

Sophisticated Euclidean maps in forest chimpanzees

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We examined the spatial orientation abilities of wild chimpanzees, *Pan troglodytes verus*, in Tai National Park, Côte d'Ivoire. Predictions resulting from the hypothesized use of topological maps and Euclidean maps in a tropical forest were tested using quantified measurements of travel direction, distance travelled and routes based on landmarks. The results strongly suggest that the chimpanzees knew precisely where they were going, travelled in a straight line to reach food resources, and were aware of the distance they were going to walk. They also returned to a food resource from many different directions rather than repeatedly using the same paths. Furthermore, the initial direction taken to reach a food source corresponded exactly to the general direction needed to reach that resource suggesting that they did not navigate by landmarks to reach the goal. To control for the possibility that chimpanzees may remember numerous landmarks allowing them to navigate as precisely as if with a Euclidean map but in reality only using a topological one, we compared movement patterns in the core and peripheral areas of the territory, as they used the latter 75% less frequently. We found no variation in the linearity of movement, but a reduction in the distance travelled at the periphery, which corresponds to the possibility that the chimpanzees used a Euclidean map to navigate between resources. All these results provide additional support for the use of a Euclidean map in chimpanzees and we discuss how particular ecological conditions could favour the development of such sophisticated spatial orientation abilities in primates.

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Living in a tropical forest involves coping with a complex environment with an unpredictable spatial and temporal distribution of resources. These characteristics have been hypothesized to favour the development of greater mental abilities in primates (Milton 1981). With such capacities, primates know 'where' the resources are (Garber 1989; Garber & Paciulli 1997; Janson 2007), 'when' to look for them (Janmaat et al. 2006a, b) and 'what or how much' there is likely to be (Cunningham & Janson 2007a, b), and this is true when the resources are tools rather than food sources (Boesch & Boesch 1984). Equipped with such a powerful spatial memory, primates have been seen navigating efficiently when moving towards food resources, and often finding the closest ones (Menzel 1973; Boesch & Boesch 1984; Garber 1988; Janson 1998) or the most productive ones (Garber 1988; Janson 1998; Cunningham & Janson 2007a, b; Valero & Byrne 2007).

Although there are some studies on spatial memory in animals in their natural habitat, little is known about the exact mechanisms involved in navigation. Two main mechanisms have been proposed

and discussed in the context of primate foraging (Byrne 2000; Garber 2000). The first implies a representation of space, in which the animal is not able to compute distance and direction to a known location directly, but uses a route based on landmarks, which is like a succession of instructions containing approximate local information about direction and distance, but shown to be insufficient for the provision of general ideas of direction, distances and short cuts (Piaget & Inhelder 1956; Byrne 1979). This mechanism is called a topological or network map (Byrne 2000), and is based upon the topological relation between objects (Piaget & Inhelder 1956). There is some such evidence in animals for the use of landmarks along familiar routes (MacKinnon 1974; Milton 1980, 2000; Sigg & Stolba 1981; Cartwright & Collett 1983; Wehner et al. 2006; Di Fiore & Suarez 2007). The second mechanism is a representation of space that allows the animal to compute distance and direction from any one place to any other known place. This mechanism has been called a mental or cognitive map (Tolman 1948; O'Keefe & Nadel 1978) or vector map (Byrne 2000), and is based on a Euclidean representation of space (Piaget & Inhelder 1956). We use the term Euclidean map to characterize such a mechanism. The Euclidean map is recognized as the most efficient mechanism. In a well-known area where the topological map can be efficient, the Euclidean map offers an important additional flexibility. In human

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children, the Euclidean notion of space emerges from the topological representation at around 6 or 7 years of age, allowing more complex and flexible spatial operations (Piaget & Inhelder 1956). Its development has been shown to be a function of socioecological living conditions (Wassmann & Dasen 1998; Boesch 2007). Recently, Burgess (2006), following Piaget & Inhelder (1956), noted that human spatial memory could rest on the combination of egocentric and allocentric representations of space.

