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### Journal

International Journal of Comparative Psychology, 25(4)

### ISSN

0889-3675

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### Publication Date

2012

### DOI

10.46867/ijcp.2012.25.04.02

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## **Orangutans' Use of Contiguous Versus Distal Social and Non-social Cues in an Object-choice Task**

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In this experiment, orangutans' ability to use social versus non-social cues on an object-choice task was examined. In addition, the role of spatial proximity was investigated, by matching the distance between the cue and the target object across both social and non-social conditions. Subjects took significantly fewer trials to learn to use social cues (a finger touching the target object and an experimenter's face hovering above the target object) than non-social cues (paper markers). There was no statistical difference between their performance with cues that were physically contiguous with the target object and those that were distal spatially, regardless of whether the cue was social or non-social in nature. Evidence for spontaneous cue use was strongest for the social-contiguous condition (a finger touching the target object). These results suggest that spatial proximity alone cannot explain apes' performance on these types of tasks. Although subjects may have difficulty deriving information from human-based gestures, they still appear to be more attuned to these cues than to abstract physical markers that are matched in terms of spatial relationship and reliability.

In rainforest environments, food resources are often sparsely dispersed across space and time. For non-human primates (hereafter, 'primates'), the ability to exploit cues in order to locate hidden food, either from perceptible stimuli or from the behaviour of conspecifics, could confer a major evolutionary advantage. However, in captivity, they have difficulty spontaneously using these types of cues in object-choice experiments. For instance, primates appear to be unable to use direction of gaze to locate food (Anderson, Montant, & Schmitt, 1996; Anderson, Sallaberry, & Barbier, 1995; Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Call, Hare, & Tomasello, 1998; Itakura, Agnetta, Hare, & Tomasello, 1999; Peignot & Anderson, 1999; Povinelli, Reaux, Bierschwale, Allain, & Simon, 1997), or an experimenter's touch or point (Bräuer et al., 2006; Povinelli et al., 1997; Tomasello, Call, & Gluckman, 1997; but see Itakura & Tanaka, 1998; Peignot & Anderson, 1999, for contradictory results).

Although there may be evolutionary benefits of exploiting such cues, it is unlikely that an animal in its natural environment would point to a food source for another's benefit (Bräuer et al., 2006). It seems similarly improbable that primates would be naturally predisposed to use a human's direction of gaze or point when faced with an artificial foraging task. Bräuer et al. (2006) have argued that apes are sensitive to causal cues based on physical stimuli, but not to communicative social cues. Indeed, the inability of primates to succeed on these tasks is used to support the idea that they do not perceive the communicative intentions of experimenters (Anderson et al., 1995; Call, Agnetta, & Tomasello, 2000; Tomasello et al., 1997). However, this ability need not reflect cognitively complex processes. For instance, Emery (2000) notes that organisms could use a reflexive eye-detector mechanism to react to the direction of another's gaze.

Support for a simpler mechanism in primates comes from the finding that performance is better on object-choice tasks when the cue is spatially closer to the target. Anderson et al. (1995) speculated that capuchin monkeys' superior performance using pointing versus gaze direction might have resulted from the closer proximity between the experimenter's hand and the target object. Further, in Itakura et al. (1999), primates solved an object-choice task when an experimenter or conspecific was physically close to the target, regardless of gaze direction. Thus, spatial proximity may predict cue use. This is consistent with the natural foraging conditions of primates, in which the mere presence of a conspecific often signals an increased probability of food (Call et al., 2000).

Subjects' attention may also be a factor in their ability to exploit cues. In Povinelli, Parks, and Novak (1991), rhesus monkeys had difficulty using an experimenter's point to locate hidden food, however, one subject showed marked improvement when the experimenter wore a distinctive glove. Similarly, Itakura et al. (1999) found an improvement in chimpanzees' ability to use gaze direction if the experimenter made a concurrent vocalization. These findings suggest that local enhancement, i.e. drawing a subject's attention to a cue, might play a role.

