Searching in the Middle—Capuchins’ (Cebus apella) and Bonobos’ (Pan paniscus) Behavior During a Spatial Search Task

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In this study we show that bonobos and capuchin monkeys can learn to search in the middle of a landmark configuration in a small-scale space. Five bonobos (Pan paniscus) and 2 capuchin monkeys (Cebus apella) were tested in a series of experiments with the expansion test paradigm. The primates were trained to search in the middle of a 4- or 2-landmark configuration, and were then tested with the same configuration expanded. Neither species searched in the middle of the expanded 4-landmark configuration. When presented with a 2-landmark configuration and a constant or variable inter-landmark training distance, the subjects sometimes searched preferentially in the middle of the expanded configuration. We discuss 2 alternative explanations of the results: extracting a middle rule or averaging between different goal-landmark vectors. In any case, compared to adult humans, primates appear highly constrained in their abilities to search in the middle of a configuration of detached landmarks. We discuss some of the factors that may influence the primates’ behavior in this task.

Keywords: bonobos, capuchins, landmark configuration, middle rule, vector averaging

Animals need to be able to navigate through their environment to find goals such as food locations or shelter. These goals, however, may sometimes be concealed and not directly visible, so that animals have to exploit other, perceptible elements in the environment as reference points to locate their targets. Elements that can function as reference points are often called landmarks.

Landmarks can be used by animals in three different ways. First, through an associative mechanism: A goal is associated with the immediately surrounding landmarks that are used to define a general area of search. In that case landmarks serve as beacons to mark the position of the goal. Second, through an elemental mechanism: The distance and direction of the goal from one landmark (i.e., a vector) can be encoded and if multiple landmarks exist, each landmark is used as a separate origin of one vector. To be able to compute the distance and direction of the goal from a landmark, animals must possess additional information about their own position in space. This information can be accessed for example, through an internal directional sense or a fixed point of departure. Finally, through a configurational mechanism: The distance and direction of the goal are encoded in relation to a set of multiple landmarks, so that the goal position is coded as being for example, in the middle of a set of two or more landmarks. In sum, understanding and using a spatial configuration of multiple elements means understanding and representing the spatial relations among these elements as a whole, independent of the viewer’s position and perspective. This means, that a representation can be formed that is not solely based on perception but rather based on generating an abstract geometrical rule.

To assess what mechanism a subject exploits in landmark use, an “expansion test” paradigm is often used (Cartwright & Collett, 1982; Collett, Cartwright, & Smith, 1986). Typically, a learning task is given in which an invisible goal bears a con-
sistent spatial relation to an array of two to four landmarks, for
example, can always be found in the middle between four
landmarks (see Figure 1a for an example). The landmarks and
the goal have no fixed position in the search space, so that the
subject can only rely on the landmarks to find the goal. Once the
subject manages to find the reward consistently, it is tested with a
transformed array. Different kinds of transformations have been
used: diagonal; vertical; or horizontal expansions, contractions,
and rotations. The search pattern of a subject in response to an
expanded array usually provides good evidence concerning the
mechanism it originally used to code for the reward location (see
Figure 1b for an example). For example, if one finds that the
subject primarily searches in the vicinity of the landmarks, it is
very likely that the landmarks served as beacons. If the subject
searches in the trained direction and distance from one or more
landmarks, it can be assumed that it encoded a vector, to identify
the reward location. Finally, if the subject searches in the middle
of the expanded array it may have coded the configuration of the
whole array and extracted some kind of abstract rule such as
“always search in the middle of the array” (middle rule).

An alternative explanation for searching in the middle is that the
animals learn vectors from goal landmark and search in the middle
of a transformed array of landmarks by averaging the different
vectors. The vector-sum model was first proposed by Cheng
(1988), who later revised it as a consequence of the finding that
instead of averaging whole vectors pigeons average the direction
and distance components separately (Cheng, 1995). In addition to
pigeons, Clark’s nutcrackers were found to make separate deci-
sions about directional and distance information (Kamil & Jones,
1997). Thus, vector averaging in the animal literature is different
from vector averaging in the mathematical sense proper (see also
Kamil & Jones, 1999). If the inter-landmark distance of a land-
mark array is increased, the learned goal-landmark vectors end
short of the middle point between the landmarks. In addition, the
landmarks are farther away from the goal than in the original array.
Trying to compromise between the learned goal-landmark dis-
tances the animal may thus end up searching in the middle.
However, it has been argued that in the case of new inter-landmark
distances exceeding the range of the training distances, searching
in the middle cannot be readily explained by the use of specific
vectors from individual landmarks (Jones, Antoniadis, Shettle-
worth, & Kamil, 2002). In fact, up to now, no nonhuman species
trained with a constant inter-landmark distance and detached ob-
jects as landmarks searched in the middle of an expanded array.
Exceptions involved a different methodology and will be discussed
later below.

When tested with the expansion test paradigm, human adults
have been shown to adopt the middle rule strategy irrespective of
the experimental conditions: large-scale (i.e., within which the
subjects move, see Acredolo, 1988) or small-scale spaces, constant
training distances, variable numbers of landmarks, (Spetch, Cheng,
& MacDonald, 1996; Spetch et al., 1997). Human children develop
the ability to code a goal position as being at a certain distance and
direction from a landmark at around 3 years of age (Sutton, 2006).
When the expansion test paradigm is used to assess their perfor-
ance, they are strongly affected by the complexity of landmark
configurations and the nature of the search space. From 4 years of
age on, human children can search in the middle when presented
with expanded two-landmark configurations in a continuous (i.e.,
with no precise possible hiding sites) large-scale search space: an
open field of a prairie preserve with high grass (Uttal, Sandstrom,
& Newcombe, 2006). However, when a four-landmark configura-
tion is used, children from 5 to 9 years experience difficulties in
using the middle rule (MacDonald, Spetch, Kelly, & Cheng, 2004),
and show no significant improvement with age. Furthermore,
MacDonald et al. tested children aged 3 to 5 years in either a
discrete search space (i.e., with paper cups on a board precisely
indicating the possible hiding sites) or a continuous search space
(i.e., a box lined with confetti). On the one hand, children had more
difficulty learning the task in the continuous space than in the
discrete space, but, on the other hand, an overall higher proportion
of children used the landmark configuration relationally in the
continuous space. However, only one child (aged 42 months)
exclusively searched in the middle of the configuration in the
continuous space above chance. The other four children searched
both near the landmarks and in the middle above chance. In all the
above cited studies the children received only one inter-landmark
distance during training.

In addition to humans, a variety of nonprimate species have
been tested with the expansion paradigm, mainly in a continuous
large-scale space. When trained with constant inter-landmark dis-
tances, during the expansion trials the animals searched either next
to the landmarks (i.e., adopted a beacon strategy, e.g., chickens,
Della Chiesa, Speranza, Tommasi, & Vallortigara, 2006) or they
searched at the learned goal-landmark distances (e.g., bats, Winter,
von Merten, & Kleindienst, 2005; Clark’s nutcrackers, Kelly,
Kippenbroch, Templeton & Kamil, 2008; pigeons, Spetch et al.,

Using a different methodology based on variable training dis-
tances, different species of birds such as Clark’s nutcrackers,
pigeons, and jackdaws searched in the middle of an expanded
two-landmark array (e.g., Jones et al., 2002; Kamil & Jones, 1997,
2000), although some differences between species existed due to
their different life histories (Jones et al., 2002). It is generally
accepted that the birds in those experiments learned to use the
middle of the landmark-landmark distance to find food. The dif-
ferent findings for the pigeons and the nutcrackers strongly suggest
that the training conditions (constant vs. variable training dis-

![Figure 1. An expansion test with four landmarks and diagonal expansion is depicted. In (a) a training configuration is shown and in (b) an expanded configuration. The filled dark circles stand for the landmarks, the cross in (a) for the reward position during training. The light filled circles indicate possible search areas. B = beacon search; M = middle rule; V = vector search.](image-url)
ances) may have a crucial influence on which strategy is preferentially used (Kelly et al., 2008).

