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Functionally Referential Communication in a Chimpanzee

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Summary

The evolutionary origins of the use of speech signals to refer to events or objects in the world have remained obscure. Although functionally referential calls have been described in some monkey species [1, 2], studies with our closest living relatives, the great apes, have not generated comparable findings. These negative results have been taken to suggest that ape vocalizations are not the product of their otherwise sophisticated mentality and that ape gestural communication is more informative for theories of language evolution [3, 4]. We tested whether chimpanzee rough grunts, which are produced during feeding contexts [5–8], functioned as referential signals. Individuals produced acoustically distinct types of "rough grunts" when encountering different foods. In a naturalistic playback experiment, a focal subject was able to use the information conveyed by these calls produced by several group mates to guide his search for food, demonstrating that the different grunt types were meaningful to him. This study provides experimental evidence that our closest living relatives can produce and understand functionally referential calls as part of their natural communication. We suggest that these findings give support to the vocal rather than gestural theories of language evolution.

Results and Discussion

To investigate whether chimpanzee "rough grunts" functioned as referential signals, we designed a playback experiment in which chimpanzees were played a sequence of rough grunts that mimicked the discovery of food by another group member. Our goal was to determine first whether other individuals hearing these call sequences could draw inferences about the calls' referent (that is, the food found by the caller) and second whether recipients used this information to guide their own search for food.

Subjects were 11 chimpanzees living in an outdoor enclosure with an adjoining indoor area at Edinburgh Zoo, Scotland (see the Supplemental Data available with this article online). We first determined the food-preference hierarchy for each individual. All subjects unanimously treated bread as a high-value food item, whereas apples were collectively treated as low value. We then recorded rough grunts given by several individuals in response to bread or apples. We set up two artificial feeding trees adjacent to the enclosure, one delivering apples, the other one bread over a period of 6 weeks (Figure 1). Pieces of apple or bread were concealed in cardboard tubes and dropped from both trees, but only one set of tubes was baited in any one trial. After the chimpanzees had learned these contingencies, we conducted a playback experiment. We mimicked the discovery of food by a group member by broadcasting a sequence of rough grunts from the vicinity of the food trees. Empty tubes, containing no food, were dropped from both trees. Grunts given to apples or bread were then broadcast to the first individual to emerge from the indoor enclosure. The search behavior of this individual was filmed and analyzed.

We refrained from interfering with the daily routine of the animals and from any training regime as a result of the concern that this may have altered the animals' natural use of vocalizations. In particular, we did not restrict the individuals' access to any part of the enclosure. One consequence of these precautions was that we were only able to collect systematic data from one individual, a 5-year-old male chimpanzee (LB) who nearly always emerged first from the inside enclosure. Although potentially limited, studies of single animals have crucially contributed to our understanding of a species' cognitive capacities [9–13].

Acoustic Structure of Rough Grunts Varies as a Function of the Food Encountered by the Caller

We conducted an acoustic analysis, which confirmed that calls given to bread and apples fell into two acoustic subtypes with relatively little overlap (Figure 2; Table 1; Supplemental Data). We analyzed 82 calls from 19 different bouts recorded from three different individuals (see Supplemental Data). Univariate analysis of variance revealed that six out of the seven parameters varied significantly as a function of the food that elicited them (Table 1). Rough grunts given to apples were characterized by a low fundamental frequency, a high level of nonperiodic sound, a low first-formant frequency, and a high second- and third-formant frequency. In contrast, rough grunts given to bread were characterized by a high fundamental frequency, a low level of nonperiodic sound, a high first-formant frequency, and low second- and third-formant frequencies. There were no differences in call duration.

We then conducted a discriminant function analysis to explore whether rough grunts given to apples and bread could be statistically grouped. The seven acoustic parameters had variance inflation factors of less than 8, indicating that there were no colinearity problems. The discriminant function resulting from the seven parameters explained a significant amount of variation between grunts given in response to bread and apples (Wilks's lambda = 0.187, $F_{6,12} = 8.005$, $p = 0.001$). The function correctly classified 100% of the calls according to the food that elicited them (78.9% with cross-validation discriminant analysis). In sum, our analyses clearly demonstrated that there is subtle but