It is notoriously difficult to make conclusions about the existence of a Euclidean map for animals in their natural environment, first, because there is no natural condition where animals would face a new environment to show novel short cuts, detours or path innovation in the case of a Euclidean map (Bennett 1996), and second, because a topological map with many landmarks could be as precise as a Euclidean map (Byrne 2000). Nevertheless, a Euclidean map remains more flexible, allowing the discovery of novel short cuts and detours under changing conditions, and navigation remains highly efficient in less well-known areas. Thus, since it is difficult to test wild animals in a new environment, another way to differentiate between these two mechanisms is to delineate the areas where animals are less frequently present. Territorial animals navigating in a clumped habitat, such as Tai chimpanzees, *Pan troglodytes verus*, are renowned for preferentially using the core area rather than the peripheral area (Boesch & Boesch-Achermann 2000; Herbinger et al. 2001). Therefore, we expect different movement patterns between the core area and the peripheral area, as the further they move from the core area, the fewer available landmarks they have to guide their movements.

Chimpanzees living in Tai National Park, Côte d'Ivoire, are perfect subjects for a study on spatial orientation. On the one hand, the forest is homogeneous throughout the territory and resources are generally evenly dispersed (Anderson et al. 2005). On the other hand, chimpanzees live in a fission–fusion society, and it is therefore possible to tease apart the contribution of individual orientation from social or sexual influences. In the first part of the study, we tested whether chimpanzees know where they are going by analysing the pathway selected to reach the resource in a low-visibility environment with many potential food sources. The linearity index is a good measure of determining how close to a straight line they travel from one resource to another and how efficiently they can reach their goal (Noser & Byrne 2007a, b; Valero & Byrne 2007). Whereas a low linearity index would indicate a lack of goal directedness during navigation, a high linearity index is not enough by itself to identify the mechanism involved in navigation because it is possible that animals might follow a simple 'straight-line' strategy that would be efficient in a habitat rich in resources without using any kind of Euclidean map (Janson & Byrne 2007). Alternatively, a simple topological map with many landmarks could also result in high linearity. Therefore, travel speed has been proposed to be a useful quantification of the anticipation of reaching a goal, particularly when associated with high linearity or long travel distances (Janson & Di Bitetti 1997; Janmaat et al. 2006b; Noser & Byrne 2007b). Constant speed throughout travel between two resources would represent a lack of goal directedness (which could be caused by a lack of knowledge about the resources' locations but also a lack of motivation). In contrast, variation in travel speed while the resource is still out of sight and scenting range could indicate that chimpanzees know that they are approaching the resource. The expected variation in travel speed is important and can be predicted in both directions. On the one hand, acceleration would be the expected result if motivation increases as the chimpanzees near their goal. On the other hand, under the typical fission organization of chimpanzees in their natural habitat, individuals may slow down as they near the resource in case other silent group members are already present at it. For these reasons,

a significant variation in speed would suggest that the chimpanzees have a notion of distance.

Furthermore, if chimpanzees only use a topological map, they would be more likely to approach a known resource from the same directions, that is, from the same landmarks every time. They would only be able to use several routes to reach the same resource if they had many landmarks. Therefore, when a known food source is revisited, the prediction from a topological map is very different from that from a Euclidean map, as the latter allows individuals to arrive at a resource from all possible directions. In addition to testing for the notion of direction, we compared the difference between the initial direction when leaving a resource with the general direction adopted to reach the next. If chimpanzees were using a Euclidean map, this difference should be negligible, whereas if they were following landmarks it would be higher because they would reorient along the way when encountering landmarks or nodes (Di Fiore & Suarez 2007).

Finally, we tried to distinguish between Euclidean and topological maps by investigating differences in the movement patterns between the peripheral and central areas of the territory. Since chimpanzees preferentially use the core area, we expected the navigation to be less linear to reach a resource located at the periphery when using a topological map. Alternatively, with a Euclidean map, the ability to compute direction and distance to a known place maximizes efficiency in terms of high linearity. We also expected linearity to remain constant between the periphery and the core area. However, distance travelled might vary according to the number of resources known. If no variation in movement patterns were detected at the periphery, it would suggest that the chimpanzees had accumulated a similar knowledge of the periphery as of the core area.

