

Evolutionary Psychology of Spatial Representations in the Hominidae

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Summary

Comparatively little is known about the inherited primate background underlying human cognition, the human cognitive “wild-type.” Yet it is possible to trace the evolution of human cognitive abilities and tendencies by contrasting the skills of our nearest cousins, not just chimpanzees, but all the extant great apes, thus showing what we are likely to have inherited from the common ancestor [1]. By looking at human infants early in cognitive development, we can also obtain insights into native cognitive biases in our species [2]. Here, we focus on spatial memory, a central cognitive domain. We show, first, that all nonhuman great apes and 1-year-old human infants exhibit a preference for place over feature strategies for spatial memory. This suggests the common ancestor of all great apes had the same preference. We then examine 3-year-old human children and find that this preference reverses. Thus, the continuity between our species and the other great apes is masked early in human ontogeny. These findings, based on both phylogenetic and ontogenetic contrasts, open up the prospect of a systematic evolutionary psychology resting upon the cladistics of cognitive preferences.

Results and Discussion

To examine spatial memory strategy across the Hominidae, we compared the performance of all four nonhuman great apes (henceforth, apes), prelinguistic human infants (1-year-olds), and human children (3-year-olds). We used a simple object-search task in which subjects had to choose between using a place- or feature-based strategy. An experimenter (E) distributed three containers open side up on a table. All three containers

had distinct rich featural attributes. Subjects observed while E produced the reward and inverted all the containers, so that one of the containers hid the reward. The apparatus was then occluded, and two of the containers were switched out of sight of the participant. In the *feature* condition, the reward moved with the distinctive container; in the *place* condition, the reward remained in its original place, now under a different container. The *place* and *feature* conditions were administered in two consecutive blocks for each individual, counterbalanced for order across subjects. The transition between the two blocks was unmarked—that is, the strategy that had yielded rewards in the prior block suddenly no longer did, and the alternative strategy was now the winning one. Randomly interleaved within both blocks were control trials in which all containers stayed in their original location (the *no switch* condition). After these manipulations (~7 s after presentation), the occluder was raised, and the subject chose one of the three containers (no correction allowed) and got the reward, if any, under it (Figure 1 and Movie S1 in the Supplemental Data available online).

Twenty-five apes of four different species belonging to all three nonhuman great ape genera—*Pongo*, orangutans (*Pongo pygmaeus*); *Gorilla*, gorillas (*Gorilla gorilla*); and *Pan*, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*)—were tested with this apparatus. In addition, twenty-six human prelinguistic infants between 12 and 13 months were tested, along with the same number of three-year-olds (for subject and analysis details, see Experimental Procedures). In a comparison of the average number of correct trials, results showed, first, no significant differences in strategy preference among ape genera (see Analysis Details below), so they were grouped to compare them with the two human groups. All three remaining groups showed clear preferences between the two strategies (ANOVAS: for apes, $F_{2,46} = 33.30$, $p < 0.001$; for 1-year-olds, $F_{2,48} = 7.90$, $p < 0.01$; and for 3-year-olds, $F_{2,48} = 18.27$, $p < 0.001$; for descriptive statistics, see Figure 2 and Table S1). However, the three subject groups (apes, 1-year-old infants, 3-year-old children) differed in their strategy preferences (Figure 2). Both 1-year-olds and apes performed better when the food stayed in the same location regardless of the movement of the container (i.e., in the *place* condition) than when it moved with its container (both $p < 0.01$, paired *t* tests). In contrast, three-year-old subjects performed better at retrieving the reward when it moved with the container (i.e., in the *feature* condition) than when it stayed in its place ($p < 0.05$, paired *t* test). Figure 2 presents a summary score obtained after subtracting the respective chance levels for percent correct scores in the *place* and *feature* conditions. A more detailed analysis looked at subjects' choice of strategy rather than their correct performance. We classified the subjects' choices as place based, feature based, or errors (i.e., neither the selected location nor the container had been rewarded before occlusion). An analysis of choices at

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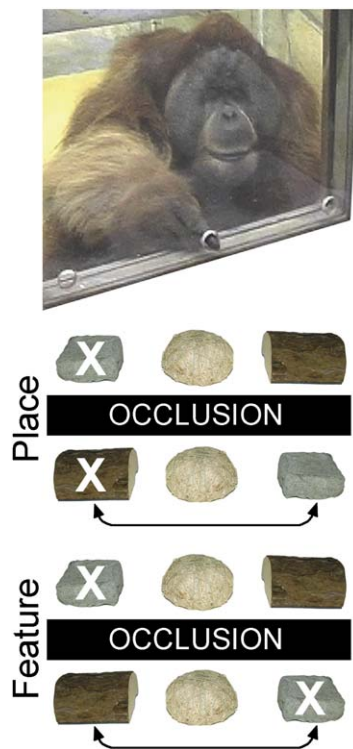