One way to assess whether these possibilities can account for primates' difficulties on these tasks is to contrast their behaviour using social cues and physical markers that are matched in terms of distance from the target object. A few experiments have examined primates' ability to use physical cues: Call et al. demonstrated that great apes could use non-visual stimuli, such as auditory cues, to locate a hidden food item (Bräuer et al., 2006; Call, 2004), as well as visual markers (Bräuer et al., 2006; Call & Tomasello, 1998; Tomasello et al., 1997). Importantly, in Bräuer et al. (2006), apes used visual and auditory cues that were independent of any experimenter interaction (i.e., subjects did not watch experimenters place the markers or shake the target object). However, in each of these cases, the role of cue proximity was not examined.

The present research investigated the role of sociality and physical proximity in the cues that great apes (in this case, orangutans) use to solve an object-choice task. Orangutans were chosen as test subjects because their cognitive abilities are comparable to other great apes across a number of paradigms (e.g., Barth & Call, 2006; Herrmann, Wobber, & Call, 2008; Poss & Rochat, 2003), including object-choice tasks (Call & Tomasello, 1998; Tomasello et al., 1997), yet they are the only ape species that does not live in large social groups in natural settings. Thus, exploring their ability to follow social versus non-social cues provides an important contrast to experiments involving group-living ape species.

The current experiment compared conditions in which a cue was given socially (by a human) and non-socially (by a physical marker). This variable was compared between conditions in which the cue was physically contiguous with the target object and those in which it was distal, to test whether performance was enhanced when the cue actually made contact with the target object. In contrast to previous work (e.g., Call et al., 2000; Call & Tomasello, 1994; Itakura et al., 1999; Tomasello et al., 1997), subjects' behaviour was examined not only with respect to spontaneous cue use, but also in terms of the relative ease with which subjects learned to use a particular cue. Thus, rather than presenting subjects with a limited number (< 30) of critical test trials (which might be confounded by the use of

multiple conditions, in which subjects must redirect attention and inhibit responses to previous cues), they were given the chance to learn to attend to and exploit cues that reliably predicted the location of food, as in their natural environment.

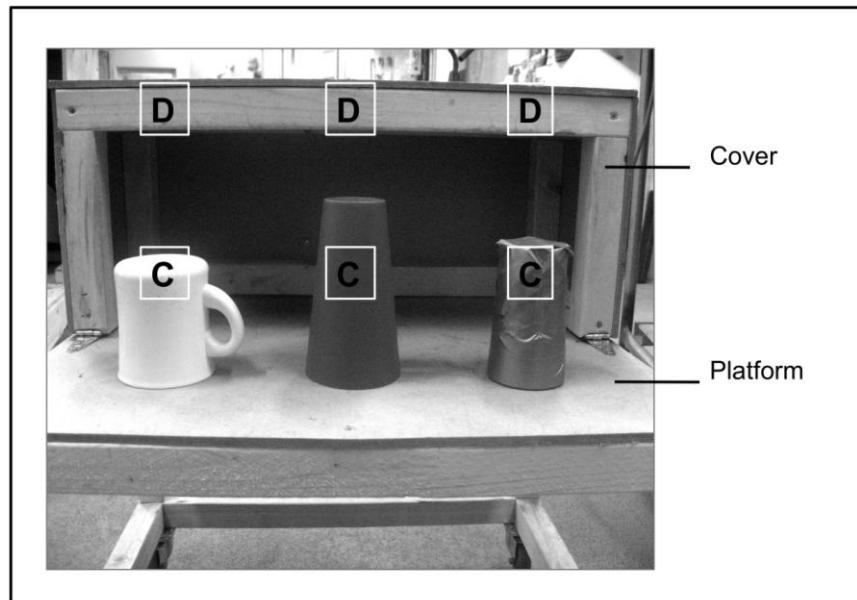
## Method

### Subjects

Five captive-born, mother-reared orangutans<sup>1</sup> (*Pongo abelii*) participated (two males, aged 4 and 32, and three females, aged 13, 18, and 25) at the Toronto Zoo, when off exhibit. The older male died during the course of the experiment. All subjects had participated in cognitive studies on concept learning, memory, and spatial cognition, but none involving social or non-social cues in an object-choice task. All subjects had been trained to respond to zookeepers' verbal commands, for management purposes (e.g., present a limb, or shift to a different holding area). Water was always available, and favoured food rewards (grapes) were used for motivation.

