administering to dogs a progressive elimination task using the same procedure and the same spatial arrays used with cats in Dorais Pagé and Dumas' study (2003).

1. Experiment 1

Experiment 1 aimed at studying the effect of the distance between the starting point and the targets. There were two experimental conditions. In Condition 1 all targets were equidistant from the starting point whereas in Condition 2 that distance differed for each target. One must remember that the starting point corresponds to the position of the dog before initiating search.

2. Method

2.1. Subjects

The subjects were 10 (3 males and 7 females) domestic dogs (*Canis familiaris*), which were tested in their owners' homes. All dogs were experimentally naive and they were divided equally in two experimental groups. The youngest subject was 10 months old and the oldest one was 11 years old ($M = 3$ years 7 months, $S.D. = 3$ years and 0 month).

2.2. Procedure

Food was unavailable for at least 2 h before training and testing sessions. However, water was available ad libitum. The same procedure was used in the two experiments reported here.

2.2.1. Training

First, an experimenter (E1) gently restrained the animal at the starting point before letting the dog eating a piece of food (e.g., a food pellet of a commercial brand) in a bowl (5.7 cm \times 10.5 cm) placed at the starting point. On the next four training trials, the distance between the starting point and the feeding bowl was gradually increased up to 2 m. Then, on each of the 20 following trials, the position of the bowl was randomly chosen among 20 predetermined positions in a 1.5 m \times 1.5 m area located at approximately 2 m in front of the starting point. None of these positions corresponded to any of the three target positions used in each of the two experimental conditions. To succeed on any training trial the dog had to walk (on the first trial distance was 0) from the starting point to the feeding bowl and to eat the piece of food within 30 s otherwise the trial was failed. After each successful or failed trial, the dog was turned 180° so that it could not see the other experimenter (E2) both moving the bowl to position relevant to the next trial and (if necessary) re-baiting the bowl. The side (left or right) through which the dog was turned was counterbalanced across the trials as was the side through which E2 came back behind the starting point. Once the manipulations had been completed the dog was turned 180° again so that it could have visual access to the experimental set up before being released. The same procedure was used throughout both

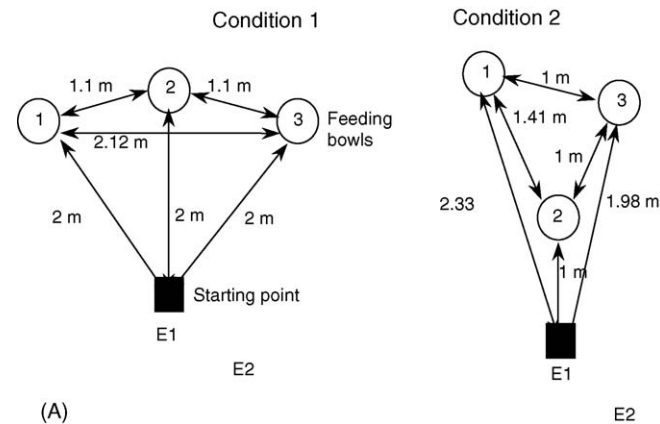
the training and the experimental trials in the two experiments reported in this article. During each trial, E2 stood behind the starting point and noted whether the dog succeeded or not. Each training session included 25 trials. Training was completed when the dogs could empty the baited Bowl 2 out of 25 trials within a single session. All dogs needed only one session to satisfy the criterion.

2.2.2. Experimental trials

On the session following the end of training, the experimental trials were administered. Three identical bowls were used (5.7 cm × 10.5 cm) and a piece of food was placed in each bowl. The piece of food was not visible from the starting point or from bowl to bowl. In Condition 1 (see Fig. 1A), each of the three

feeding bowls was at the same distance from the starting point and the distance between the adjacent bowls was constant. In Condition 2 none of the three bowls was at the same distance from the starting point. However, two interbowl distances were equivalent whereas the third interbowl distance was larger than the two other ones. The side (i.e., left or right) on which the larger interbowl distance was located was counterbalanced across trials for each subject.