With respect to primate species, only a few monkey species were tested with the expansion paradigm. MacDonald et al. (2004) tested three marmoset monkeys with a four-landmark configuration in a discrete space (i.e., with paper cups on a board precisely indicating the possible hiding sites). The scale of the search space was large because the marmosets moved within the space. Marmosets showed evidence of using a combination of a beacon and a vector strategy. Furthermore, when two squirrel monkeys were tested with a four-landmark or a two-landmark array in a discrete space (i.e., in which the possible hiding sites were precisely indicated by holes drilled on a board) they never searched in the middle (Sutton, Olthof, & Roberts, 2000). Finally, two capuchin monkeys tested with a four-landmark and a two-landmark array in a discrete large-scale space did not search in the middle of the expanded array (Potì, Bartolommcei, & Saporiti, 2005). Rather, depending on the complexity of the landmark configuration, the capuchins searched either near the landmarks (with a four-landmark array) or they searched at the vector distance and direction from the landmarks (with a two-landmark array). All the above cited studies used constant inter-landmark training distances.

Even though some primate species were tested with the expansion test paradigm, so far none of the great ape species was investigated. As great apes, especially bonobos and chimpanzees, are phylogenetically most closely related to humans (see, e.g., Enard & Pääbo, 2004), studying these species can help to shed light on the question whether humans are unique in their ability to spontaneously use an array of landmarks configurationally (without training with varying inter-landmark distances). Therefore, we investigated how bonobos would perform when presented with the expansion test paradigm, and how they would perform compared to a monkey species like capuchins that possesses complex spatial skills (see, e.g., Cummins-Sebree & Fragaszy, 2005). As the capuchins did not search in the middle in previous experiments (e.g., Potì et al., 2005), we hypothesized that reducing the size of the search space might elicit a different performance.

In our first experiment we wanted to investigate whether bonobos and capuchins would search in the middle of a four-landmark configuration in small-scale discrete search space after training with constant inter-landmark distances. In a series of follow-up experiments (Experiments 2a through 2c) we used simpler landmark configurations to find out whether the complexity of the landmark configuration might have an influence on the subjects’ behavior. In Experiments 2b through 2c we tested the bonobos with configurations that differed from those used for the capuchins in Experiment 2a, as the two species had revealed a striking difference in performance during training in Experiments 1a and 1b. In the last experiments (3a and 3b) we investigated whether training the subjects with variable inter-landmark distances would facilitate searching in the middle as it was the case with a number of avian species (e.g., Jones et al., 2002).

**Experiment 1**

We trained subjects to find a food reward in the middle of an imaginary square whose vertices were indicated by four identical landmarks. Because the landmarks and the goal occupied different positions in space across trials the subjects were forced to use the landmarks to locate the reward. After training, the subjects were tested with an expanded array by moving all of the landmarks by one hole in diagonal direction. The search space was a small-scale vertical plane. Besides allowing a complete view of the space, this arrangement reduced the influence of any perspective biases.

**Experiment 1a—Capuchins**

**Method**

**Subjects.** Subjects were two adult males, Gal and Robot, housed in the National Research Council (CNR) lab in Rome. Each subject lives in a social group of five capuchin monkeys (Cebus apella). The capuchins are housed in indoor—outdoor cages furnished with tree trunks, perches, and slides (indoor cages: 1.90 m × 2.33 m × 2.47 m high; first-subject outdoor cage: 4.84 m × 8 m × 2.75 m high; second-subject outdoor cage: 4.84 m × 4 m × 2.75 m high). All cages are connected by sliding doors. The monkeys are fed with monkey chow (Rieper Ag SpA via B. v. Guggenberg-Strasse 6 I-39030 Vintl/Vandoies BZ). In addition, fresh fruits and vegetables are given every afternoon. Three times a week the monkeys receive a mixture of curd cheese, vitamins, egg, bran, oats, and sugar. Water was given ad libitum. During the experiment the subjects were never food deprived. Both the subjects had participated in a number of cognitive tests. In particular, Gal had already participated in the Potì et al. (2005) study. They were tested individually five times a week in a familiar experimental cage (74 cm long × 57 cm wide × 75 cm high).

**Apparatus.** The search space was a vertical square plane on which a grid of 9 × 9 holes was drilled. Food was hidden in a compartment behind a hole in the middle of a square configuration of landmarks. A rectangular white wooden board 55 cm long × 55 cm wide × 1 cm deep was mounted vertically on a trolley table (55 cm long × 55 cm wide × 90 cm high). On the board we drilled 81 holes measuring 2 cm in diameter, which were all at the same distance from one another along the orthogonal axes in a 9 × 9 square grid. The landmarks—red round metal ball grips measuring 3 cm in diameter—could be placed in the holes. At the beginning of each trial the trolley carrying the board was placed in front of the experimental cage and aligned with its vertical mesh so that all of the holes were visible and reachable through the mesh. On the experimenter’s side of the board, a wooden box measuring 2.9 cm in length × 2 cm in width × 1.5 cm height was attached below each hole. The animal could reach and inspect each box by inserting one or two fingers in the corresponding hole. We filled all boxes with cat litter so that they served as possible hiding places for a food reward. The food reward was a quarter of a peanut or a raisin. During intertrial intervals the apparatus was taken out of view of the subject.

**Procedure.**

**Familiarization and training.** Landmarks were arranged so as to form the corners of an imaginary square. A food reward was hidden in the box behind the hole in the middle of the landmark configuration, which was contiguous with all four landmarks (see Figure 2a). The position of the landmark configuration and of the food reward changed from trial to trial so as to force the subjects to use the landmarks to locate the reward. The landmarks were never placed in the holes along the perimeter of the board and the reward was never placed behind the hole in the middle of the board to prevent the subjects from using these absolute cues. Consequently, in the training configuration the reward occupied 24
alternative positions on the board. The subjects received sessions of 12 trials each and so the 24 reward positions were presented in two consecutive sessions. The order of presentation of trials within a session was random with the restriction that successive configurations could not share more than one side of the imaginary square. In the first two sessions the experimenter showed the animals where she put the reward. In the following six sessions the food reward was left visible for the first 4 trials, whereas it was totally hidden in the remaining 8 trials. Thus, there were in all 24 visible trials with reward partly visible and 48 trials with reward totally hidden. The 24 visible trials constituted one full series of positions, whereas the 48 not visible trials constituted two different series. The remaining sessions only included trials with the reward not being visible. The subjects were trained to retrieve the reward from the middle hole with their first search. Multiple searches of the same hole were counted only if the subject searched in another hole before returning to the hole. Each hole was identified by a different alphanumerical code. Each trial ended as soon as the animal retrieved the reward, or 1 min elapsed from when the animal started searching. Intertrial interval was 2 min. The animals received daily experimental sessions of 12 trials 5 days a week. All the trials were recorded with a videocamera. The animals received training until satisfying a performance criterion. The criterion was at least 17 first searches in the middle hole in two consecutive sessions (i.e., 24 trials), this is significantly better than chance according to one-tailed binomial test \( p < 0.05 \) with alpha set at .05. Overall, Gal and Robot received 408 and 288 training trials with the food not being visible, respectively. In the last two sessions of training (i.e., 24 trials) each subject retrieved the reward on its first search in 71% of the trials.