### Materials

The apparatus consisted of a wooden platform (surface: 60 cm x 40 cm; height: 30 cm) on wheels, with a cover that could be flipped down in front to hide the surface from subjects (see Figure 1). Three inverted opaque cups (diameter: 9 cm; height: 9 cm) were placed on top of the platform, 22 cm apart, centre to centre.



*Figure 1.* Photo of the experimental apparatus, consisting of a platform with a cover that could be flipped up to reveal three inverted cups (cover is pictured in the flipped up position). Letter 'C's denote where contiguous cues (finger point and paper marker) were placed, and letter 'D's denote where distal cues (experimenter's head and paper marker) were placed.

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<sup>1</sup>One orangutan, Sekali (18 year-old, female), was hand-raised briefly and then was reared by a surrogate orangutan mother.

## Procedure

An experimenter, familiar to subjects, sat behind the apparatus, and wore a baseball cap and surgical mask, to cover facial features and prevent inadvertent cuing (subjects were familiar with these items from previous studies). At the beginning of a trial, the cover of the apparatus was closed, so that subjects could not see the cups. The experimenter leaned over, hiding her arms under the cover, and placed a grape under one of the cups. In non-social cue conditions, she also stuck the marker to the prescribed location (see below). Her face was oriented downward so there were no directional cues to the hiding location. Once a cup was baited, the experimenter raised the cover to reveal the cups to subjects. In social cue conditions (see below), the experimenter placed her hand or head (depending on the condition) in the prescribed location as she opened the cover. On all trials, once the cover was open, the experimenter remained motionless. Subjects selected a cup by touching it with a stick (as they had done in previous experiments). If a correct choice was made, the orangutan was given the food. If an incorrect choice was made, the experimenter lifted the cup to show that it was empty, and showed where the food was hidden. Regardless of choice, the next trial began immediately. The experimenter recorded subjects' choices in real time.

Subjects completed four conditions: two involved 'social' cues from the experimenter, and two involved 'non-social' cues, with a physical marker. The order in which conditions were completed was randomly assigned and counterbalanced between subjects. For each set of social and non-social conditions, one used a cue that was physically contiguous with the baited cup, and one used a distal cue. Specifically, in the *Non-social-contiguous* condition, a square paper marker (2.5cm x 2.5cm) was appended to the side of the baited cup. In the *Non-social-distal* condition, a larger paper marker (5 cm x 5 cm) was appended to the cover of the apparatus, 15 cm above the baited cup. In the *Social-contiguous* condition, the experimenter's finger touched the baited cup. In the *Social-distal* condition, the experimenter placed her head 15 cm above the baited cup. Although a human may not be an ecologically valid 'social' partner, previous research suggests that substituting conspecifics for humans does not improve primates' performances on these tasks (Itakura et al., 1999). Further, these were captive-born orangutans, who interacted with humans daily.

For each condition, training sessions lasted twenty minutes, leading to approximately 40-60 trials per session. Subjects completed two sessions per day, three to four days per week, with a minimum of twenty minutes interceding consecutive sessions. The criterion for acquisition was 70% or more trials correct, for three consecutive sessions, which is significantly above chance level for 40 or more trials ( $p < 0.001$ ). If subjects did not reach criterion within 2000 trials, the condition was aborted, and they were advanced to the next one. This was necessary for practical reasons (because testing could not go on indefinitely), and to prevent outliers from biasing the results. If subjects reached criterion, they completed forty control trials (across two sessions), in which everything was identical to regular testing (including reinforcement), except that no cue was given. These trials tested whether subjects relied on extraneous cues to solve the task, such as auditory or scent cues, or unintentional experimenter-based cues.

## Data Analysis

To test for spontaneous cue use, each subject's performance on the first session for each condition was compared to chance level (33.3%) using binomial  $z$  tests. Performance on the remainder of training trials was not compared to chance because, by definition, if subjects reached criterion, their performance was significantly above chance level. Binomial  $z$  tests were used to compare performance on control trials to chance level. Because such a large number of binomial  $z$  tests was conducted, a Bonferroni-corrected alpha level of  $\alpha = 0.003$  was used. A repeated-measures, 2 (Sociality) x 2 (Proximity) ANOVA compared the mean number of trials to criterion between conditions, at  $\alpha = 0.05$ .