METHODS

Study Site and Subject

We collected data on the chimpanzees of the south group of the Tai chimpanzee project in the Tai National Park, Côte d'Ivoire (Boesch & Boesch-Achermann 2000; Boesch et al. 2006, 2008). This lowland rainforest of 4540 km² represents the largest remaining protected forest block in West Africa. The study site is located on the western side of the Park, 15 km East of Tai village. Four chimpanzee communities are studied in the research area. The north community has been studied since 1979 (Boesch & Boesch-Achermann 2000), the south and middle communities since 1995 and the east community more recently since 2000. In this study, the south group was studied for 15 months (April 2006–July 2007) and at the beginning of the study comprised 35 individuals, of which five were adult males, 11 adult females, three adolescent males, 10 infants and five juveniles. Early in 2007, two young adult females immigrated to this community. Fifteen of the adult chimpanzees were followed (five adult males and 10 of the 11 adult females) for 217 days. One adult female was not followed because she was not totally habituated to humans, and following her could have influenced her movement patterns. Hygienic measures have been established in the study area to prevent the transmission of diseases between humans and chimpanzees (Leendertz et al. 2006; Boesch 2008). In accordance with these rules, the chimpanzees were followed at a minimum distance of 7 m.

Behavioural Data Collection

On each day of data collection, one target individual was followed from the time at which the chimpanzees left their sleeping site in the morning until the evening when they were building new nests. The position of the target was automatically recorded every

minute with a GPS Garmin cx60, each of these data points including the exact time and date. The coordinates were recorded in UTM (Universal Transverse Mercator) which provides data in metres and allows easier calculations of distances and linearity (Fig. 1).

We determined GPS accuracy from a constant position while the chimpanzees were eating or resting for more than 1 h, by calculating the distances between two points recorded on a minute basis. The variation was ± 14.2 m ($N = 12\,615$ positions obtained during 123 stable positions from 100 days). For example, for a distance travelled of 50 m (which represents the mean distance between two points), the consequences of the inaccuracy of the GPS (14.2 m) to measure the correct angle would be 15.82° and the linearity index would become 0.9619 instead of 1 theoretically for a straight line.

The position of the target chimpanzee and its activity were recorded every minute. The number of adults in the group and the number of males and females were also recorded to determine the female ratio of the group, equal to the number of adult females

divided by the total number of adult chimpanzees. A female ratio of 1 would represent an entirely female group and 0 an entirely male group. We tried to follow solitary chimpanzees or those in small groups to reduce the complication factors of social interactions in large groups and to allow us to test the influence of simple social factors on navigation between resources. Every resource eaten was considered and characterized by measurements of the journey from the previous resource visited: distance travelled, linearity index, mean travel speed, initial and final travel speeds (calculated over the first and last thirds of the journey), initial direction, general direction, group size, female ratio, time of day and location within the territory (periphery or core area).

Simulation of Revisiting a Resource from Different Direction

We considered a resource as revisited only when the revisit occurred less than 30 days after the first visit to be certain that the