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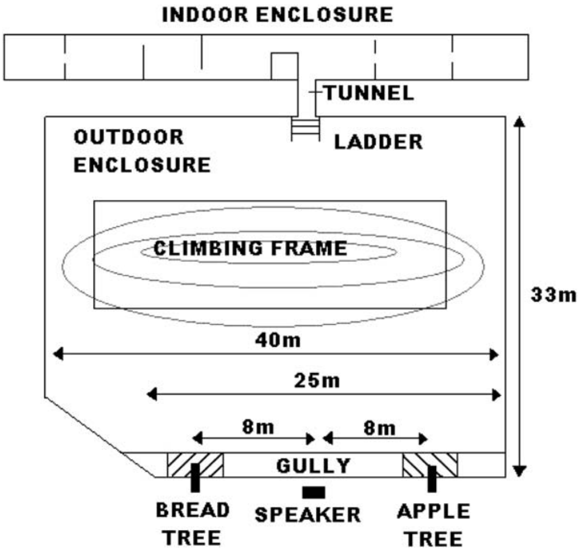

Figure 1. Plan of the Chimpanzee Enclosures at Edinburgh Zoo

Illustrated are the indoor/outdoor enclosure, the location of bread and apple trees, and the corresponding feeding sites underneath. All measurements are in meters (m).

consistent acoustic variation present within this particular call type, which can be explained by the food encountered by the caller.

Playbacks Had a Significant Effect on the Subject's Behavior

Our initial prediction was that, after hearing a playback stimulus, LB would rush to the food tree that corresponded to the rough grunts used as playback stimuli. This was true during four of the six initial playback trials, but thereafter LB developed an idiosyncratic search strategy by consistently approaching the bread tree first, presumably because he did not obtain a reward in previous trials and there were no costs involved in visiting both trees (note that no food was provided during any of the experimental or control trials).

We therefore analyzed a number of subtler behavioral measures: (1) time spent on the ladder before descending into enclosure, (2) time spent searching, and (3) number of tubes searched. Because both locations regularly contained empty tubes from previous feeding events, we corrected search effort for the number of tubes present at each location (see Supplemental Data). We extracted these measures from a total of 17 test trials (nine apple, eight bread), which we compared to ten control trials.

Hearing a series of grunts had a number of effects on LB's behavior (two-tailed Mann-Whitney U tests). First, before approaching the trees, LB remained on the ladder significantly longer in test than in control trials ($\text{mean}_{\text{test}} = 9.33$, $\text{mean}_{\text{control}} = 5.40$, $U = 42.50$, $p = 0.031$), demonstrating that he perceived and presumably processed the playback stimuli.

We then analyzed whether rough grunts affected his overall search efforts (Figure 3). As predicted, LB searched more tubes ($\text{mean}_{\text{bread}} = 48.87\%$, $\text{mean}_{\text{apple}} = 21.15\%$, $U = 85.5$, $p = 0.043$) and searched for longer ($\text{mean}_{\text{bread}} = 1.13$sec/tube, $\text{mean}_{\text{apple}} = 0.36$sec/tube, $U = 81.5$, $p = 0.030$) underneath both trees after hearing grunts given to bread compared to grunts given to apples. Somewhat surprisingly, his search behavior in control trials did not differ from that in bread trials (tubes searched: $\text{mean}_{\text{control}} = 49.3\%$, $U = 179$, $p = 0.983$; search time: $\text{mean}_{\text{control}} = 1.44$sec/tube, $U = 178$, $p = 0.960$) although he searched significantly more in control than in apple trials (tubes searched: $U = 71.0$, $p = 0.004$; search time: $U = 77.0$, $p = 0.007$). To correct for multiple pair-wise comparisons, we adjusted the critical α level from 0.050 to 0.017 with a Sidak correction [$\alpha_{FW} = 1-(1 - \alpha_{COMP})^{\text{No COMP}}$].

These differences in global search effort indicated that LB was searching with clear expectations. In particular, they seem to reflect LB's expectations of finding highly prized bread. Due to the ongoing baiting procedure, finding bread was more likely during control trials (when new tubes were present, but no grunts were heard) than after apple trials (when new tubes were present, and grunts given to apples were heard). It was therefore only after hearing grunts given to apples that LB could safely abandon the possibility of finding bread, and his overall search effort was accordingly reduced.