The adult male that died completed only two of the four conditions, leaving two missing values in the data set. These were missing at random, because the order of conditions was randomly assigned and counterbalanced. To preserve the sample size and include an appropriate estimate of error, multiple imputation was used to estimate the two missing values (see Keselman, Algina, & Kowalchuk, 2001, for a discussion on dealing with missing data in repeated-measures designs). For this estimation, a linear regression model was used, with three imputations.

## Results and Discussion

### Control Trials and Order Effects

Subjects' performance did not vary by the order of conditions,  $F(1,3) = 0.116$ ,  $p = 0.939$ ,  $\eta_p^2 = 0.259$ . No subject's performance on control trials differed from that expected by chance (highest level of accuracy on control trials = 19/40). Therefore, it is highly unlikely that subjects relied on extraneous cues to determine where the food was hidden.

### Acquisition and Effect of Sociality and Proximity of Cues

The strongest evidence of spontaneous cue use was found in the social-contiguous (hand pointing) condition, in which two of the five subjects performed significantly above chance levels from the first session (see Table 1). In addition, the youngest subject appeared to use the social-distal (experimenter's head) and non-social contiguous (marker attached to cup) cues spontaneously. Finally, one subject performed significantly above chance in the first session of training in the non-social distal condition, however her performance dropped to below chance level in the subsequent two sessions. This casts doubt on the likelihood of her spontaneous use of the cue. All subjects reached criterion within 2000 trials in all four conditions, with two exceptions: One of the adult females and the older male each failed to reach criterion on the non-social distal condition.

Table 1

*Percentage of correct choices made by orangutans on an object-choice task, during the first training session (with  $n$  trials) of four different cue conditions.*

Cue type	Subject (age, sex)									
	Budi		Jahe		Sekali		Ramai		Molek	
	(4, M)		(13, F)		(18, F)		(25, F)		(32, M)	
	%	n	%	n	%	n	%	n	%	n
Social-contiguous	46.7	60	<b>86.7</b>	60	43.9	41	<b>70.0</b>	60	37.5	40
Social-distal	<b>60.0</b>	40	42.5	40	43.3	60	20.0	60	--	--
Non-social-contiguous	<b>57.5</b>	40	41.7	60	40.0	60	40.0	40	--	--
Non-social-distal	40.0	40	50.0	60	38.3	60	<b>53.3</b>	60	40.0	40

*Note:* Values in **bold** are significantly higher than that expected by chance at a Bonferonni-corrected alpha level of  $p < 0.003$ , based on binomial  $z$  tests.

Dash = data is not available because the subject died before completing all four conditions.

No significant interaction was found between sociality and proximity,  $F(1,4) = 0.14$ ,  $p = 0.726$ ,  $\eta_p^2 = 0.034$ . A main effect was found for sociality, with subjects taking significantly fewer trials to reach criterion on social cue conditions,  $M = 410.1$ , 95% CI [293.9, 526.3], than non-social,  $M = 1065.2$ , 95% CI [393.6, 1736.8],  $F(1,4) = 8.81$ ,  $p = 0.041$ ,  $\eta_p^2 = 0.688$  (Figure 2). With respect to spatial proximity, although close to statistical significance, a difference was not found

between contiguous cue conditions,  $M = 594.2$ , 95% CI [269.68, 919.13], and distal ones,  $M = 881.1$ , 95% CI [415.2, 1347.0],  $F(1,4) = 6.91$ ,  $p = 0.058$ ,  $\eta_p^2 = 0.633$  (Figure 2).