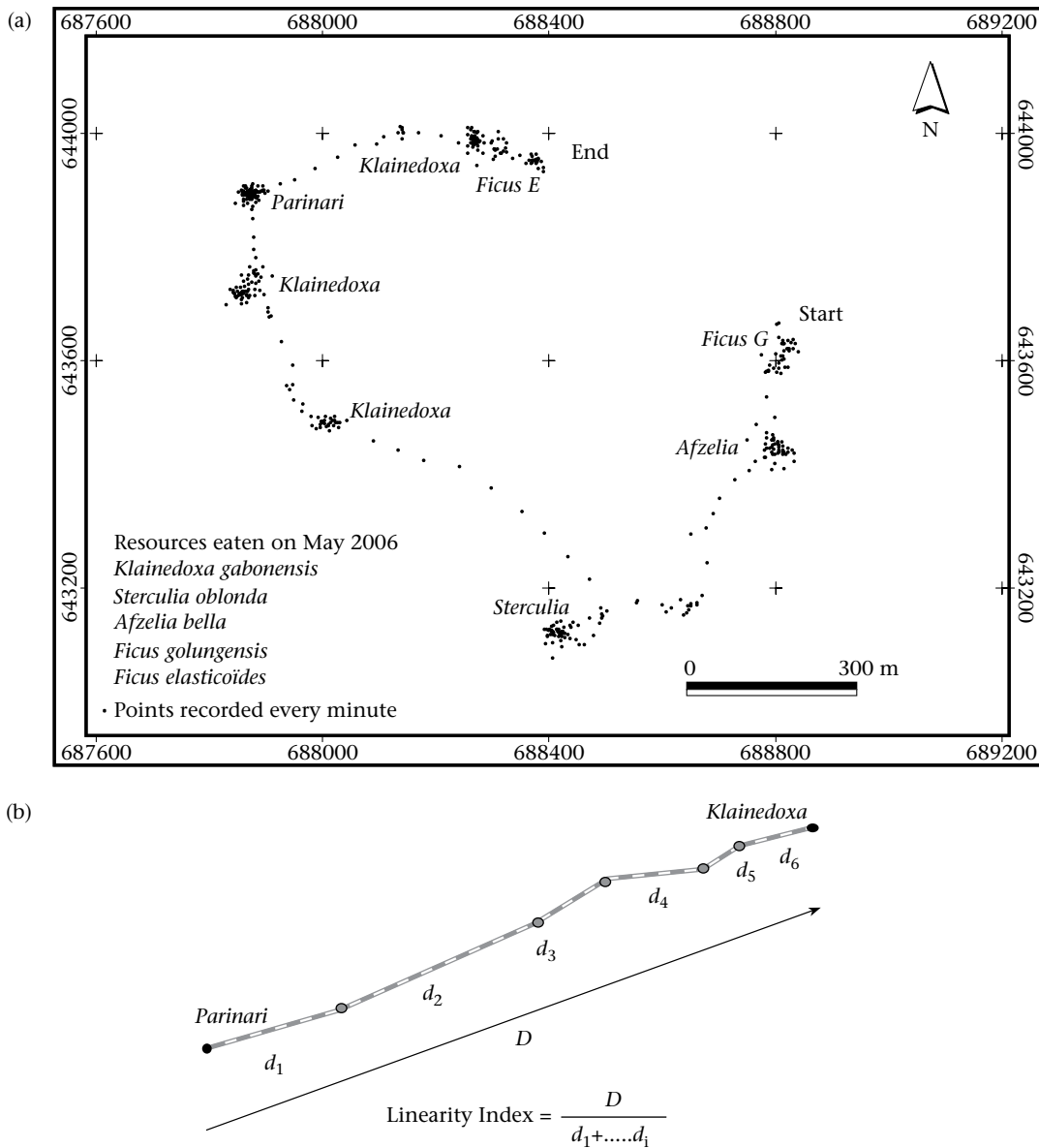


Figure 1. Illustration of the data collected during a day following the Tai chimpanzees. Example of 24 May 2006. (a) Resources eaten during day and automatic points recorded with a GPS every minute. The areas where the points are grouped represent places where chimpanzees were not moving. (b) A step between Parinari and Klainedoxa trees with its characteristic movement patterns: distance travelled (D) and linearity index (LI) which is the distance travelled (D) divided by the sum of the distances between points ($d_1 \dots d_i$).

revisit occurred during the same fruiting season (revisits = 288, revisited trees = 126). We compared the different directions used to reach one tree to see whether a Euclidian or topological map was being used. If, for example, a chimpanzee visited the same resource four times using two different routes from their topological map, during which they arrived at the tree from angles of 17°, 18°, 120°, 122°, we would then calculate the mean deviation angle as the following: $[(18 - 17) + (120 - 18) + (122 - 120) + (122 - 17)]/4$ which is equal to 52.5°. On the other hand, if a chimpanzee visited a tree four times with a Euclidean map, thereby using no routes and arriving from the different directions of 15°, 56°, 145°, 324°, with the same calculation we would obtain a mean deviation angle of 82.5°. Therefore, to distinguish between the two maps, we needed to simulate what would be the mean deviation angle if chimpanzees used only one, two or five different routes per tree or returned to the resource from any direction. If the deviation angle was larger than 180°, we subtracted 360° to keep the deviation between 0° and 180°. We compared the observed deviations with the simulated mean deviation for the four conditions.