Deployment of Search Effort Was Affected by the Type of Rough Grunts Heard by the Subject

In a final analysis, we compared the search efforts LB deployed under each tree (two-tailed Wilcoxon-matched pair tests). For control trials, we predicted no difference in search effort under the two trees, which was the case (tubes searched: $W = 21.0$, $p = 0.556$; search time: $W = 21.0$, $p = 0.556$). For test trials, we predicted more intense searching underneath the correct tree, i.e., the one referred to by the grunts. This was also the case. After hearing grunts given to apples, LB searched significantly longer and tended to search more tubes underneath the apple than the bread tree ($W = 4.0$, $p = 0.028$; $W = 5.0$, $p = 0.078$; Figure 4). In contrast, after hearing grunts given to bread, he searched significantly more tubes and tended to search longer underneath the bread tree than the apple tree ($W = 6.0$, $p = 0.046$; $W = 7.0$, $p = 0.074$; Figure 4).

We conducted a power analysis to assess how meaningful the p values of 0.10–0.05 were. An a priori test revealed that in order to achieve a moderate level of power of 0.500, a total of 183 trials would have been required (effect size = 0.3, α level = 0.05, two-tailed t test, Pitman Asymptotic Relative Efficiency score = 0.955 for nonparametric testing). Because our sample sizes for analysis only ranged from 8 to 27 trials, the corresponding power levels were much lower, ranging from 0.063 to 0.219. Hence, it seems safe to conclude that our failure to reach significance at the $\alpha = 0.05$ level is attributable to the low statistical power associated with the small number of trials. Simply running more trials on LB was not an option because in the last weeks, he was already beginning to show signs of frustration when responding to playback stimuli (which never lead to finding any food, as a result of our experimental design). Continuing with more trials would have simply led to extinction.

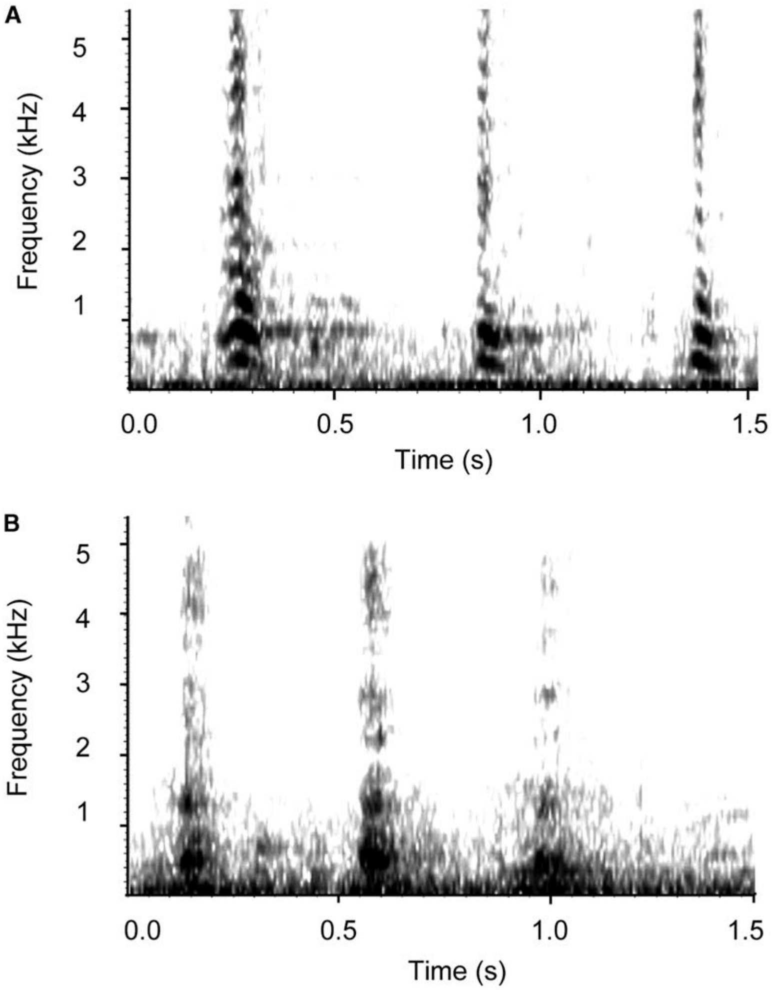

Figure 2. Time-Frequency Spectrograms of Rough-Grunt Calling Bouts Given by the Adult Male Louis

Grunts given to bread (A) have more energy (depicted by the darkness of the image) at higher frequencies and have a clear harmonic structure, in comparison to the lower-pitched, noisy grunts given to apples (B).