**Testing.** Test trials of two types were introduced: control and expansion trials. During control trials animals received the training configuration, but no reward. During expansion trials the distance among the landmarks was doubled along two dimensions so that the landmarks were separated by three holes, and there was no reward (see Figure 2a). Given the general restrictions to prevent the subjects from using absolute cues, the middle of the expanded configuration occupied eight alternative positions on the board. Another 8 trials served as controls. So, each subject received a total of 16 test trials consisting of 8 control trials and 8 expansion trials. The subjects received four sessions. Each session comprised 8 training trials, 2 control trials, and 2 expansion trials. In each session the order of trials was random with the following restrictions: (a) the first 2 trials...
in each session were training trials; (b) the middle of the configuration did not occupy the same position in 2 successive trials; (c) each expansion trial was preceded by a training trial; and (d) the imaginary square of the training trial preceding an expansion trial did not overlap with the imaginary square of the expansion trial following it. Each test trial ended as soon as the animal searched in the middle of the configuration or 1 min elapsed from when the animal started searching.

Data scoring and analysis. All sessions were recorded with a digital videocamera that was placed in front of the apparatus on the experimenter’s side. The videotapes were then later used to code the searches during the control and expansion trials of the test phase. A search was defined as inserting one or two fingers into a hole and moving them around. We analyzed two types of searches. First, to assess whether the subjects’ search was guided by the position of the landmarks, we determined whether the subjects searched more often inside than outside the landmark boundary area using a binomial test. The landmark boundary area was defined as all the holes inside the landmark configuration plus a 1-hole perimeter around the configuration and included 21 holes in the training configuration, and 45 holes in the expanded configuration. We used binomial tests to determine whether searches directed toward the inner landmark area differed from chance. Second, we analyzed in more detail the searches directed to the inside of the landmark boundary area (see Figure 2). In control trials we distinguished three regions that represented the accuracy of the search behavior with respect to the landmark configuration (see Figure 2a): middle (M, 1 hole), inner area (IA, 4 holes), and outer area (OA, 16 holes). In expansion trials we distinguished the following regions that corresponded to the three search strategies that were mentioned earlier (see Figure 2a): M (1 hole), vector (V, 4 holes), and beacon (B, 32 holes). As the holes in the vector area were also part of the beacon area (see Figure 2a), searches in these holes counted for both areas. Because each area contained a different number of holes, we analyzed the number of searches directed to each area in relation to the number of holes available in each area. We used chi-square tests to determine whether searches directed toward each area differed from what would be expected by chance. For example, we compared the frequency of searches in the vector and beacon areas to the expected frequency of searches in those two areas as based on the number of holes per area (e.g., 4 and 32, respectively). We assumed that if the subjects chose randomly, they would be equally likely to target any hole in the respective areas, so that the expected frequency of searches equaled the number of holes per respective area. All statistical tests were evaluated with a significance level of .05. Exact, two-tailed p values are reported where applicable. Two observers separately coded the subjects’ overall searches in all test trials (i.e., in control trials and in expansion trials). For the reliability analysis we only considered cases in which both observers could see a subject’s searches on the board. Interobserver reliability was calculated by means of a weighted kappa. At first, weighted kappas were determined on the basis of individual trials, in which only those trials were considered in the analysis that contained 5 or more searches. These weighted kappas were then averaged over trials. Weighted kappas were calculated using an R program based on a weighting procedure as described in Bortz, Lienert and Boehnke (1990). Average agreement (weighted kappa) was 100%.

Results

In the control condition, both subjects directed at least 80% (expected: 27%) of their searches to the inside of the landmark boundary area (binomial test: p < .001, in all cases). Similarly, they directed at least 94% (expected: 58%) of their searches to the inside of the landmark boundary area in the expansion condition (binomial test: p < .001, in all cases). Focusing exclusively on the inside of the landmark boundary area (see Table 1), the capuchins searched significantly more often in the middle than in any other subarea in the control condition whereas in the expansion condition, their searches were distributed among the three subareas according to the values expected by chance. The capuchins’ distribution of first and overall searches relative to the landmark configuration can be inspected more thoroughly in Figure 3. The subjects’ searches were not a consequence of using absolute cues such as the middle of the board because in control trials the target area was never in the middle of the board whereas in expansion trials the target area always fell in the area enclosed by the holes adjacent the central hole. Yet, the subjects did not target this area preferentially.

Experiment 1b—Bonobos

Method

Subjects. Five adult bonobos (Pan paniscus; Joey, Kuno, Limbuko, Ulindi, Yasa) from the zoo in Leipzig were tested in the facilities of the Wolfgang Köhler Primate Research Center. The bonobos are housed as a social group in spacious indoor and outdoor enclosures, where they have access to climbing trees, ropes, and different kinds of enrichment devices. They are fed four times a day; their diet consisting mainly of vegetables and fruits. In addition they receive enrichment items—such as small food packages or raisin-filled bamboo sticks—once a day five times a week. All the subjects have undergone cognitive tests in the past and participated in a variety of tests on a daily basis (7 days a week) while the landmark study was being conducted. The subjects were tested individually four times a week on average—depending on availability. All testing was conducted in the subjects’ sleeping room where the individuals could be separated during the test with the exception of one subject (Ulindi) who was tested with her still dependent 2.5-year-old infant.

Apparatus. Again the search space was a vertical square plane on which a grid of 9 × 9 holes was drilled. Food was hidden in a compartment behind a hole in the middle of a square configuration of landmarks. The test apparatus consisted of a black board in which we drilled 81 holes in an area of 47 cm × 47 cm. The holes measured 3 cm in diameter and were regularly spaced (1.5 cm between holes) along the orthogonal axes in a 9 × 9 square grid. The board was mounted on a metal grid measuring (58 cm high × 79 cm wide × 4 cm deep) that aligned with the holes and allowed full access to them. On the back of the board behind each hole, we attached square boxes of 4.5 cm × 4.5 cm in width and 12 cm in depth that opened toward the experimenter’s side of the apparatus. The metal grid was then screwed in vertical position on
a frame on one side of the subjects’ sleeping cage with a distance of 41.5 cm to the floor. An opaque plastic panel could be inserted into a slot in front of the board to block the subject’s access to it completely during intertrial intervals. The back of the apparatus, carrying the boxes, was located outside the cage and easily accessible for the experimenter. The landmarks used in the experiment were made out of film containers (3 cm in diameter, 5 cm in height) that were glued onto plastic tubes of 10 cm length and wrapped with strong red tape. When the landmarks were inserted into the holes of the apparatus they appeared as plane red dots to the subjects. In addition, a Plexiglas panel was inserted at the back of the box to hold the landmarks in place while the subject was inspecting the holes. The food reward was a raisin that was hidden in a corner behind the corresponding hole on the experimenter’s side of the apparatus, so that the subject could not see it from his side of the apparatus.