At the beginning of each trial, the dog was gently restrained by E1 at the starting point. Then the dog was released and it was allowed to choose one bowl. If the dog chose a baited bowl it was allowed to eat the food pellet before being brought back to the starting point and it was released again. If the dog chose a non-baited bowl (i.e., the one it had already visited) it was immediately brought back to the starting point (i.e., a non-correction procedure was used) and it was released again. Each time within a trial that a dog visited a non-baited (i.e., already visited) bowl was counted as an error. The bowl at which the error was directed was also noted. Choice was defined as any head movement (i.e., bending the head in the bowl, leaning toward the internal part of the bowl) that allowed the dog to have visual access to the content of the bowl. E2 noted which bowl was chosen on each attempt. A trial was completed when all three bowls had been emptied. Each dog had to complete 30 trials. When the animal did not initiate search four times in a row or when it quit the experimental setting and ran away in another room the session was ended. On average, the dogs needed 2.40 sessions (S.D. = 0.84) to complete all 30 trials. There was only one experimental session per day.



3. Results

For each dog the order in which the three bowls were emptied was registered on each trial. This was referred to as the pattern of elimination. For example, pattern 2-1-3 means that Bowl 2 (i.e., intermediate bowl) was emptied first, then Bowl 1 (i.e., left bowl) and finally Bowl 3 (i.e., the right bowl). As there were three bowls there were six possible patterns of elimination. The rejection level adopted for all analyses in both experiments reported in this article was $p < 0.05$; post hoc comparisons used the Newman–Keuls test.

Individual data are presented in Table 1. Given that in Condition 2 the mean frequency for pattern 1-2-3 was 0, a nonparametric test was used to compare both conditions. A statistical analysis revealed that the distribution of patterns of elimination (see Fig. 1B) significantly differed, $\chi^2(5) = 151.44$, between Condition 1 and Condition 2. In Condition 1, a one-way ANOVA computed on the mean number of times each pattern of elimination was chosen, with pattern of elimination as a within-subject factor, did not reveal any significant difference. In other words, in Condition 1, the patterns of elimination were equiprobable. In Condition 2, a descriptive analysis revealed that the dogs first chose Bowl 2 (i.e., the intermediate bowl) on 143 trials out of 150. The left bowl was chosen first on only one trial and the right bowl was chosen first only on six trials. In other words, the dogs first chose the bowl that was the closest target to the starting point. A statistical analysis did not reveal any significant difference, paired t (d.f. = 4) = 0.57, ns, between pattern 2-1-3 ($M = 12$.

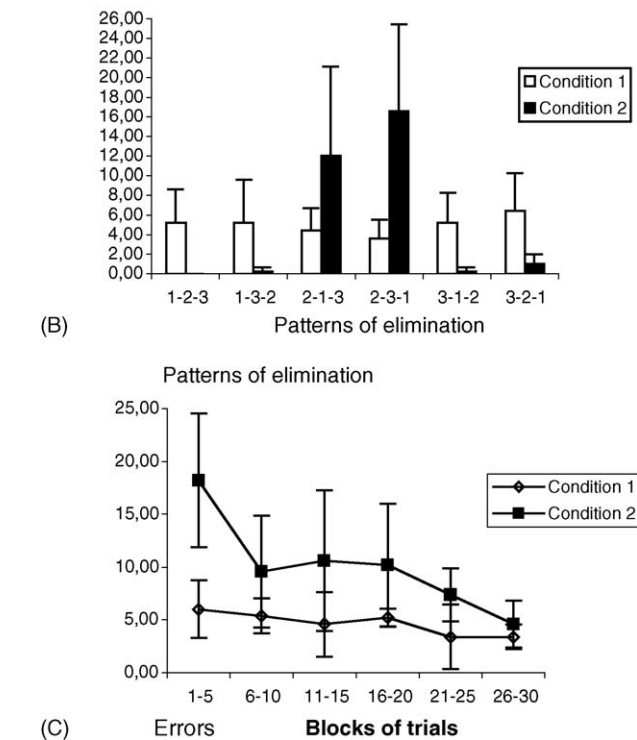


Fig. 1. (A) A schematic representation of the spatial configuration of the baited bowls in each condition in Experiment 1. E1 = experimenter 1, E2 = experimenter 2. (B) Mean number of times each pattern of elimination was chosen in each condition. (C) Mean number of errors per block of trials for each condition. 1 = left, 2 = intermediate, 3 = right.