Finally, we tested whether this observed deviation could be influenced by group composition, since individual knowledge could lead to different routes, by a peripheral position of the resource, and also by the time interval between revisits, since the period of time during which the revisits occurred could influence the use of a particular route in the case of the topological map. We ran a multiple regression to control for the number of revisits to the same tree, as this variable clearly affects the angle deviation obtained by these methods. For the variation in group composition between revisits, we distinguished cases when one individual revisited the tree alone from other cases. For the revisit interval, we determined the interval between revisits in days and we took the mean interval when considering more than two visits to the same tree.

Analyses

Considering the accuracy of the GPS, we discarded the second of two points (the points that were recorded automatically by the GPS every minute) that were less than 30 m apart. Daily journeys are represented as series of coordinates with a mean distance between two points of 48 m ($N = 15\,101$ on 216 days). The journey between two successive food resources is referred to as a step. All food resources in production at the time of the journey were considered, except ephemeral ones such as mushrooms or insects. A step is characterized by the distance travelled, the straight-line distance between the two resources, the travel speed and the linearity index (=direct distance divided by distance travelled, where 1 would represent a straight line and 0 would represent back tracking). We discarded all steps during which chimpanzees stopped for other activities such as resting, inspecting resources, joining other members of the community, grooming and eating insects and mushrooms.

To test the association between travel speed and linearity index we applied a multiple regression, controlling for social influence, daily organization (Noser & Byrne 2007a, b) and position in the territory (influence of the peripheral area). To study the effect of being at the periphery on distance travelled we ran a second multiple regression controlling for any effects of social factors and daily organization (time of day) on distance travelled.

To control for social factors, we tested the effects of female ratio and group size (larger groups with more leadership could cause travel deviations). Then to control for daily organization, we included of variable time of day. Finally, to test differences in movement patterns between core area and peripheral area, where we expected chimpanzees to have less knowledge about landmarks

or resource locations, we defined a variable indicating whether the resource was eaten at the periphery or core area. The periphery is defined as the area within the territory where chimpanzees spend only 25% of the time. Figure 2 illustrates how chimpanzees use their territory and shows that peripheral areas are less frequently used the further away they move from the core area.

To ensure the data approximated to a normal distribution, a necessary condition for using multiple regression analyses, we log transformed the variables travel speed, time of day and distance travelled. The linearity index (LI) was highly skewed towards 1, and a log transformation was not strong enough to produce a normal distribution; we therefore applied a fourth-root transformation. This transformation is based on considerations of the logistic regression, and the corresponding transformation is $1 - (1 - LI)^{1/4}$. After transformation, we ensured normal distribution of our data by investigating the Z scores of each variable. Since fewer than 1% of the Z scores were larger than |3|, and fewer than 5% larger than |2|, we concluded that the data were in an appropriate form for multivariate testing (Zar 1999). A squared term was added for time of day to account for any nonlinear relationship with linearity index or distance travelled.

RESULTS

Notion of Direction

Under a Euclidean map hypothesis, a high linearity index would indicate that individuals 'know' where they are going. We found an average linearity index of 0.962 ($N = 852$ steps). This linearity index is not significantly different from a straight line once a correction was made for GPS inaccuracy (linearity index obtained when including only the GPS measurements error = 0.9619; t test: $t_{851} = 0.28$, $P = 0.773$; Fig. 3).

A test for interactions between linearity and travel speed controlling for social influence, daily organization and navigation at the periphery showed that the faster the chimpanzees were moving, the more linear their movement within that step (Table 1). This supports the notion that individuals 'know' where they are going. The variation in linearity was not associated with a particular type of social or daily organization, nor by any differential