**Procedure.**

**Familiarization, training, and testing.** Everything was as in Experiment 1a with the following exceptions. First, during the first 6 sessions of training the reward was fully visible to the subject once the occluder was removed. Second, intertrial interval was approximately 20 to 30 s. Third, each test trial ended either if the animals stopped searching or if 1 min elapsed from when the animal first started searching. Note, that the criterion to end trials was different from the one that was used for the capuchins. Fourth, the bonobos seemed to have trouble learning to target the middle with their first search. As we did not find any improvement after 60 sessions we decided to discontinue training and test them anyway. In the last 2 sessions of the training Joey retrieved the reward with his first search in 38% of the trials, Kuno in 29% of the trials, Limbuko in 25% of the trials, Ulindi in 29% of the trials, and Yasa in 54% of the trials.

**Data scoring and analysis.** Everything as in Experiment 1a. Average agreement (weighted kappa) was 93.87%.

### Results

In the control condition, all subjects directed at least 82% (expected: 27%) of their searches to the inside of the landmark boundary area (binomial test: \( p < .001 \), in all cases). Similarly, they directed at least 96% (expected: 58%) of their searches to the inside of the landmark boundary area in the expansion condition (binomial test: \( p < .001 \), in all cases). Focusing exclusively on the inside of the landmark boundary area (see Table 1), one bonobo (Kuno) searched significantly more often in the middle than in any other area, whereas the remaining four bonobos searched significantly more often in the middle and in the inner area than in the outer area. In the expansion condition, two bonobos (Kuno and Yasa) searched more often in the vector area than in the beacon area (see Table 1). The distribution of the subjects’ first and overall searches relative to the landmark configuration can be inspected more thoroughly in Figure 4. As in Experiment 1a, the subjects’ behavior was not a consequence of searching near the middle of the board. They searched in the middle of the configuration when it was outside in the middle of the board (i.e., in the control condition), whereas they did not search in the middle of the configuration when it was in the middle of the board (i.e., in the expansion condition).

### Discussion (Experiments 1a and 1b)

All subjects focused their searches in the landmark boundary area both in the control and the expansion conditions thus providing evidence for the use of landmarks but no evidence supporting the use of a middle rule to guide their search. In control trials, the subjects mostly directed their searches toward the middle of the configuration and the inner area (in the case of four bonobos), whereas they searched the least in the outer area. However, during expansion trials, the subjects did not search in the middle of the configuration any longer. Two bonobos searched preferentially in

<table>
<thead>
<tr>
<th>Subject</th>
<th>% M</th>
<th>% IA</th>
<th>% OA</th>
<th>N</th>
<th>Pairwise comparison*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gal</td>
<td>40</td>
<td>30</td>
<td>30</td>
<td>20</td>
<td>M &gt; IA &gt; OA</td>
</tr>
<tr>
<td>Robot</td>
<td>35</td>
<td>30</td>
<td>35</td>
<td>20</td>
<td>M &gt; IA &gt; OA</td>
</tr>
<tr>
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<td>19</td>
<td>76</td>
<td>—</td>
<td></td>
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<tr>
<td>Joey</td>
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<td>42</td>
<td>47</td>
<td>130</td>
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<tr>
<td>Kuno</td>
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<td>59</td>
<td>17</td>
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<tr>
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<tr>
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<td>41</td>
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<tr>
<td>Expectedb</td>
<td>5</td>
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</table>

Note. In the expansion condition the holes in the vector area were also part of the beacon area, consequently all the searches that were counted for the vector area were also counted for the beacon area. Therefore, the sum of the percentage of searches in all areas exceeds 100%. M = middle; IA = inner area; OA = outer area; V = vector; B = beacon.

* This test analyzed whether values of the different subareas differed from each other using chi-square tests comparing expected and observed values. The direction of the difference is indicated by the symbols greater than (>) and less than (<). * Values as expected by chance: If the subjects chose by chance they would be equally likely to target any hole in the respective areas, so that the expected frequency of searches equals the number of holes per respective area.

### Table 1

**Percentage of Searches Directed to the Subareas of the Inner Boundary Area During the Test Phase of Experiments 1a and 1b**

<table>
<thead>
<tr>
<th>Subject</th>
<th>% M</th>
<th>% IA</th>
<th>% OA</th>
<th>N</th>
<th>Pairwise comparison*</th>
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<td></td>
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<td></td>
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<tr>
<td>Expansion</td>
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<table>
<thead>
<tr>
<th>Subject</th>
<th>% M</th>
<th>% V</th>
<th>% B</th>
<th>N</th>
<th>Pairwise comparison*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gal</td>
<td>40</td>
<td>30</td>
<td>30</td>
<td>20</td>
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<td>5</td>
<td>19</td>
<td>76</td>
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<tr>
<td>Joey</td>
<td>11</td>
<td>42</td>
<td>47</td>
<td>130</td>
<td>M, IA &gt; OA</td>
</tr>
<tr>
<td>Kuno</td>
<td>24</td>
<td>59</td>
<td>17</td>
<td>95</td>
<td>M &gt; IA &gt; OA</td>
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<tr>
<td>Limbuko</td>
<td>20</td>
<td>57</td>
<td>23</td>
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<td>M, IA &gt; OA</td>
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<td>Ulindi</td>
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<td>69</td>
<td>M, IA &gt; OA</td>
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<td>Yasa</td>
<td>20</td>
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<td>27</td>
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<td>M, IA &gt; OA</td>
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<td>Expectedb</td>
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Average agreement (weighted kappa) was 93.87%.
The vector area of the expanded configuration, which indicates that they might have learned goal-landmark vectors.

The finding that the capuchins and the bonobos did not preferentially search in the middle of an expanded four-landmark configuration is consistent with previous findings in other species like marmosets, capuchins or Clark’s nutcrackers that were tested in a large search space (Kelly et al., 2008; MacDonald et al., 2004; Poti et al., 2005). Apparently, reducing the size of the search space in the current study did not facilitate searching in the middle in capuchins or bonobos. Alternatively, in the case of the bonobos, it is possible that the performance in the expansion condition was affected by the poor performance during training. It is unclear, why the bonobos failed to reach the training criterion while the capuchins did so with ease. In conclusion, human adults seem to be the only species that spontaneously search in the middle of an expanded four-landmark array irrespective of for example, the size of the search space (Spetch et al., 1996).

**Experiment 2**

As the results in Experiments 1a and 1b might have been influenced by the number of landmarks and the complexity of the landmark configuration, we decided to conduct the expansion test with simpler landmark configurations, to test whether less complex configurations could facilitate searching in the middle of an expanded landmark array. We administered different tasks to the capuchins and the bonobos because the bonobos showed more difficulties than capuchins in learning to search in the middle hole during training. Capuchins were tested in Experiment 2a with a two-landmark configuration in two different orientations, and bonobos in Experiment 2b and 2c with two-landmark configurations with one orientation, but different inter-landmark distances.

**Experiment 2a—Capuchins**

The capuchins received a task very similar to one used by Poti et al. (2005) in a large-scale space, to investigate whether they would search in the middle in a small-scale space. In fact, the main difference between the tasks in the two studies was the scale of space. One subject of the present study (Gal) also participated in the previous one. A two-landmark configuration was used and the reward placed midway along the virtual line connecting the landmarks. The landmarks were separated by three holes, so that the middle hole was not adjacent to the landmarks. We used a two-
Figure 4. The bonobos’ distribution of first and overall searches relative to the landmark configuration in Experiment 1b is shown. (a) Shows the distribution of searches in the expansion condition, and (b) shows the distribution in the control condition. Black circles represent landmarks, gray squares represent overall searches and black squares represent first searches. The number of searches per position is represented by the size of the squares, in which the largest square represents the maximum number of searches in one position and all other squares are scaled accordingly. The configuration is shown in the middle of the square, but, in fact, it never was in the exact middle of the board in real trials. Max = maximum.
landmark configuration with two different orientations to the board, which were analogous to rotations of the landmark line. By using two different orientations, we wanted to rule out the possibility that the capuchins might learn to use the alignment of the landmarks with the board’s side to determine the direction of their search. During training we used one inter-landmark distance. When the subjects reached a performance criterion, expansion trials were introduced during which the landmarks were separated by five holes.