Table 1
Number of times each pattern of elimination was chosen in each condition for each subject in Experiment 1

Subject	Pattern of elimination					
	1-2-3	1-3-2	2-1-3	2-3-1	3-1-2	3-2-1
Condition 1						
1	7	8	7	2	2	4
2	5	10	2	3	3	7
3	2	0	2	7	9	10
4	2	1	6	3	8	10
5	10	7	5	3	4	1
Condition 2						
1	0	1	10	16	1	2
2	0	0	23	7	0	0
3	0	0	3	27	0	0
4	0	0	20	9	0	1
5	0	0	4	24	0	2

0; S.D. = 9.13) and pattern 2-3-1 ($M = 16.6$; S.D. = 8.85) regarding the mean number of times each pattern was chosen first.

Errors were also analyzed (see Fig. 1C). A 2 (condition) \times 6 (block) ANOVA with repeated measures on block, computed on the number of errors, revealed a significant effect of condition, $F(1, 8) = 12.54$, and a significant effect of block, $F(5, 40) = 6.45$. The condition \times block interaction also reached significance, $F(5, 20) = 2.89$. The dogs made more errors in Condition 2 than in Condition 1. Further analysis revealed that there was a significant, $F(1, 4) = 20.64$, linear trend in Condition 2 across the blocks of trials but not in Condition 1. Hence performance significantly improved across trials in Condition 2.

Finally a 3 (bowl) \times 2 (choice) ANOVA computed on the number of errors in Condition 1, with bowl as and choice as within-subject factors, only revealed a significant effect of choice, $F(1, 4) = 26.48$. That is the errors were equally distributed among the three bowls and the dogs made more errors after the second correct choice than after the first one. A similar ANOVA in Condition 2 revealed a significant effect of bowl, $F(2, 8) = 22.10$, a significant effect of choice, $F(1, 4) = 33.83$, and a significant bowl \times choice interaction, $F(2, 8) = 4.73$. A one-way ANOVA on Choice 1 with bowl as a within-subject factor revealed a significant effect of bowl, $F(2, 8) = 52.67$. A posteriori comparisons revealed that the dogs erred more often at Bowl 2 than at the two other bowls. There was no difference between Bowl 1 and Bowl 3. A similar ANOVA on Choice 2 also revealed a significant effect of bowl, $F(2, 8) = 8.49$. A posteriori comparisons revealed that the dogs erred more often at Bowl 2 than at Bowl 1, but that there was no difference between Bowl 3 and Bowl 1. No other comparison reached significance.

4. Discussion

The results of Experiment 1 revealed that when the targets were equidistant from the starting point (i.e., Condition 1) the dogs randomly selected among the targets. In addition the errors were equally distributed among the targets. When the distance between the starting point and the targets varied (i.e., Condition

2), the dogs relied on the least distance rule and most of the errors were directed at the closest target (i.e., intermediate target).

First, the fact that the dogs randomly selected among equidistant targets (i.e., Condition 1) is discrepant with what has been previously observed in this species. In Fabrigoule and Sagave's study (1992) the starting point was located at the center of a circular array so that each baited site was equidistant from the starting point. The dogs were released from the starting point and they were brought back only when all baited sites had been emptied. Under such circumstances, once the dogs had made their first choice they had to choose among targets whose distance with the initially chosen target varied. That methodological difference can account for the fact that in Fabrigoule and Sagave's study (1992) the dogs relied on the least distance rule. In Frabrigoule's study (1974) the dogs were administered a similar task to the one administered in Condition 1; that is they had to visit four baited bowls located 5 m in front of them, the distance between the adjacent bowls being 1.3 m. Each time the dogs visited a baited bowl they were brought back to the starting point. If they visited an already visited bowl they were let free to search for another baited target before being brought back to the starting point. The data revealed that the dogs relied on divergence instead of choosing the targets in a random order. That is they chose as their second choice the farthest target in relation to the initially chosen one. However in Fabrigoule's study (1974) the distance between the targets and the starting point was 5 m whereas it was 2 m in our study. As in both studies the distance between the adjacent targets was the same (1.3 m versus 1.2 m), angular deviation between the adjacent targets was necessarily smaller in Fabrigoule's study than it was in Condition 1 in Experiment 1. This suggests that divergence can be linked to small angular deviation between adjacent targets.