Figure 1. Experimental Conditions

(Top) Adult orangutan male performing the task. (Bottom) Experimental conditions. The X indicates the hidden reward before and after occlusion. *Place*: During occlusion, the experimenter (E) switches two containers while the reward stays in its original location. *Feature*: E again switches two containers during occlusion but moves the reward with its container.

the first switch trial revealed that distributions match the error data. Comparison of frequencies of strategies adapted on trial 1 showed that distribution of first-choice strategy in older children differed significantly from those of 1-year-olds (Fisher exact test, $p < 0.001$) and apes (Fisher exact test, $p < 0.001$), which were in turn very similar to each other (Fisher exact test, $p > 0.5$). Whereas 3-year-old children tended to use a feature

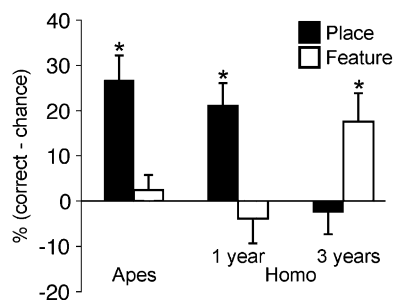


Figure 2. Strategy Preferences: Performance

Mean percent correct ($\pm$ SE) for the *place* and *feature* conditions only. Means are adjusted for the respective chance levels of the different subject groups: 33.33% for 3-year-old human children and nonhuman great apes (1 out of 3 containers) and 50% for 1-year-old human infants (1 out of 2 containers). Conditions marked with * were significantly different from chance in one-sample t tests. Unmarked bars were not significantly different from chance (see Analysis Details).



Figure 3. Strategy Preferences: First Choice

Percentage of subjects choosing to use either place or feature cues to retrieve the reward on trial 1 of the experiment (before receiving any feedback).

strategy on their very first switch trial, apes and 1-year-olds initially chose place (Figure 3). Overall, the performance of young human infants and all other hominid genera showed a similar pattern, which differed substantially from that observed in older, human children, who preferred to use feature rather than place information.

Conclusions

All species feeding upon dispersed resources in space and time need to remember locations and know how to find them. There are two main strategies for remembering object location: the use of object features and the use of place features as defined by a spatial frame of reference. Earlier studies have examined the use of place and feature cues in a range of species from goldfish to pigeons, humans to rats. In tasks that allow the subject species to freely combine both kinds of cues, all tested species seem able to use both kinds according to circumstance, although some seem able to combine both more readily than others [3]. However, in tasks that oppose the two kinds of cues, some species prefer place-based strategies (e.g., fish [4, 5], lizards [6], rats [3, 7], and dogs [8]), whereas others predominantly use feature-based strategies (e.g., toads [9], chicks [10], and human children [11]). No studies, however, have systematically tracked these preferences across the phylogenetic tree. Here, we investigated a complete family, systematically examining this particular cognitive preference across all the extant genera in the Hominidae (see Figure 4, bottom), including humans at two different ontogenetic phases.

We show that all nonhuman great ape genera share a preference for locating things in space in terms of abstract place or position rather than in terms of the features of a container object. Indeed, the continuities between human and ape spatial cognition are striking: Apes and humans show similar ontogenetic development across the Piagetian stages up to stage 6 [12], commit similar errors [13], and can cope with a variety of object displacements [14–16]. Here, we have shown that at 1 year of age, humans exhibit just the same spatial-cognition biases found in all other genera of the family (Figure 4). The standard method of comparative cognition thus suggests a common phylogenetic inheritance of a preference for place-based spatial strategies from the ancestor shared by all four genera. Object-location memory is a central cognitive function underlying more complex foraging behavior. Hence, this finding is