**Method**

**Subjects.** Subjects were the same two adult male capuchins of Experiment 1. One subject (Gal) first participated in Experiment 2a and then in Experiment 3. The other subject (Robot) first participated in Experiment 3 and then in Experiment 2a.

**Apparatus.** The apparatus was the same as in Experiment 1. Only two landmarks were placed on the board on an imaginary straight line and they were separated by three holes during training (see Figure 2b). During the expansion trials the landmarks were separated by five holes (see Figure 2b). Moreover, the imaginary line between the landmarks could be parallel to either side of the board, called horizontal and vertical orientations of the landmark configuration.

**Procedure.**

**Training.** The training procedure was the same as in Experiment 1, with the following exceptions. The middle hole of the training configuration could occupy 40 different positions, 20 for each orientation. To give the subjects daily sessions of 12 trials, we sorted randomly 18 out of the 20 different trials per orientation, which resulted in a full series of 36 trials. A full series was administered in three consecutive sessions before starting a new one. During the first three sessions the food reward was left visible in the box behind the hole in the middle of the configuration of landmarks. In each of the following six sessions the food reward was left partly visible in the litter in the first 4 trials, whereas it was totally hidden in the remaining 8 trials. Thus, there were in total 24 trials with the reward being partly visible (12 with vertical and 12 with horizontal orientation) and 48 trials with the reward being completely hidden (24 with vertical and 24 with horizontal orientation). The remaining sessions only included trials with the food not being visible under the litter. Gal and Robot received 132 and 216 training trials with the food not being visible, respectively. In the last two sessions of the training (i.e., 24 trials) Gal and Robot retrieved the reward on their first search in 83% of trials and 71% of trials, respectively.

**Testing.** The testing procedure was the same as in Experiment 1, with the following exceptions. During expansion trials the distance among the landmarks was doubled, so that the landmarks were separated by five holes (see Figure 2b). The middle of the expanded configuration occupied 24 alternative positions, 12 per orientation. Another 24 trials served as control trials. So, each subject received a total of 48 test trials, 24 control trials (12 per orientation) and 24 expansion trials (12 per orientation). The subjects received 12 sessions. Each session comprised 8 training trials, 2 control trials, 1 per orientation, and 2 expansion trials, 1 per orientation. In each session the order of trials was random with the same restrictions applying as in Experiment 1 and the following exceptions: First, the same orientation could not be given more than twice in a sequence, and second, in case an expansion trial had the same orientation as the preceding trial, the two configurations could not share any other parts, whereas in case an expansion trial and preceding trial had different orientations, the corresponding middle positions had to differ. Each test trial ended as soon as the animal searched in the middle of the configuration or 1 min elapsed from when the animal started searching.

**Data scoring and analysis.** Data scoring and analysis were the same as in Experiment 1 with the following exceptions. The landmark boundary area included 19 holes in the training (see Figure 2b) and 25 holes in the expanded configuration (see Figure 2b). In control trials in the M included 1 hole, the IA 2 holes, and the OA 16 holes. In expansion trials in the M comprised 1 hole, the V 2 holes, and the B 16 holes. Moreover, we conducted two further analyses. First, we assessed whether the subjects used an absolute cue such as the middle of the board to guide their search during expansion and control trials. In particular, we wanted to control for the possibility that the subjects might have been more likely to search in the middle of the landmark array when it coincided with the middle of the board. We defined the middle of the board as those holes adjacent to the central hole, whereas the periphery included all the remaining holes. We then calculated expected frequencies based on the number of trials in which the middle of the landmark configuration could be found in the middle of the board or in the periphery (e.g., out of 6 trials, 2 trials fell in the middle and 4 trials in the periphery). Finally, we compared the expected frequencies with the frequencies of middle searches (middle of the landmark array) in the respective trials (chi-square goodness-of-fit tests). If we found no significant differences, then the subjects’ were not more likely to make middle searches when the middle of the landmark array coincided with the middle of the board. Second, we assessed whether the subjects changed their search behavior in the course of testing. We wanted to control for the possibility that the subjects might show an effect of learning and search more often in the middle of the landmark configuration at the end of the experiment than at the beginning. Thus, we compared the frequencies of the subjects’ middle searches in the first and second half of trials in both control and expansion condition using Wilcoxon’s test. Average agreement (weighted kappa) between two independent observers was 99.92%.

**Results**

In the control condition, the capuchins directed at least 71% (horizontal orientation) and 56% (vertical orientation; expected: 24% in both configurations) of their searches to the inside of the landmark boundary area (binomial test: \( p < .001 \), in all cases). Similarly, they directed at least 65% (horizontal orientation) and 65% (vertical orientation; expected: 32% in both orientations) of their searches to the inside of the landmark boundary area in the expansion condition (binomial test: \( p < .001 \), in all cases).

Focusing exclusively on the inside of the landmark boundary area (see Table 2), in the horizontal orientation Gal searched significantly more often in the middle than in inner area and the outer area, and Robot searched significantly more often in the middle and in the inner area than in the outer area. In the vertical orientation, Gal also searched more often in the middle and the inner area than in the outer area, and Robot searched more often in
the middle and the inner area than in the outer area. In the expansion condition, Gal searched in the middle and vector area of the horizontal orientation significantly more often than in the beacon area whereas Robot searched significantly more often in the middle than in the beacon area of the vertical orientation. The capuchins’ distribution of first and overall searches relative to the landmark configuration can be inspected more thoroughly in Figure 5.

The capuchins did not preferentially target the middle of the configuration when it coincided with in the middle of the board. In fact, there was no significant difference between the expected distribution of middle searches in the middle and periphery and the observed distribution (the maximum chi-square value was: $\chi^2 = 0.750, df = 1, N = 6, p = .671$). Moreover, the capuchins’ search of in the middle of the configuration did not change over trials (Wilcoxon’s test: $z < 1.42, p > .49$ in all cases).

**Discussion**

The capuchins’ searches were guided by the landmarks, as they concentrated their searches in the landmark boundary area independently of in the middle of the board. Moreover, during control trials the capuchins searched mainly in the middle hole. During expansion trials the capuchins searched preferentially in the middle of the configuration although only with respect to one orientation (and a different one for each subject).

The capuchins’ behavior was quite different when similar horizontal and vertical orientations were used in a large scale space in a study by Potì et al. (2005). In that study two capuchins (among them Gal) did not search in the middle but they searched preferentially at the learned goal-landmark distances in both landmark orientations. Given that the main difference between the tasks in the two studies was the scale of space, we suggest that a small-scale space may facilitate the behavior of searching in the middle of a two-landmark configuration in capuchins.