Second, the data revealed that the errors were equally distributed among the targets when the distance between the starting point and the targets was constant (i.e., Condition 1). Under the same circumstances the cats (Dorais Pagé and Dumas, 2003) erred more often at the intermediate target than at the two other targets. Dorais Pagé and Dumas (2003) argued that a target located at a short distance in line with the bodily axis of the cat mimics a naturally occurring setting in which the cat is ready to pounce on its prey (see Leyhausen, 1979). According to this interpretation, dogs should also be prone to the interference created by the intermediate target as they also pursue and kill prey. Hence that interpretation has to be revised. One likely interpretation states that because dogs have to share their attention between the prey and the conspecifics during the hunt any interference in memory linked to any target (e.g., the intermediate target) would be detrimental to memory updating. Solitary hunters like cats do not have to share attention among multiple targets.

Third, the fact that the dogs randomly selected among the equidistant targets in Condition 1 replicated what had been observed in cats (see Condition 1 in Experiment 1 in Dorais Pagé and Dumas, 2003). This clearly suggests that dogs and cats share the same basic decision making system. Dogs and cats appear to assess the distance between the targets and the starting point

before initiating search. If the outcome of that evaluation is negative both species will select the targets in a random order. If the outcome of the evaluation proves to be positive (i.e., Condition 2 in Experiment 1) both cats and dogs first search for the closest target. In addition, previous research (Dorais Pagé and Dumas, 2003) showed that the cats also used the distance between the adjacent targets as a source of information (at least when all targets are equidistant from the starting point, see Dorais Pagé and Dumas, 2003). The cats first chose the two adjacent targets that were separated by the shortest distance (all targets being equidistant from the starting point). Hence, it remains to be seen whether the distance between the adjacent targets, which can also be referred to as angular deviation between the adjacent targets, can influence search behavior in dogs.

5. Experiment 2

Experiment 2 aimed at verifying whether dogs will use angular deviation (i.e., distance between adjacent targets) as a source of information. In order to study the impact of angular deviation between the adjacent targets, we used the same spatial array as that one used in Condition 1 in Experiment 1 (i.e., all bowls being equidistant from the starting point), except that the position of the intermediate bowl was no longer in line with the bodily axis of the dog (see Fig. 2A). Actually we used the same spatial array as that one used with cats in Condition 1 in Experiment 2 in Dorais Pagé and Dumas’ study (2003). In their study, Dorais Pagé and Dumas also included in Experiment 2 another condition in which the least distance rule was in conflict with both the intermediate position per se and the bodily axis of the cat. In that particular condition, the intermediate location was in line with the bodily axis of the cat but it was farther from the starting point than were the left and the right targets, which were equidistant from the starting point. Unexpectedly, the data revealed that, instead of randomly first choosing between the left and the right target, the cats systematically first chose the right target. Experiment 2 also aimed at verifying whether dogs would exhibit a similar bias than that exhibited by cats.

6. Method

6.1. Subjects and procedure

The subjects were 12 (4 males and 8 females) domestic dogs (*C. familiaris*), which were tested in their owners’ homes. All dogs were experimentally naive and they were divided equally in two experimental groups. The youngest subject was 18 months old and the oldest one was 8 years old ($M=4$ years 9 months, $S.D.=2$ years 4 months). The dogs were trained and tested following the same procedure (and criterion) as in Experiment 1. Experiment 2 included two conditions. In Condition 1 the intermediate bowl was closer to one external bowl than it was for the other bowl. For three dogs it was closer the right bowl, and for the other three dogs it was closer to the left bowl (see Fig. 2). In Condition 2, both the left and right bowls were equidistant from the starting point but they were closer to starting point than