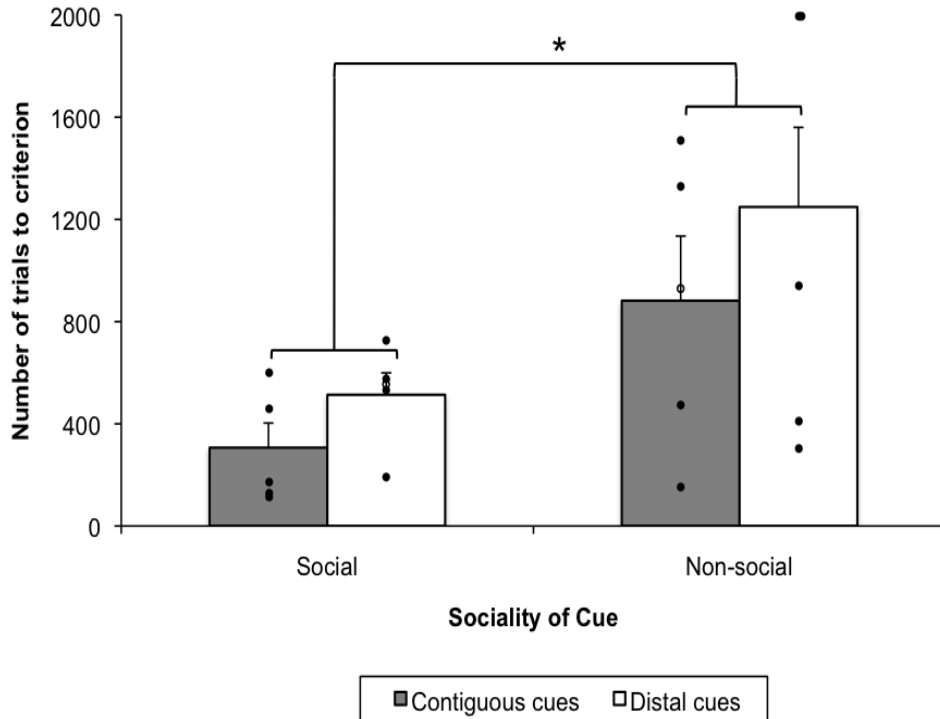


Figure 2. The mean number of trials required for orangutans to learn to use social and non-social cues that varied with respect to physical proximity to a target object, in an object-choice task. Black-filled circles show individual results, and open circles show values that were estimated using multiple imputation. The bracket with asterisk indicates a significant difference between social conditions, at an alpha level of 0.05.

In this experiment, subjects used social cues more readily than non-social cues, and some subjects appeared to do so spontaneously. These results contrast with the work of Bräuer et al. (2006), who found that apes had more difficulty with social cues than physical ones. There are a few possible explanations for this. First, Bräuer et al. (2006) postulated that apes were adept at exploiting physical cues, whereas dogs were superior at using social cues, due to their shared evolution with humans and accompanying domestication. It is possible that ‘domestication’ during an individual’s ontogeny might also affect its ability to use social cues. Indeed, ‘enculturated’ apes tend to be better at using communicative cues (e.g., Call & Tomasello, 1996; Call et al., 2000; Itakura & Tanaka, 1998). Further, training apes to perform interactive behaviours with humans (such as presenting a limb) appears to improve performance on these types of social communicative tasks (Call & Tomasello, 1996). Thus, although orangutans have not had human-mediated evolutionary processes to shape their behaviour, the subjects in the present experiment were captive reared, and trained and fed by humans. This may

help explain their attention to the experimenter's cues. Further research could examine whether wild orangutan populations show a similar pattern.

Secondly, it is possible that some methodological differences between this experiment and that of Bräuer et al. (2006) may have led to the differences in the results (*c.f.*, Lyn, 2010; Miklósi & Soproni, 2006; Mulcahy & Hedge, 2012). For instance, Bräuer et al. (2006) focused only on spontaneous cue use, whereas in the present experiment, subjects were allowed to learn to attend to cues across many more trials. Even so, at least two subjects in the present experiment appeared to use the experimenter's hand point spontaneously from the first session. Mulcahy and Hedge (2012) argued that the way an object-choice task is presented (centrally versus peripherally) affects apes' ability to succeed. This factor cannot account for the differences between the present results and those of Bräuer et al. (2006), because both used centrally presented object arrays. However, it demonstrates that methodological factors likely affect apes' propensity to use human communicative cues spontaneously, and therefore, this issue should be addressed in future research.