Still, both capuchins targeted the middle of the configuration with only one of the two orientations, so that the individual search behaviors seem to be strongly influenced by the landmark orientation. In addition, one capuchin searched in the Vector area as much as in the middle. In the light of these results, we decided to adopt the method of varying the inter-landmark distance during training which has successfully elicited acquisition of the middle rule in different avian species (see Experiment 3a).

**Experiment 2b—Bonobos**

Only bonobos were tested in this experiment. Given the difficulties the subjects experienced during the training in Experiment 1, a simplified configuration was used in Experiment 2b. The bonobos were trained with a two-landmark configuration with one hole between landmarks assuming that they would acquire the new configuration with more ease. In the expansion condition the distance between landmarks was increased to three holes.

**Method**

**Subjects.** Three of the five bonobos (Kuno, Limbuko, Yasa) from Experiment 1 participated in this study. The subjects were again tested in their sleeping cages and received on average four sessions per week.

**Apparatus.** The apparatus described in Experiment 1 for bonobos was used. During training and control trials the landmarks were in horizontal orientation and separated by one hole, whereas during expansion trials the landmarks were separated by three holes (see Figure 2c).

**Procedure.**

**Training.** The training procedure followed the one outlined in Experiment 1 with the following exceptions. The reward was hidden from the start of experiment. The subjects were trained with an array of two identical landmarks that were arranged in a horizontal array with one hole between landmarks (see Figure 2c). Trials were arranged according to the rules of Experiment 1 and the following rule: Configurations did not share a landmark in two consecutive trials. Performance criterion was as in Experiment 1. Kuno, Limbuko, and Yasa reached the criterion after 48 trials, 288 trials, and 72 trials, respectively. In the last two sessions of the training Kuno retrieved the reward on his first search in 87.5% of the trials, Limbuko in 79.2% of the trials, and Yasa in 75% of the trials.
Testing. The testing procedure was the same as in Experiment 1 with the following exceptions. In the expanded configuration the landmarks were separated by three holes (see Figure 2c). The five vertical reward positions on the left and right side of the apparatus were omitted, so that 14 positions remained to be tested. The subject received a total of seven sessions with two expansion, two control and eight training trials. Trials were arranged according to the same rules as in Experiment 1 and the following rules: The configuration in the expansion trial and the preceding training trial did not overlap or share a landmark. Each test trial ended either when the animals stopped searching or 1 min elapsed from when the animal first started searching.

Data scoring and analysis. Data scoring and analysis were the same as in Experiments 1 and 2a, with the following exceptions. The landmark boundary area included 12 holes in the training (see Figure 2c) and 16 holes in the expanded configuration (see Figure 2c). In control trials the M included 1 hole and the OA 12 holes. In expansion trials the M comprised 1 hole, the V 2 holes, and the B 16 holes. Again, the holes in the vector area were also part of the beacon area so that searches in these holes counted for both areas. Average agreement (weighted kappa) between two independent observers was 99.13%.

Results

In the control condition, the bonobos directed at least 90% (expected: 16%) of their searches to the inside of the landmark boundary area (binomial test: \( p < .001 \), in all cases). Similarly, they directed at least 93% (expected: 24%) of their searches to the inside of the landmark boundary area in the expansion condition (binomial test: \( p < .001 \), in all cases). Focusing exclusively on the inside of the landmark boundary area (see Table 3), all three subjects searched in the middle more often than in the outer area in the control condition. In the expansion condition, Kuno and Limbuko searched in the vector area significantly more often than in any other area, whereas Yasa searched in the middle and the vector area more often than in the beacon area (see Table 3). The bonobos’ distribution of first and overall searches relative to the landmark configuration can be inspected more thoroughly in Figure 6.

The bonobos did not preferentially target the middle of the configuration when it coincided with the middle of the board (the maximum chi-square value was: \( \chi^2 = 2.133, df = 1, N = 24, p = .200 \)). Moreover, the bonobos’ search of the middle of the configuration did not change over trials (Wilcoxon’s test: \( z < 1.64, p > .25 \) in all cases).
Discussion

Two of the three bonobos quickly learned to use the new landmark configuration to guide their search, so reducing the complexity of the configuration appeared to facilitate the acquisition process. Moreover, in the expansion condition, two of the three bonobos (Kuno and Limbuko) searched preferentially in the vector area, and thus seemed to have coded the goal-landmark distances to locate the food reward. The remaining bonobo (Yasa) also searched in the middle more often than in the beacon area. As with capuchins, this last finding is quite unusual in the relevant literature and it may indicate geometric rule learning by bonobos—an issue which we return later in the general discussion.

We wondered whether the fact that the food reward could always be found in a position adjacent to the landmarks during training, made coding vectors from the respective landmarks an easy default. Therefore, in a follow-up experiment, we administered a task with a two-landmark configuration and three holes inter-landmark distance during training to the bonobos.

Experiment 2c

In this experiment we used a two-landmark configuration and placed the reward midway along the virtual line connecting the landmarks. The landmarks were separated by three holes and the middle hole was not adjacent to the landmarks. We used one inter-landmark distance during training. Compared to Experiment 2a the task was easier because only the horizontal orientation of the configuration was used.

Method

Subject. One bonobo (Kuno) from Experiments 1 and 2b participated in this study. The subject was tested in his sleeping cages and received on average four sessions per week.

Apparatus. The apparatus described in Experiment 1 for bonobos was used. During training the landmarks were in horizontal orientation and separated by three holes (see Figure 2b, horizontal orientation), whereas during expansion the landmarks were separated by five holes (see Figure 2b, horizontal orientation).

Procedure. Training. The training procedure was the same as in the previous experiments with the following exceptions. The subject was given 1 session per day with 10 trials per session. The subject was trained with an array of two identical landmarks that were arranged in a horizontal array with three holes between landmarks (see Figure 2b, horizontal orientation). The training lasted for 30 sessions. In the last 2 sessions of the training Kuno retrieved the reward on his first search in 55% of the trials.

Testing. The testing procedure was the same as in the previous experiments with the following exceptions. In the expanded configuration the inter-landmark distance was increased to five holes (see Figure 2b, horizontal orientation). Only six horizontal positions in the middle of the apparatus were used. The subject received a total of four sessions consisting of seven training trials, and either two expansion trials and one control trial or one expansion trial and two control trials. The order of the different types of sessions was a, b, a, b, so that the subject experienced a total of six control and six expansion trials. Each test trial ended either if the animal stopped searching or if 1 min elapsed from when the animal first started searching.

Data scoring and analysis. Data scoring and analysis were the same as in Experiment 2b with the following exceptions. The landmark boundary area included 19 holes in the training (see Figure 2b, horizontal orientation) and 25 holes in the expanded configuration (see Figure 2b, horizontal orientation). In control trials the M included 1 hole, the IA 2 holes, and the OA 16 holes. In expansion trials the M comprised 1 hole, the V 2 holes, and the B 16 holes. Average agreement (weighted kappa) between two independent observers was 100%.

Results

Kuno directed 87% of his searches to the inside of the landmark boundary area both in the control and expansion conditions (binomial test: \( p < .001 \) in both cases; expected: control = 24%, expansion = 52%).
expansion = 32%). Focusing exclusively on the inside of the landmark boundary area (see Table 3), Kuno searched in the middle of the configuration and the inner area significantly more often than in the outer area in the control condition. In the expansion condition, he searched significantly more often in the middle of the configuration than in the beacon area or the vector area, and he searched in the vector area more often than in the beacon area (see Table 3). Kuno’s distribution of first and overall searches relative to the landmark configuration can be inspected more thoroughly in Figure 7.