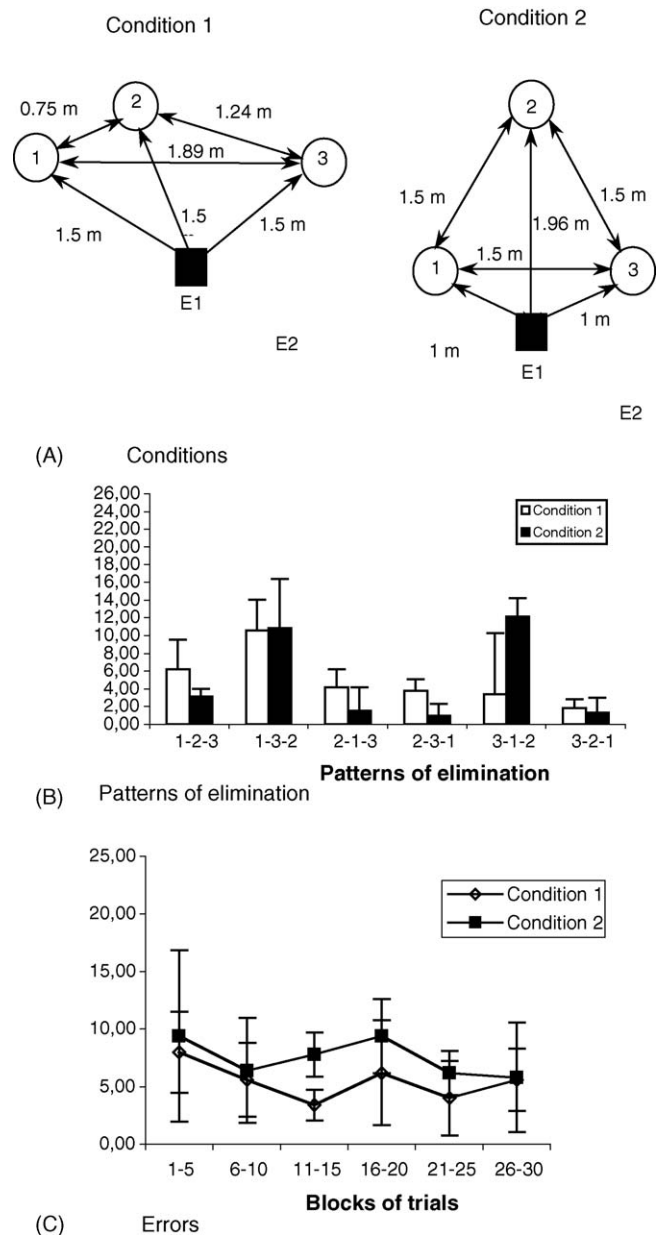


Fig. 2. (A) A schematic representation of the spatial configuration of the baited bowls in each condition in Experiment 2. E1 = experimenter 1, E2 = experimenter 2. (B) Mean number of times each pattern of elimination was chosen in each condition. (C) Mean number of errors per block of trials for each condition. 1 = left, 2 = intermediate, 3 = right.

was the intermediate bowl. In addition, the distance between the adjacent bowls was constant. On average, the dogs needed only one session to complete training and 1.67 sessions ($S.D.=0.65$) to complete the 30 experimental trials. There was only one session per day. Three additional dogs were eliminated because of a lack of motivation.

7. Results

Individual data are presented in Table 2. A 2 (condition) × 6 (pattern of elimination) ANOVA with pattern of elimination as a within-subject factor computed on the number of times

Table 2

Number of times each pattern of elimination was chosen in each condition for each subject in Experiment 2

Subject	Pattern of elimination					
	1-2-3	1-3-2	2-1-3	2-3-1	3-1-2	3-2-1
Condition 1						
1	7	5	6	5	3	4
2	7	9	3	3	5	3
3	13	3	10	3	0	1
4	6	10	6	5	2	1
5	6	9	6	2	6	1
6	5	20	0	4	1	0
Condition 2						
1	5	16	4	0	4	1
2	2	13	4	3	7	1
3	2	9	0	1	16	2
4	9	8	0	0	8	1
5	0	12	1	2	7	3
6	1	7	0	0	22	0

Note: In Condition 1 the smallest angular deviation was on the left for subjects 1, 2 and 3 and on the right for subjects 4, 5, and 6.

each pattern of elimination (see Fig. 2B) was chosen, revealed a significant effect of pattern, $F(5, 50) = 9.30$, and a significant pattern \times condition interaction, $F(5, 50) = 5.46$. A one-way ANOVA in Condition 1 revealed a significant effect of pattern, $F(5, 25) = 3.96$. Post hoc comparisons revealed that the pattern of elimination 1-3-2 was chosen more often than pattern 3-1-2, 3-2-1 and 2-3-1. That is the dogs avoided as a first choice the bowl that was on the right position. Indeed they chose the target on the left position as their first choice whether the least angular deviation was on the right or on the left. A similar ANOVA in Condition 2 also revealed a significant effect of pattern, $F(5, 25) = 10.21$. Post hoc comparisons revealed that the patterns 3-1-2 and 1-3-2 were chosen more often the other patterns. In other words, the dogs first visited the two bowls that were the closest targets to the starting point.