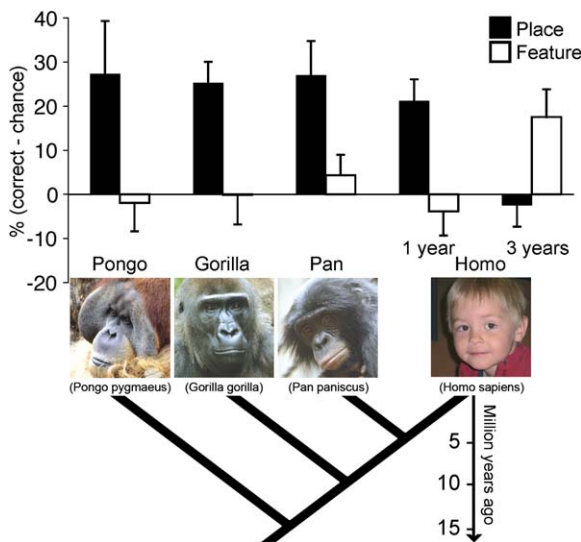


Figure 4. Strategy preferences across the Hominidae

Mean percent correct ($\pm$ SE) for the *place* and *feature* conditions for all nonhuman great ape genera and human 1- and 3-year-old children. Means are adjusted for the respective chance levels of the different subject groups (see Figure 2). No statistics were computed for the separate nonhuman genera because of relatively small sample sizes in some of the groups. Qualitatively, *Pongo*, *Gorilla*, and *Pan*, as well as 1-year-old human infants, all display a similar pattern. In contrast 3-year-old infants show the opposite preference. Below is the phylogenetic tree displaying the evolutionary relationships among the four Hominid genera (*Pongo*, *Gorilla*, *Pan*, *Homo*). The photographs display individuals of four representative species. All five extant species of Hominids participated in the reported study: orangutan (*Pongo pygmaeus*), gorilla (*Gorilla gorilla*), bonobo (*Pan paniscus*), chimpanzee (*Pan troglodytes*), and human (*Homo sapiens*). Here, we assume a taxonomy based on monophyletic groups. In this framework, Hominidae include all the great apes including humans but not the Hylobatidae or small apes.

of considerable interest for the interpretation of the fossil record—it suggests dominantly place-based foraging strategies in the common ancestor of the Hominidae, which may thus have foraged in rather different ways than modern human hunter-gatherers: Place-based strategies are highly effective for foraging within a stable territory; feature-based strategies are advantageous for foraging in novel environments (e.g., finding mushrooms close to trees of a particular species). Thus, strategy preferences might indicate foraging and lifestyle preferences. Through a comparative analysis of cognition across a complete phylogenetic clade, we have been able to reconstruct in our common ancestor behavioral preferences that cannot be found directly in the fossil record.

We also find that human infants share the same cognitive preference as apes, but this changes into a preference for features during early human ontogeny. Why should three-year-old children differ in their preferred spatial strategy from human infants and other great apes? One possibility is that 1-year-old human infants (as well as apes) lack certain cognitive abilities that are needed to solve a feature-based search task (e.g., response inhibition [17] or exhaustive search strategies [18]) and that excel in humans after the first year of life. However, in previous experiments, various animal species [4, 19] and human infants [20, 21] demonstrated

the ability to use feature cues to retrieve hidden targets. In fact, all of our subject groups tended to improve on their dispreferred strategy at least when it was rewarded in the first block of trials. Alternatively, the preference for place over feature cues for spatial memory in 1-year-olds and apes might not be due to a lack of ability to solve the *feature* condition, but to a proclivity to use place- over feature-based strategies whenever available. In that case, the switch in humans would be due to reconstructive events in human ontogeny between the first and the third years, events that reweigh preferences, not create abilities. Clearly, this is a period where much happens in cognitive development. Maybe most prominently, infants are inducted into social life through the acquisition of interpersonal skills [22], such as, for example, increasing understanding of others' mental states and the acquisition of spoken language, the combination of which opens up the full affordances of human culture [23]. Language in particular has long been argued to play a reconstructive role in human cognitive development [24–28]. Indeed, the first words learned by German children are nouns [29], and nouns specifically name bundles of object features, thus making featural specificity prominent. In fact, previous research has shown naming to draw attention to featural distinctions between objects in young infants [26]. Further experimentation would be needed to demonstrate a causal role for language for the present task, e.g., by examining infants of the same age but different language capacities. What the present data tell us is that the “wild-type” in our family exhibits a proclivity for place over feature in spatial tasks, and that humans reverse this early in childhood.

Experimental Procedures

Apparatus

An imitation hollow stone, an imitation bird's nest, and a hollow piece of wood were used as containers. All were approximately 15 cm wide and placed on a plastic plank (70 × 40 cm) 20 cm (center to center) apart. An opaque plastic screen (70 × 40 cm) or a dark curtain was used as an occluder. Apes received grapes or slices of banana as rewards, whereas children received small toy animals that they collected in a bag and returned at the end of the session. The toys used as rewards with 1-year-olds were slightly bigger than those for older children to avoid risk of swallowing. All subjects were verbally encouraged for a correct choice, and children that did not immediately produce a response were prompted with the words, “Can you find it? Show me!” There were no other verbal instructions.