Kuno did not preferentially target the middle of the configuration when it coincided with in the middle of the board (the maximum chi-square value was: \( \chi^2 = 0.071, df = 1, N = 12, p > 0.999 \)). Moreover, his search in the middle of the configuration did not change over trials (Wilcoxon’s test: \( z = 0.00, p > 0.999 \) in both cases).

**Discussion**

Kuno’s searches were guided by the landmarks. In the control condition, he searched between landmarks whereas in the expansion condition, he searched in the middle of the configuration more often than in any other area. Two factors may have contributed to the result: First, during training the reward could no longer be found in a position adjacent to the landmarks as in the previous experiment, and second, Kuno had had a lot of experience with the task from participating in previous experiments. As we wanted to investigate whether training with variable training distances would also facilitate searching in the middle in bonobos, we presented them in Experiment 3 with two different inter-landmark distances during training.

**Experiment 3**

The subjects were trained with a variable inter-landmark distance. They were trained to find a food reward midway along the virtual line connecting two landmarks, with the landmarks separated by either one or three holes. When the subjects reached a performance criterion expansion trials were introduced with the landmarks separated by five holes.

**Experiment 3a—Capuchins**

**Method**

**Subjects.** The same two capuchins (Gal and Robot) of Experiments 1a and 2a participated in this study.

**Apparatus.** The apparatus described in Experiment 1 was used. During training the landmarks could be separated by either one or three holes (see Figure 2d). Only the vertical orientation of the landmark line to the board was used, the same as in Experiment 2a. During expansion trials the landmark were separated by five holes (see Figure 2d).

**Procedure.**

**Training.** The training procedure followed the one outlined in Experiment 1 with the following exceptions. The two inter-
landmark distances were balanced in each session, and the same distance was not presented more than twice in a row. The middle hole of the landmark configuration could occupy 34 different positions on the board when landmarks were separated by one hole, and 20 positions when landmarks were separated by three holes. To give the subjects daily sessions of 12 trials, we sorted randomly 18 out of the 34 and 18 out of the 20 different positions per inter-landmark distance, which resulted in a full series of 36 trials. A full series was administered in three consecutive sessions before starting a new one. During the first three sessions the food reward was left visible in the middle of the configuration of landmarks. In each of the following six sessions the food reward was left visible for the first 4 trials (balanced for each of the two inter-landmarks distances), whereas it was totally hidden for the remaining 8 trials (balanced for each of the two inter-landmarks distances). Thus, there were in all 24 trials with the reward being partly visible and 48 trials with reward being totally hidden. All remaining sessions only included trials with the food not being visible. Both capuchins needed 72 trials with the reward being totally hidden to reach the training criterion. In the last two sessions of the training Gal retrieved the reward on his first search in 83.33% of the trials, and Robot in 92% of the trials.

**Testing.** The testing procedure was the same as in the previous experiments with the following exceptions. Each session of 12 trials comprised 8 training trials, 2 control trials, with training configuration and no reward, 1 for each inter-landmark distance, and 2 expansion trials. Each subject received six sessions of 12 trials. So, each subject received 12 control trials (6 for each inter-landmark distance) and 12 expansion trials overall. Within each session, training trials were balanced according to inter-landmark distance. In each session the order of trials was random with the same restrictions as in the previous experiments and the following restriction: The same inter-landmark distance could not be given more than twice in a sequence. Each test trial ended as soon as the animal searched in the middle of the configuration or 1 min elapsed from when the animal started searching.

**Data scoring and analysis.** Data scoring and analysis were the same as in Experiment 1 with the following exceptions. In the training configuration, the landmark boundary area included 13 and 19 holes with the 1-hole and the 3-hole inter-landmark distances, respectively (see Figure 2d). In the expanded configuration the landmark boundary area included 25 holes in the expanded configuration (see Figure 2d). In control trials the M included 1 hole and the OA 12 for the 1 hole inter-landmark distance. For the 3 holes inter-landmark distance the M included 1 hole, the IA 2 holes, and the OA 16 holes. In expansion trials the M comprised 1 hole, the V 4 holes, and the B 16 holes. Average agreement (weighted kappa) between two independent observers was 100%.

**Results**

In the control condition, the capuchins directed 100% (one hole, expected: 16%) and at least 90% (three holes, expected: 24%) of their searches to the inside of the landmark boundary area (binomial test: $p < .001$, in all cases). Similarly, they directed at least 70% (expected: 32%) of their searches to the inside of the landmark boundary area in the expansion condition (binomial test: $p < .001$, in both cases). Focusing exclusively on the inside of the landmark boundary area (see Table 4), in control trials the capuchins searched significantly more often in the middle of the configuration than in any other area regardless of the inter-landmark distance. In the expansion condition, Gal searched in the middle and the vector area significantly more often than in the beacon area whereas Robot searched in the
middle more often than in any of the two other areas (see Table 4). The capuchins' distribution of first and overall searches relative to the landmark configuration can be inspected more thoroughly in Figure 8.

Capuchins did not preferentially target the middle of the configuration when it coincided with in the middle of the board. In fact, there was no significant difference between the expected distribution of middle searches in the middle and periphery and the observed distribution (the maximum chi-square value was: $\chi^2 = 0.000$, $df = 1, N = 6, p > .999$). Moreover, capuchins' searching in the middle of the configuration did not change over trials (Wilcoxon's test: $z = 0.00$, $p < .999$ in all cases).

### Experiment 3b—Bonobos

#### Method

**Subjects.** Two bonobos (Kuno and Yasa) from Experiments 1 and 2 participated in this study.

**Apparatus.** The apparatus described in Experiment 1b was used. During training the landmarks could be separated by either one or three holes (see Figure 2d). Only the vertical orientation of the landmark line to the board was used, the same as in Experiment 2a. During expansion trials the landmark were separated by five holes (see Figure 2d).

**Procedure.** It was as in Experiment 3a with one exception: Each test trial ended either when the animals stopped searching or when 1 min elapsed from when the animal first started searching. Note, that the criterion to end trials was different from the one that was used for the capuchins. Moreover, the bonobos were given 30 training sessions with the reward being hidden. In the last 2 sessions of the training Kuno retrieved the reward on his first search in 62.5% of the trials, and Yasa in 50% of the trials.

**Data scoring and analysis.** Everything as in Experiment 3a. Average agreement (weighted kappa) was 99.63%.

#### Results

In the control condition, the bonobos directed at least 84% (one hole, expected: 16%) and 94% (three holes, expected: 24%) of their searches to the inside of the landmark boundary area (binomial test: $p < .001$, in all cases). Similarly, they directed at least 93% (expected: 32%) of their searches to the inside of the landmark boundary area in the expansion condition (binomial test: $p < .001$, in both cases). Focusing exclusively on the inside of the landmark boundary area (see Table 4), in control trials the bonobos searched significantly more often in the middle than in the outer area with respect to the one-hole inter-landmark distance, and significantly more often in the middle and the inner area than in the outer area with respect to the three-holes inter-landmark distance (see Table 4). In the expansion condition, the bonobos searched in the middle and the vector area significantly more often than in the beacon area (see Table 4). The bonobos’ distribution of first and overall searches relative to the landmark configuration can be inspected more thoroughly in Figure 8.

The bonobos did not preferentially target the middle of the configuration when it coincided with in the middle of the board (the maximum chi-square value was: $\chi^2 = 2.000$, $df = 1, N = 9, p = .288$). Moreover, the bonobos’ search of in the middle of the configuration did not change over trials (Wilcoxon’s test: $z < 1.35, p > .49$ in all cases).