A third possibility is that the 'social' cues used in this experiment were not truly communicative cues, at least in the sense described by Bräuer et al. (2006). For instance, the static positioning of the experimenter's head over the target object might be viewed as more similar to a physical landmark that signals food is nearby than as a social cue, because it is not a natural communicative gesture. In this sense, subjects might have attended more to the experimenter's head because it was intrinsically more interesting to look at than the paper markers. In addition, although finger pointing is a natural communicative gesture among humans, the apes' success with this cue might have, instead, resulted from repeated associations between the experimenter's hands and food rewards (given after correct trials).

Regardless, although primates have shown difficulty using human communicative cues in previous experiments, based on the present results, orangutans are still more proficient at following human social cues than they are non-social physical markers. This suggests that, while they may not have read the experimenter's communicative intentions, they still applied more significance to her behaviour than to an abstract physical object.

Although the orangutans in general responded more readily to the social cues, the youngest subject, Budi, showed some divergent results with respect to his ability to spontaneously use cues. Specifically, unlike the others, he showed evidence of spontaneous use for the social-distal and non-social contiguous conditions. One possible explanation for this involves his training background. In contrast to the other subjects, who had been trained many years ago to present limbs and transfer between holding areas, Budi had undergone training for these procedures only shortly before the present experiment began. It is possible this recent training primed heightened vigilance toward experimenter cues (such as in the social-distal condition) (see Call & Tomasello, 1996). Another interesting consideration is that, as the only juvenile subject, his smaller stature would have afforded him a different viewpoint than the other subjects, with his eye level closer to the height of the overturned cups. As such, the non-social contiguous paper markers were directly in his line of vision, and so may have been more obvious for Budi than for the other subjects. Of course, it is also possible that there are



developmental differences in cue responsiveness between juvenile and adult apes. Most experiments on this topic have included only adult and near-adult subjects (*c.f.*, Anderson et al., 1995, 1996; Call et al., 2000); however, Buttelmann, Call, and Tomasello (2008) and Herrmann, Melis, and Tomasello (2006) used comparable object-choice tasks, with samples that included 4-7 year old subjects, and found no significant effect of age.

Another noteworthy result of the current research is that proximity was not found to be a significant predictor of the number of trials required to reach criterion. This contrasts with the well documented finding that minimizing the distance between cues, responses, and rewards enhances learning (Miller & Murphy, 1964; Murphy & Miller, 1955). Yet, subjects showed more evidence of spontaneous cue use in contiguous conditions, and the only condition in which subjects failed to reach criterion was one of the distal ones. Thus, it is possible that the marginal significance found with respect to the number of trials to criterion might instead be a reflection of the limited sample size, given that the effect size was considerable.

Conversely, it is also possible that the role of proximity was obscured by a slight confound in design. Specifically, the type of social cue differed between the two proximity conditions: in the contiguous condition, it was a hand point whereas in the distal condition, it was the position of the experimenter's head. This use of different cues may have led to differing subjective levels of salience between conditions, making the effect of proximity less clear (although it is possible that the cues were equally salient to subjects, for the reasons mentioned above regarding training history). However, if proximity was a key factor, one might have expected to find a significant interaction between proximity and social condition, with a significant difference between the non-social conditions across levels of proximity, since the same cues were used in those conditions. This was not the case. More importantly, Anderson et al. (1996) performed an experiment that explicitly contrasted the effect of distance between a human-based cue (direction of gaze) and a target object, and found, like the present research, that proximity did not play a significant role in capuchins' abilities to use the social cues. Although that research was conducted with a different primate species, it makes a compelling case for the idea that using the same two social cues in the present experiment would still have led to the same pattern of results: no effect of proximity. Because this is the first study to explicitly examine this variable across social and non-social conditions, further research is warranted to determine which of these possibilities is correct.

Taken together, it appears that the roles of sociality and physical proximity in orangutans' use of cues on an object-choice task are not entirely straightforward. Based on the current findings, orangutans appear to follow experimenter-given cues more readily than non-social physical ones, whether spontaneously or after repeated exposure. Although physical proximity may contribute to subjects' propensity to attend to a cue, this factor, at least in isolation, cannot account for primates' behaviour in these tasks. Future research should explore the role of methodology and individual ontogeny in this process.