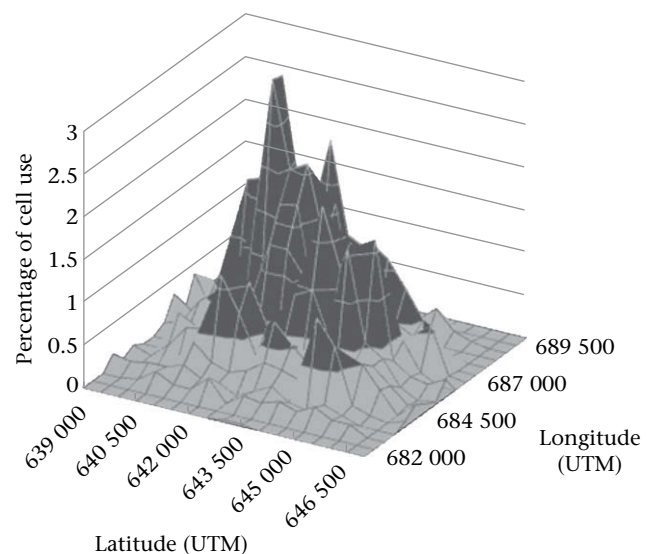


Figure 2. Areas where chimpanzees found resources during the study (from March 2006 to July 2007), showing the core area (dark grey) and the peripheral area (light grey). Cells are defined as 500 m² areas.

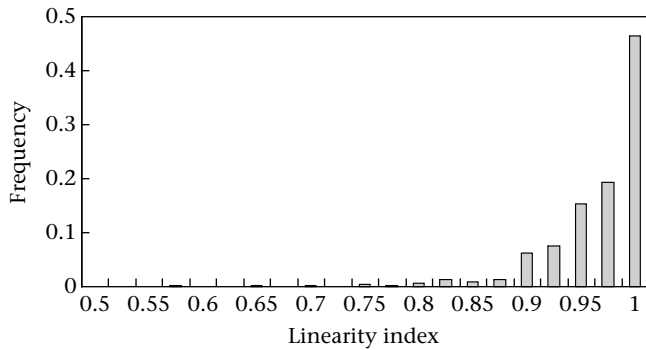


Figure 3. Linearity index frequency. An index of linearity of 0.9619 represents a straight line taking into account the error of the GPS.

knowledge of the environment at the periphery. However, the more females there were in the group, the more linear the group's navigation between resources.

If chimpanzees have a notion of direction, we should expect the initial direction adopted when beginning a step to be equal to the general direction taken during the entire step. However, if they were using landmarks to orient themselves, we would expect greater differences between the two. We compared the difference between the initial direction taken from the previous resource and the general direction taken between two resources, while taking into account the GPS measurement error (15.84°). Only steps with more than four points ($N = 399$; minimum step length = 124 m; mean step length = 294 m) were considered for this test to avoid the bias of short steps which would, in the case of a topological map, be linked to too few landmarks. The initial direction did not differ from the general direction (mean deviation from a straight line = 17.05°) when taking GPS error into account (t test: $t_{398} = 1.582$, $P = 0.114$).

Notion of Distance

Under a Euclidean map hypothesis, chimpanzees know in which direction to travel to reach their goal, as well as how far away it is. We would therefore predict that target chimpanzees would change their travelling speed before arriving at the food source. To test for this, we compared the initial and final speeds (comparing the first with the last two points for steps of less than 300 m and the first with the last three points for longer steps). A paired t test showed ($t_{1033} = 10.7$, $P < 0.001$) a significant deceleration when approaching a resource. Thus, it seems that target chimpanzees 'know' when they are nearing their goals and adapt their speed accordingly.

Revisiting of Resources

Under a Euclidean map hypothesis, we would expect chimpanzees to revisit a tree from all possible directions, as they are not

affected by the availability of topological landmarks. The mean observed deviation (deviation = 66.1°) was significantly higher than the simulated deviation of revisiting a resource using a unique route (deviation = 0° ; $t_{392} = 23.725$, $P < 0.001$), two different routes (deviation = 35.7° ; $t_{392} = 10.907$, $P < 0.001$) and five different routes (deviation = 59.7° ; $t_{392} = 2.289$, $P = 0.023$), but not significantly different to the simulation of going back to a tree from any possible direction (deviation = 68.2° ; $t_{392} = -0.763$, $P = 0.446$). This result means that chimpanzees do not use routes to return to a resource and thus can find a resource from all possible different directions.