Conclusions

Our results have demonstrated that a chimpanzee can extract information about the nature of a food source encountered by conspecifics by listening to their calls. Our focal animal adjusted his foraging behavior on the basis of the calls he heard, in the absence of any additional contextual information. Crucially, our study was not based on any training or conditioning regime, nor did it rely on artificial segregation of individuals. Instead, animals were given the opportunity to use and respond to vocalizations freely and spontaneously within an ecologically relevant framework.

Our results are consistent with the hypothesis that chimpanzee food grunts are functionally referential signals. In what ways are these findings important for understanding the origins of linguistic reference, a core feature of human speech? In contrast to speech, nonhuman-primate vocal behavior is probably not the result of a conscious desire of individuals to inform one another. In this sense, nonhuman-primate signals differ

Table 1. Descriptive Statistics and Univariate Analysis of Variance for 82 Analyzed Rough Grunts Given in Response to Apples or Bread

	Apples (n = 42)		Bread (n = 40)			
	Mean	SD	Mean	SD	F	p value
Call rate (calls/s)	2.23	0.517	1.89	0.411	10.45	0.002
Call duration (s)	0.13	0.110	0.11	0.056	0.85	0.360
Fundamental frequency (Hz)	365.60	218.853	559.15	160.226	20.71	<0.001
First-formant frequency (Hz)	684.07	143.581	739.05	97.983	4.06	0.047
Second-formant frequency (Hz)	1661.12	267.113	1490.35	174.856	11.61	0.001
Third-formant frequency (Hz)	2973.57	256.530	2705.95	246.187	23.19	<0.001
Noise-to-harmonic ratio	0.54	0.167	0.28	0.197	38.54	<0.001

The degree of freedom for univariate analysis of variance = 1, 80.

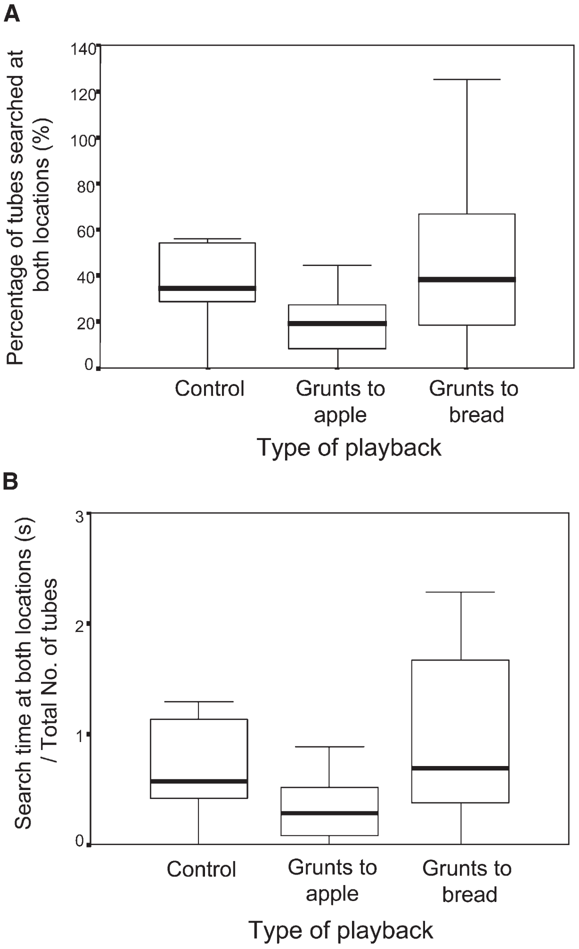

Figure 3. Box Plots Illustrating Percentage of Tubes Searched and Time Spent Searching at Both Locations with Total Number of Tubes Available at Each Location Controlled for

Box plots illustrate medians, interquartile ranges, and highest and lowest values, excluding outliers. Each tube searched was scored as a search event, even if it had been searched previously in the trial; i.e., relative scores could be higher than 100%.

from human speech in an important way: Signalers and recipients may not know that producing a signal is the same as receiving one [14]. Nevertheless, primate calls can be functionally referential because individuals produce acoustically distinct vocalizations in response to distinct external events. Recipients can therefore infer specific information about external events witnessed by the caller. Whereas this process appears to mirror human semantic capacities from the perspective of the recipient [2], the production of signals may well be driven by a substantial motivational component. When finding apples or bread, chimpanzees may experience unique psychological states that drive their vocal production more or less directly. Nevertheless, because the grunts vary reliably with the food type encountered, the calls obtain functional relevance as referential signals and become meaningful to recipients. The same argument also applies for the better-known cases of the vervet or Diana monkey alarm calls [1, 2] or the functionally referential food calls of rhesus monkeys [15]. Further work will have to explore the nature of the psychological mechanisms that drive call production. At the moment, our study only shows that a chimpanzee can infer information about external events from conspecifics' rough grunts, demonstrating that these vocalizations qualify as functionally referential signals.