A 2 (condition) \times 6 (block) ANOVA with repeated measures on block, computed on the number of errors, revealed only a significant effect of block, $F(5, 50) = 2.93$. Further analysis revealed that there was a significant, $F(1, 10) = 5.58$, linear trend across the blocks of trials. Thus, the dogs' performance improved across trials in both conditions (see Fig. 2C).

Finally, a 2 (choice) \times 3 (bowl) ANOVA, computed on the number of errors in Condition 1 with choice and bowl as within-subject factors, revealed only a significant effect of choice, $F(1, 5) = 58.76$. That is the errors were equally distributed among the three bowls and the dogs made more errors after the second correct choice than after the first one. As in Condition 2 Bowl 2 was chosen last most of the time, the cats almost never erred at this bowl. Accordingly, a 2 (choice) \times 2 (bowl: Bowl 1 versus Bowl 3) ANOVA, computed on the number of errors with choice and bowl as within-subject factors, revealed only a significant effect of choice, $F(1, 5) = 14.11$. In other words, the cats erred as often at Bowl 1 than at Bowl 3 (and almost never at the intermediate bowl) and they made more errors after the second choice than after the first one.

8. Discussion

The results of Experiment 2 revealed that, when angular deviation between the adjacent targets was made relevant as a source of information, the dogs chose the target on the left side of the bodily axis first. On their second choice, contrary to what was observed in cats, the dogs chose the divergent target (i.e., the right target) on many trials. Given that the results of Fabrigoule's study (1974) and those of Experiment 1 suggested that small angular deviation can induce divergence, it could be that the least angular deviation used in Condition 1 in Experiment 2 was small enough to induce divergence. Divergence can certainly be of adaptive value to cooperative hunters. However that cannot account for the fact that the dogs first searched at the left target even when the smallest angular deviation was on the right. Dorais Pagé and Dumas (2003) argued that bias positions observed in cats when they were administered a progressive elimination task was linked to some conflict in the cat's decision making system. Although the nature of such a conflict still remains to be clarified in dogs, the data suggest that the fact that all targets were equidistant from the starting point could have been the source of the conflict. But more research is needed to clarify this point.

The results also revealed that, contrary to what was observed in cats, the dogs did not show any position bias when having to choose between the left and the right target when these targets were equidistant from the starting point and the least distance rule was activated (i.e., the intermediate location being farther from the starting point than were the two other targets). Under the same circumstances the cats systematically chose first the right target (Dorais Pagé and Dumas, 2003). Given that the cats pursue only one prey at a time, a second target at the same distance will distract the cat. In other words the cats would not easily share attention between the two targets. As dogs are cooperative hunters they need to share attention between the prey and the conspecifics so that having to choose between two equivalent closest target does not create any difficulty to the decision making process.

9. General discussion

The present research aimed at testing Gibson's hypothesis (1990) which predicted that there would be differences between cats and dogs' search behavior given that information processing demands differ between cooperative and solitary hunters. In order to do so, dogs were administered a progressive elimination task using the same procedure and the same spatial arrays as those used with cats in Dorais Pagé and Dumas' study (2003).

The results revealed that dogs and cats shared the same basic decision making system. Both species select the targets in a random order under the same circumstances, that is when both the distance between the targets and the starting point was constant and the distance between the adjacent targets was constant. When the distance between the starting point and the targets varied, dogs like cats relied on the least distance rule, which replicated what had been found in other mammals (e.g., Menzel, 1973). When the distance between the adjacent targets varied,

the cats relied on the smallest angular deviation rule whereas dogs rather seem to rely (at least partly) on divergence. Divergence could be of adaptive value to cooperative hunters. Being too close to a conspecific while hunting could decrease success. Previous research (Poucet et al., 1983) revealed that cats could also rely on divergence. But in cats divergence emerged after extensive training and it was interpreted as a way to decrease memory load. In dogs, divergence emerged spontaneously and as such can be linked to optimization of foraging strategies rather than strategies to increase memory efficiency (see Cohen et al., 2003; Roberts, 1998). But more research is needed to clarify the conditions under which mammal species will rely on the least distance rule or on divergence.