#### Discussion (Experiments 3a and 3b)

In the control condition the capuchins and the bonobos targeted the middle of the configuration and they did so by referring to the landmarks rather than to other cues. In the expansion condition at least one subject (Robot) searched in the middle of the configuration more than in any other area. The other subjects searched both in the middle and the vector areas.

The results of Experiment 3 again suggest that for capuchins the scale of the search space counts. In another study with two capuchins the expansion paradigm was used in a large-scale space (Poti et al., 2005). No capuchin ever searched in the middle of the expanded configuration with either four- or two-landmark arrays. Furthermore, Poti and collaborators conducted an experiment with one capuchin that was trained with variable inter-landmark training distances as in our Experiment 3, but in a large-scale space. When presented with the expanded configuration the subject
searched along the landmark line but at the two training distances from one landmark, and again not in the middle (Poti, Bartolommei, & Saporiti, 2004), which is in contrast to the findings from the current studies. Unfortunately, similar evidence for bonobos concerning the influence of the size of the search space is not available and may be a question for further investigations.

General Discussion

In this study we show that bonobos and capuchin monkeys can learn to search in the middle of a landmark configuration in a small-scale space. They do so to a limited extent, however.

When confronted with a four-landmark configuration the subjects learned to search inside the landmark boundary, but showed no evidence of searching in the middle of the expanded array. Two bonobos, however, showed evidence of coding vectors from the landmarks to the goal location. For bonobos and capuchins, this result is similar to the one obtained previously in a large-scale space (Poti et al., 2005). It is also similar to the results reported for a number of nonhuman species as already discussed above.

When presented with a two-landmark configuration and a constant inter-landmark training distance, the subjects sometimes...
searched preferentially in the middle of the configuration. More specifically, if during training the food reward could be found in a position directly adjacent to the landmarks (Experiment 2b), two bonobos preferentially searched the vector area, and one bonobo searched both the vector area and in the middle. When the inter-landmark distance was greater during training (so that the reward could no longer be found adjacent to the landmarks), one bonobo preferentially searched in the middle, and the two capuchins did so occasionally. The capuchins’ search behavior appeared to depend on the landmark orientation that was used (horizontal or vertical). In sum, not all subjects searched in the middle, but among those who did, at least two subjects searched in the middle more than any other place, whereas the other subjects searched both in the middle and in the vector area. Clearly, the primates did not simply learn to search near one or more landmarks, that is, they did not use the landmarks as beacons. However, two competing hypotheses could explain the subjects’ behavior. The first hypothesis is that the primates learned both goal-landmark vectors and the abstract geometrical middle (i.e., to code the food location in terms of the relation between the landmarks). However, primates might be able to learn this middle rule only if the configuration is simple, there are not other variables to be taken into account (such as orientation), and the scale of the space is small.

Learning to search in the middle does not exclude searching in other areas as well. For example, young children learned both goal-landmark vectors and the middle of a two-landmark configuration (Ut tall et al., 2006). Similarly, McDonald et al. (2004) reported that three children in a four-landmark array mentioned “middle” when searching in the expanded array, which indicates that they may have learnt the abstract geometrical rule. However, only one of them (aged 42 months) exclusively searched in the middle of the configuration in the continuous space above chance whereas another searched both near the landmarks and in the middle above chance.

Why did not all primates adopt the middle rule and/or not in all conditions? The middle rule is an abstract construct and as such very likely to be learned and applied only in certain conditions, and by different subjects with different ease. This is in fact what happens with young children (e.g., MacDonald et al., 2004), who searched more near one landmark than in the middle.

Our results with two landmarks and a constant training distance (Experiment 2) may be the first indication that a nonhuman species can learn a middle rule with this method. No nonhuman species trained with constant inter-landmark distances ever searched in the middle of an expanded configuration of landmarks in any of the previous studies, at least so far as distinct objects were used as landmarks (e.g., bats, Winter et al., 2005; chickens, Della Chiesa et al., 2006; Clark’s nutcrackers, Kelly et al., 2008; gerbils, Collett et al., 1986; pigeons, Spetch et al., 1996, 1997). A different behavior was observed when continuous surfaces such as the walls of a room were the possible landmarks. For example, in a study by Tommasi and collaborators (Tommasi, Vallortigara & Zanforlin, 1997), chickens were trained to peck in the middle of a round or square room (with no distinct frames or objects). When chickens were placed in an enlarged square room, they showed two separate peaks in the middle and at the training distance from the walls. The authors suggested that the chickens during training encoded information on both the absolute and the relative distance of the food from the walls of the arena. It may be that rigid boundaries like the walls of a room increase the salience of the geometry of the space (Ut tall et al., 2006).

The second hypothesis is that the subjects searched in the middle of the expanded configuration in Experiments 2a, 2b, 2c by averaging the two goal-landmark vectors they had learned during training. This hypothesis would account for the results without appealing to an abstract concept, and in this sense it would be a simpler explanation. However, it would need additional hypotheses to explain why the subjects did not always average vectors. In fact, the bonobos averaged vectors in Experiment 2 but not in Experiment 1, and in Experiment 2 capuchins and bonobos averaged vectors only sometimes. Vector averaging is supposed to be the product of a general psychological process to overcome behavioral conflict. We know that capuchins and bonobos can learn goal-landmark vectors, as some subjects clearly did in our experiments, and in the expansion test different goal-landmark vectors produce conflicting results. So, it is not clear why the primates tried to resolve the conflict in some circumstances but not in others.

In the third experiment, we further modified the training procedure and used two different inter-landmark training distances. One capuchin preferentially searched in the middle, whereas the other capuchin and both bonobos searched both in the middle and in the vector area. In the case of the capuchins, exposure to more than one inter-landmark distance during training increased the likelihood that they would prefer searching in the middle, provided however that the number of landmarks was minimal and the configuration as simple as possible. What strategy did the primates adopt to cope with the task in Experiment 3? It is unlikely that the subjects searched in the middle by vector averaging in Experiment 3, because vectors were not consistent indicators of the correct locations. So, the results of Experiment 3 could be used to support the middle rule hypothesis, but not goal-vector average hypothesis. It is conceivable that learning the middle rule is within the capabilities of primates, yet only under certain conditions. In this sense, our results are similar to those reported for some avian species that learned to search in the middle between two landmarks with a variable inter-landmark training distance (e.g., Jones et al., 2002; Kamil & Jones, 1997), even when the animals were tested with new inter-landmark distances outside of the range of the training distances. These results were explained by the animals having learned a general geometrical rule, rather than by averaging between the dictates of distinct goal-landmark vectors.

In conclusion, we found some evidence suggesting that when capuchins and bonobos are trained to search in the middle of two-landmark configurations with either constant or variable training distances, they can continue to search in the middle of the configuration when the distance between the landmarks is increased beyond the range of the training distances. Further research could determine more precisely what strategies primates adopt to cope with these tasks. Moreover, our experiments provide some evidence that the number of elements in a configuration, the type of training procedure and the scale of the search space might affect primates’ performance in the expansion task. To the extent that primates are highly constrained in their abilities to search in the middle of a simple configuration, their behavior could be compared to that of human children (MacDonald et al., 2004). Thus far, human adults remain unique in their ability to extract abstract geometrical rules from complex arrays of landmarks irrespective of the properties of the search space.
References