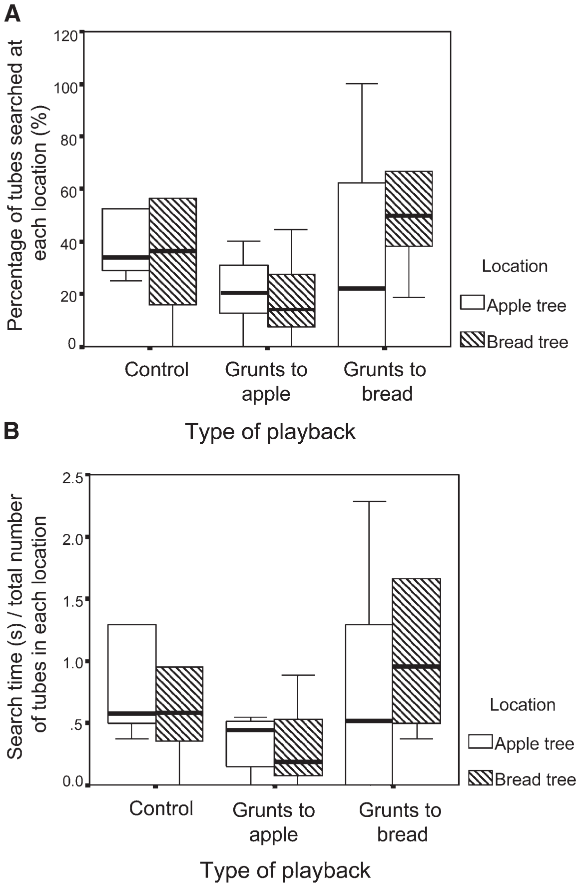

Figure 4. Box Plots Illustrating Percentage of Tubes Searched and Time Spent Searching in Each Location after Hearing Playbacks of Grunts Given to Bread or Apples

Box plots illustrate medians, interquartile ranges, and highest and lowest values, excluding outliers. Each tube searched was scored as a search event, even if it had been searched previously in the trial; i.e., relative scores could be higher than 100%.

There are two principal limitations in this study. First, as just mentioned, the exact nature of the calls' referents is difficult to describe. Currently, it may be most parsimonious to assume that the grunts were labeling some aspect of food value ("good food," "bad food"). However, the calls could also be specific to particular food types ("bread," "apple"). Further experiments are under way to explore the referential specificity in these calls. Second, as explained earlier, because we did not isolate individuals from the rest of the group, we could only collect data from one individual. This limits the generality of our findings, particularly because it remains unclear whether the behavioral capacity described is a general feature of chimpanzee communication or an isolated skill of an exceptionally gifted individual. However, given the reports from the wild [5, 6], it is very plausible that our results apply to chimpanzees in general.

Are these findings important to theories concerning human language evolution and the phylogenetic history of the cognitive capacities underlying language? Genetic evidence suggested that, until about 200,000 years ago, our hominid ancestors did not possess the orofacial motor control required for modern speech production [16]. Hence, one assumption has been that many of the cognitive capacities involved in language processing are phylogenetically older, with their evolutionary roots deep in the primate lineage and with referential communication playing a key role. However, despite evidence for functionally referential communication in a variety of animal species, and particularly monkeys [1, 2, 17–20], there has been no comparable evidence available for any of the great ape species. Some have argued that this does not pose a problem because the absence of language-like communication in nonhuman primates does not necessarily mean that language did not evolve from a primate-like communication system [21]. But then how should the monkey evidence be interpreted? Some may want to argue that it is irrelevant. However, for comparative approaches to language evolution, this creates an anomaly both because apes are more closely related to humans and because they are commonly thought to be cognitively more advanced than monkeys [22]. Unfortunately, one emerging consensus has been that chimpanzee vocal behavior is cognitively uninteresting, that is, not the product of their otherwise complex mentality. It has also led some to dismiss vocal communication as a useful tool for understanding the evolution of language, with gestural communication seen as more important [3, 4].