Our data also support previous data regarding differences between dogs and cats. Doré et al. (1996) administered both to cats and dogs variants of Piagetian object permanence tests in which spatial cues and figurative cues (e.g., visual patterns on hiding locations) were manipulated. The results revealed that both species failed to use figurative cues as a source of information to recover the hidden object. However, the dogs performed better than the cats when they were administered a test in which the screen behind which was hidden the object was moved to an empty location (i.e., where there was no screen before) while the now empty initial location was filled with another screen. But more interestingly, the cats searched for the hidden object at the initial location whereas the dogs divided search between the initial and the novel target location. That is the initial location remained activated in both the cats' and the dogs' short-term memory but it created less interference in the dogs' short-term memory. Such a difference between cats and dogs can also be interpreted in relation to Gibson's hypothesis. That is cooperative hunters need to share attention between multiple targets (prey and conspecifics) but not cats.

Overall the data supported, although in an indirect way, Gibson's hypothesis. Gibson's hypothesis relates to long-term causation whereas our study rather focused on short-term causation (i.e., conditions that influence decision making). Nonetheless Gibson's hypothesis proved to be of heuristic value in raising the issue of interspecies comparisons regarding decision making processes. The present research also support Valsecchi et al.'s claim (2000) that the progressive elimination task is a valuable tool to further our understanding of animal comparative cognition.

Acknowledgement

Support for the preparation of this article was provided by a research grant to Claude Dumas from the Natural Science and Engineering Research Council of Canada.

References

- Cohen, J., Pardy, S., Solway, H., Graham, H., 2003. Chunking versus foraging search patterns by rats in the hierarchically radial maze. *Anim. Cogn.* 6, 93–104.
- De Lillo, C., Aversano, M., Tuci, E., Visalberghi, E., 1998. Spatial constraints and regulatory functions in Monkeys (*Cebus apella*) search. *J. Comp. Psychol.* 112, 353–362.
- De Lillo, C., Visalberghi, E., Aversano, M., 1997. The organisation of exhaustive searches in a patchy space by capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 111, 82–90.
- Dorais Pagé, D., Dumas, C., 2003. Strategy planning in cats (*Felis catus*) in a progressive elimination task. *J. Comp. Psychol.* 117, 53–60.
- Doré, F.Y., Fiset, S., Goulet, S., Dumas, M.C., Gagnon, S., 1996. Search behavior in cats and dogs: interspecific differences in working memory and spatial cognition. *Anim. Learn. Behav.* 24, 142–149.
- Dukas, R. (Ed.), 1998. *Cognitive Ethology. The Evolutionary Ecology of Information Processing and Decision Making.* The University of Chicago Press, Chicago.
- Fabrigoule, C., 1974. Recherches expérimentales sur l'apprentissage spatial chez le chien [Experimental studies on spatial learning in dogs]. *Cahiers de psychologie* 17, 91–110.
- Fabrigoule, C., Sagave, I., 1992. Reorganization of cues and path organization in dogs. *Behav. Proc.* 28, 65–80.
- Gagnon, S., Doré, F.Y., 1992. Search behavior in various breeds of adult dogs (*Canis familiaris*): object permanence and olfactory cues. *J. Comp. Psychol.* 106, 58–68.
- Gibson, K.R., 1990. New perspectives on instincts and intelligence: brain size and the emergence of hierarchical mental constructional skills. In: Parker, S.T., Gibson, K.R. (Eds.), *Language and Intelligence in Monkeys and Apes.* Cambridge University Press, Cambridge, UK, pp. 97–128.
- Leyhausen, P., 1979. *Cat Behavior: The Predatory and Social Behavior of Domestic and Wild Cats.* Garland, New York.
- Menzel, E.W., 1973. Chimpanzee spatial memory organization. *Science* 182, 943–945.
- Poucet, B., Buhot-Averseng, M.C., Thinus-Blanc, C., 1983. Food-searching behavior of cats in a multiple-choice elimination problem. *Learn. Motiv.* 14, 140–153.
- Roberts, W.A., 1998. *Principles of Animal Cognition.* McGraw-Hill, New York, NY.
- Shettleworth, S.J., 2001. Animal cognition and animal behaviour. *Anim. Behav.* 61, 277–286.
- Valsecchi, P., Bartolomucci, A., Aversano, M., Visalberghi, E., 2000. Learning to cope with different food distributions: the performance of house mice (*Mus musculus domesticus*). *J. Comp. Psychol.* 114, 272–280.