## References

- Anderson, J. R., Montant, M., & Schmitt, D. (1996). Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioural Processes, 37*, 47-55.
- Anderson, J. R., Sallaberry, P., & Barbier, H. (1995). Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour, 49*, 201-208.
- Barth, J., & Call, J. (2006). Tracking the displacement of objects: A series of tasks with great apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, and *Pongo pygmaeus*) and young children (*Homo sapiens*). *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 239-252.
- Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology, 120*, 38-47.
- Buttelmann, D., Call, J., & Tomasello, M. (2008). Behavioral cues that great apes use to forage for hidden food. *Animal Cognition, 11*, 117-128.
- Call, J. (2004). Inferences about the location of food in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*). *Journal of Comparative Psychology, 118*, 232-241.
- Call, J., Agnetta, B., & Tomasello, M. (2000). Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition, 3*, 23-34.
- Call, J., Hare, B., & Tomasello, M. (1998). Chimpanzee gaze following in an object-choice task. *Animal Cognition, 1*, 89-99.
- Call, J., & Tomasello, M. (1994). Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology, 108*, 307-317.
- Call, J., & Tomasello, M. (1996). The effect of humans in the cognitive development of apes. In A. E. Russon, K. A. Bard, & S. T. Parker, (Eds.), *Reaching into thought: The minds of the great apes* (pp. 371-403). Cambridge, MA: Cambridge University Press.
- Call, J., & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and human children (*Homo sapiens*). *Journal of Comparative Psychology, 112*, 192-206.
- Emery, N. J. (2000). The eyes have it: The neuroethology, function, and evolution of social gaze. *Neuroscience and Biobehavioral Reviews, 24*, 581-604.
- Herrmann, E., Melis, A. P., & Tomasello, M. (2006). Apes' use of iconic cues in the object-choice task. *Animal Cognition, 9*, 118-130.
- Herrmann, E., Wobber, V., & Call, J. (2008). Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology, 122*, 220-230.
- Itakura, S., Agnetta, B., Hare, B., & Tomasello, M. (1999). Chimpanzee use of human and conspecific social cues to locate hidden food. *Developmental Science, 2*, 448-456.
- Itakura, S., & Tanaka, M., (1998). Use of experimenter given cues during object-choice tasks by chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *Journal of Comparative Psychology, 112*, 119-126.
- Keselman, H. J., Algina, J., & Kowalchuk, R. K. (2001). The analysis of repeated-measures designs: A review. *British Journal of Mathematical and Statistical Psychology, 54*, 1-20.

- Lyn, H. (2010). Environment, methodology, and the object choice task in apes: Evidence for declarative comprehension and implications for the evolution of language. *Journal of Evolutionary Psychology*, 8, 333-349.
- Miklósi, Á., & Soproni, K. (2006). A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*, 9, 81-93.
- Miller, R. E., & Murphy, J. V. (1964). Influence of the spatial relationships between the cue, reward, and response in discrimination learning. *Journal of Experimental Psychology*, 67, 120-123.
- Mulcahy, N. J., & Hedge, V. (2012). Are great apes tested with an object object-choice task? *Animal Behaviour*, 83, 313-321.
- Murphy, J. V., & Miller, R. E. (1955). The effect of spatial contiguity of cue and reward in the object-quality learning of rhesus monkeys. *Journal of Comparative and Physiological Psychology*, 48, 221-224.
- Peignot, P., & Anderson, J. R. (1999). Use of experimenter-given manual and facial cues by gorillas (*Gorilla gorilla*) in an object-choice task. *Journal of Comparative Psychology*, 113, 253-260.
- Poss, S. R., & Rochat, P. (2003). Referential understanding of videos in chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), and children (*Homo sapiens*). *Journal of Comparative Psychology*, 117, 420-428.
- Povinelli, D. J., Parks, K. A., & Novak, M. A. (1991). Do rhesus monkeys (*Macaca mulatta*) attribute knowledge and ignorance to others? *Journal of Comparative Psychology*, 105, 318-325.
- Povinelli, D. J., Reaux, J. E., Bierschwale, D. T., Allain, A. D., & Simon, B. B. (1997). Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. *Cognitive Development*, 12, 423-461.
- Tomasello, M., Call, J., & Gluckman, A. (1997). Comprehension of novel communicative signs by apes and human children. *Child Development*, 68, 1067-1080.