Moreover, we ran a multiple regression to test for the influence of different factors on the mean deviation angle to control for the number of revisits to the same tree. First, we tested the change in group composition between revisits and the location of the resource since a chimpanzee is more likely to reach a peripheral resource coming from the core area than coming from the far periphery. In addition to this we tested the mean revisit interval in days, as short revisit intervals could favour using the same route. Lastly, we controlled for the number of revisits that influence the mean deviation between the different directions to revisit a tree as a result of the methodology. The model is significant ($F_{4,136} = 4.489$, $P = 0.002$). However, we found no effect of periphery ($t_{135} = 0.104$, $P = 0.917$), no effect of group composition ($t_{135} = -1.534$, $P = 0.128$) and no effect of revisit interval ($t_{135} = -0.715$, $P = 0.476$). We did, however, find that the more revisits to the same tree, the smaller the deviation ($t_{135} = -3.849$, $P < 0.001$).

Effect of Periphery

Finally, to test whether the target chimpanzees were using a Euclidean rather than a topological map, we compared the linearity index between journeys in the core areas of the territory, where individuals are fully acquainted with the trees, with the peripheral areas that they frequent only 25% of the time. Contrary to our prediction for the topological map, the linearity index was not significantly different between these two areas of the territory (Table 1).

A consequence of the use of a Euclidean map in a less well-known environment could be that individuals forage between food trees that are closer to one another than in the core area. We applied logistic regressions to test for the impact of the location in the territory (peripheral position/core area) on the distance travelled, while controlling for social factors (group size and female ratio) and time of day.

The results show that distance travelled was influenced by the location in the territory, with shorter distances travelled between resources at the periphery (Table 2). Distance travelled was not influenced by the time of day or group size, but was influenced by female ratio, as was already known (Boesch & Boesch-Achermann 2000). Additionally, this effect was more pronounced for females, which travelled shorter distances than mixed groups or males ($t_{1621} = -6.467$, $P < 0.001$).

DISCUSSION

Chimpanzees appeared to know where they were going and to have a very precise notion of direction. These abilities allowed them to navigate efficiently through their territory. Chimpanzees did not use the same path when going back to a resource, and thus were able to find a tree when approaching from different directions. They also initiated navigation to a resource with the exact same direction as when they reached that resource (mean travel distance = 294 m). If they were using a topological map, chimpanzees would tend to return to the resource from the same direction. However, this would

Table 1
Results of the multiple regression testing the effect of travel speed, time of day, peripheral area, female ratio and group size on the index of linearity

Linearity index	<i>B</i>	<i>t</i>	<i>P</i>
Travel speed	0.037	4.385	<0.001
Periphery (25%)	-0.013	-1.132	0.258
Time of day (Z-scored)	0.001	0.205	0.838
Time of day (Z-scored ²)	-0.004	-0.745	0.456
Female ratio	0.042	2.787	0.005
Group size	0.000	-0.164	0.870

$F_{6,836} = 4.753$, $P < 0.001$.

Table 2

Results of the multiple regression testing the effect of periphery, time of day, group size and female ratio on distance travelled

Distance travelled	<i>B</i>	<i>t</i>	<i>P</i>
Periphery (25%)	−0.134	−2.969	0.003
Time of day (Z-scored)	−0.029	−1.574	0.116
Time of day (Z-scored)	0.025	1.288	0.198
Female ratio	−0.403	−6.467	<0.001
Group size	0.004	0.625	0.532

$F_{5,1622} = 6.180, P < 0.001$.

happen less frequently the more landmarks they could memorize. Even so, we should expect an upper limit to the number of trees they can memorize. In the 21.4 km² area of the Taï forest in which we have been following chimpanzees, we have mapped 12 500 large trees (comprising 17 species) in which chimpanzees forage (E. Normand, D. S. Ban & C. Boesch, unpublished data). About 72 species of large trees are known in Taï National Park, so we can reasonably expect twice the number we recorded of chimpanzee food trees. This gives an indication of the scale of memorization that would be required for the chimpanzees to mimic the flexibility of a Euclidean map when only using landmarks.