Recent fieldwork has demonstrated that chimpanzees use some of their calls in highly context-specific ways, and this revitalized the hypothesis that some of their calls may function as referential signals [23, 24]. Our study confirms this with experimental evidence, suggesting that the use of vocal signals to obtain information about external events evolved long before humans diverged from the rest of the primates. In light of these results, it may thus be more parsimonious to propose a direct evolutionary trajectory from ancestral primate-like vocal behavior to fully developed human speech rather than to assume a more complex route involving an intermediate stage of gestural communication [3]. Two major transitions must have occurred in human evolution during this process: (1) increased orofacial motor control allowing more sophisticated vocal abilities [16], and (2) enhanced social intelligence enabling individuals to empathize with each other's mental states [25]. These two innovations, conspicuously absent in nonhuman primates, may have been crucial to clear the way for the emergence of language in modern humans.

Experimental Procedures

Artificial Food Trees

We introduced two artificial "food trees" adjacent to the enclosure, an "apple tree" and a "bread tree" (Figure 2). Food could fall into the enclosure from these two trees at opposite ends of a concrete gully, onto two small areas measuring 2 × 4 m. During each feeding event, four tubes were dropped from both food trees remotely and simultaneously, but only one set of tubes was baited in any one trial (see Supplemental Data). Baiting of tubes was predetermined according to a randomly generated binomial sequence. Individuals quickly learned the location of each food type and that only one feeding site produced food at any given time, which made monopolizing the more valued bread location a poor strategy. Food was dropped opportunistically two to four times throughout the day over a period of 43 days until the start of the experimental phase. We continued to provide food this way throughout the experimental phase at a rate of one to three times per day to delay extinction during the experimental phase.

Experimental Phase

The experimental phase consisted of test and control trials. A maximum of one playback and one control trial were conducted each day, in addition to baited reinforcement trials. All trials were separated by at least one hour.

Subjects

It was only possible to systematically test one subject, LB. This was partly due to our attempt to minimize the interference the testing regime imposed on the natural behavior of the group. It was impossible to separate individuals from the group without the individuals subsequently encountering high aggression levels from other group members. When individuals had to be separated for veterinary reasons, severe and prolonged social upheaval was the normal outcome, suggesting that in such a situation, animals would not pay attention to subtle acoustic stimuli, the focus of this study. Therefore, we did not restrict the movements of the chimpanzees and thus focused on testing the first individuals who chose to come outside after an indoor feed. During the experimental phase, LB was always one of the first individuals outside after any feed and so was the subject on most occasions. On a few occasions, another animal emerged first, heard the playback without LB present, and began to approach the gully. However, on all these occasions LB emerged shortly afterward, saw another animal approaching the gully, and rushed to overtake the subject animal to enter the gully before him or her. LB thus prevented trials of other individuals by emerging first on most occasions, responding first to the playback when other target animals were present, and aborting other target individuals' trials by entering the gully before them. Prior to the experimental phase, LB had considerable experience with apple, bread, and unbaited tubes. He experienced 17 feeding events from the apple tree and 13 events from the bread tree prior to the experimental phase.

Trial Procedure

Before each trial, the group was given a small feed in their indoor enclosure. Once all were inside, four empty tubes were simultaneously and remotely dropped into each location (i.e., eight empty tubes total; no food was available under either tree). The first individual emerging from the inside area was the subject. Then, a test stimulus (a 3 s sequence of rough grunts) or no stimulus was played back (control trial), and the response of the subject was filmed (see Supplemental Data). Control trials provided a baseline of search behavior. We analyzed the videotapes and measured various response parameters in both test and control trials. To ensure that our coding was accurate, we asked an independent person, who was blind to the trial type and to the hypothesis of the study, to code four randomly chosen test trials and three randomly chosen control trials (25% of the total trials). Written instructions explaining the criteria used to obtain each measure were presented to the coder. The coder was then left to extract the seven measures from each of the chosen trials. These independently coded measures were then compared to the original measures with a Crombach's α test of interobserver reliability. A score of 0.87 across all trials and measures was obtained, indicating that the trials had been reliably measured.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and are available with this article online at: http://www.current-biology.com/cgi/content/full/15/19/1779/DC1/.

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