Participants

We tested twenty-six 3-year-olds with a mean age of 42 months (range: 38–46 months, mean [M] = 42.3; standard deviation [SD] = 1.9) in local kindergartens. Twenty-six human infants approximately 1 year old with a mean age of 54 weeks (range: 52–56 weeks; M = 54.3; SD = 1.3) were recruited from the local community. In the two groups, there were 12 girls and 14 boys each. All children were native German speakers of normal ability range and came from mixed socioeconomic backgrounds. We also tested twenty-five apes: five orangutans (*Pongo pygmaeus*), four gorillas (*Gorilla gorilla*), five bonobos (*Pan paniscus*), and 11 chimpanzees (*Pan troglodytes*). There were nine males and 16 females ranging from 5 to 32 years of age. All apes were housed at the Wolfgang Köhler Primate Research Center at Leipzig Zoo (Germany). They were living in social groups with conspecifics and had access to indoor and outdoor areas. During testing, the apes were fed according to their daily routine four times a day on a diet of fruit, vegetables, and monkey chow; water was at their disposal at all times.

Data Scoring

For older children and apes, each block was composed of six trials of one of the two test conditions (*place* or *feature*) and three *no switch* trials. Thus, subjects received 9 trials per block in two consecutive blocks for a total of 18 trials. We had to modify the procedure for younger children because pilot testing had revealed that they presented a strong bias toward choosing the middle position [13]. To avoid this problem, we removed the central cup from the setup. As a result, they received four trials per block in the two-container setup (two *place* trials, two *feature* trials, and two *no switch* trials each). We videotaped all trials and scored the container selected by subjects. Some trials were excluded from analysis on one or more of the following grounds: (1) The response was blocked from view on video; (2) the subjects left their hands close to one of the response places during occlusion, thereby biasing themselves toward a place-type response (1.9% of all trials excluded in total); (3) three 3-year-olds were excluded because they performed at least one block without a single correct *no switch* trial, and one additional 3-year-old was excluded because of experimenter error; (4) six 1-year-olds were excluded because they did not complete all trials. The sets of subjects reported above are the final sets, after exclusions.

Analysis Details

First, we analyzed the differences among ape genera. A mixed ANOVA with condition (*place/feature/no switch*) as within-subject factor and genera (*Pongo/Gorilla/Pan*) as between-subject factor revealed significant main effects for condition ($F_{2,44} = 17.78$, $p < 0.001$) and genus ($F_{2,21} = 3.73$, $p < 0.05$). There was no significant condition $\times$ genus interaction ($F_{4,44} = 1.325$). No simple post-hoc comparisons between genera reached significance. In tendency, *Pan* ($M = 64.9$; standard error [SE] = 2.5) outperformed *Gorilla* ($M = 52.9$; SE = 5.0) and *Pongo* ($M = 54.0$; SE = 4.5). Because we could not detect any differential preferences for one strategy over the other between genera, we collapsed all apes for further analysis. (Table S1 presents the percentage of correct trials in the three conditions for the remaining three groups).

A mixed ANOVA (condition [*place/feature/no switch*] $\times$ order [*place first/feature first*]) conducted for each group (apes, 1-year-olds, 3-year-olds) separately revealed a significant main effect of condition in all three groups (apes, $F_{2,46} = 33.30$, $p < 0.001$; 1-year-olds, $F_{2,48} = 7.90$, $p < 0.01$; and 3-year-olds, $F_{2,48} = 18.27$, $p < 0.001$). For 1-year-olds, a one-sample *t* test against chance ($chance = 0.50$) revealed that subjects were significantly above chance in all conditions ($p < 0.001$) except *feature* ($p > 0.4$). The same pattern was detected in apes: A one-sample *t* test against chance ($chance = 0.33$) revealed that subjects were significantly above chance in all conditions ($p < 0.001$) except *feature* ($p > 0.4$). For 3-year-olds, a one-sample *t* test against chance ($chance = 0.33$) revealed that subjects were significantly above chance ($p < 0.01$) in all conditions except *place* ($p > 0.5$). Descriptive statistics for all conditions in all groups are summarized in the Supplemental Data. The *p* values in all simple comparisons between the conditions reported here and in the main text were calculated and α -level corrected with a Bonferroni-Holm post-hoc test.

Supplemental Data

Supplemental Data include Experimental Procedures, one figure, one table, and one movie and are available with this article online at: <http://www.current-biology.com/cgi/content/full/16/17/1736/DC1/>.

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