None the less, we considered the possibility of a topological map including many landmarks when we tested for the effect of less well-known areas (periphery versus core area) on movement patterns. Against the topological map hypothesis, the precision in direction was not affected by the location within the territory even though the periphery was used four times less than the core area. The reduction in distance travelled per step could be interpreted as chimpanzees being limited by the distances they could precisely remember using a Euclidean map in such lesser-known areas. However, this decrease in distance travelled could also be interpreted as a behavioural adaptation to the peripheral area, owing to, for example, less time being available in those areas or potential danger relative to neighbouring groups.

Moreover, when chimpanzees travelled from one resource to another, they adapted their travel speed, slowing down when approaching the resource. This effect confirmed that chimpanzees 'knew' where they were headed. The reason for slowing down may be that in a fission–fusion society some individuals need to be careful before entering a resource area where dominant individuals might already be present.

Taken together, the different analyses discussed above point more towards the existence of a Euclidean map in wild chimpanzees. This interpretation supports a previous study of hammer transport done with the same Taï chimpanzees which reveals a very precise knowledge of the location of different stone hammers in the forest (Boesch & Boesch 1984). This was also confirmed by a study of captive chimpanzees recovering hidden food (Menzel 1973) even though here the alternative of using familiar landmarks could not be excluded (Bennett 1996). However, our results should not be viewed as excluding the possibility that chimpanzees would combine their Euclidean map with landmarks to orient themselves on the small spatial scale.

Previous studies have shown that arboreal primates (sympatric spider monkeys, *Ateles belzebuth*, and woolly monkeys, *Lagothrix poeppigii*: Di Fiore & Suarez 2007; orang-utans, *Pongo pygmaeus*: MacKinnon 1974; howler monkeys, *Alouatta palliata*: Milton 1980, 2000), but also nonarboreal primates living in semidesert areas (hamadryas baboon, *Papio hamadryas*: Sigg & Stolba 1981), use a topological map by following routes. But what exactly explains this difference between these species' spatial abilities and those of chimpanzees? We suggest that memory capacity could place an upper limit to the efficient use of a topological map, since with tens of thousands of trees, the possibility of combining landmarks

would be exceedingly high. Savannah-living baboons have fewer resources and landmarks to remember than forest-living monkeys, and while orang-utans and sympatric spider, woolly and howler monkeys are arboreal forest-living species, they may be forced to use regular pathways to navigate through the dense canopy. On the other hand, the chimpanzees' territory is much larger than those of most forest-living monkey species, so that the former might be forced by the limitations of memory to adopt a more flexible map to feed efficiently on many abundant, diverse and distant food sources.

Similarly, studies on spatial orientation in humans have shown that using landmarks is ecologically dependent. It seems that Occidental men travelling in a city follow landmarks and are unable to provide clear directions when mapping their pathways (Byrne 1979; Thorndyke & Hayes-Roth 1982). On the other hand, aboriginal people living in more open environments are more accurate in determining the direction for places that can be over 300 km away (Lewis 1976; Dasen 1984).

According to our results, female chimpanzees are more efficient at keeping their travel costs low, as they travel more linearly and for shorter distances than males. This is consistent with the challenge they face daily, needing to consume more than males to offset the costs of breast feeding and travelling with infants and juveniles. These results, however, are in contrast to numerous studies on sex differences on spatial orientation in humans, where men possess a more accurate notion of direction and distance than women, who use more landmarks (McGuinness & Sparks 1983) and possess a larger spatial memory (McBurney et al. 1997). This topic should be investigated more deeply to understand the origin of sex differences as, for example, it seems that the oestrogen level influences performance in solving spatial tasks in women (Postma et al. 1999), but also in nonhuman primates (Lacreuse et al. 2001).

This study shows that with behavioural data and a method using precise equipment to record the continuous positions of wild animals, it is possible to learn more about the knowledge the animals have of their environment. The present study supports the proposition that chimpanzees possess detailed Euclidean maps, allowing them to plan their journeys efficiently following direction and distance to the selected resources and short cuts. However, these outstanding performances observed in wild chimpanzees do not exclude the possible existence of both egocentric and exocentric representations of space working together. This proposition should be the subject of further investigations in wild chimpanzees. Such elaborate Euclidean maps are important in a dense and relatively homogeneous habitat without any obvious landmarks, as shown in humans, and further work is clearly necessary to discover the details of journey planning in such populations.

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