



Tactical use of unimodal and bimodal communication by chimpanzees, *Pan troglodytes*

DAVID A. LEAVENS*†, AUTUMN B. HOSTETTER‡, MICHAEL J. WESLEY‡ & WILLIAM D. HOPKINS‡§

*Department of Psychology, University of Georgia, U.S.A.

†Department of Psychology, School of Life Sciences, University of Sussex

‡Department of Psychology, Berry College, U.S.A.

§Division of Psychobiology, Yerkes National Primate Research Center

(Received 5 November 2002; initial acceptance 14 January 2003;
final acceptance 4 April 2003; MS. number: 7526)

Do chimpanzees tailor their communication in accordance with the attentional status of a human observer? We presented 57 chimpanzees with three experimental conditions in randomized order: an experimenter offered a banana to the focal subject (Focal), to a cagemate of the focal subject (In-Cage) and to a chimpanzee in an adjacent cage (Adjacent) while a second experimenter recorded the first and second responses of the focal subject in all three conditions. The chimpanzees' behaviour was mostly visual or bimodal in the Focal condition, changing to auditory behaviour or disengagement in the In-Cage and Adjacent conditions. Thus, with no explicit training and on their first trials in all instances, the chimpanzees tactically deployed their communicative behaviours in the visual and auditory domains in accordance with the manipulated attentional and intentional status of a human observer.

© 2004 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

There is profound theoretical interest in whether non-human primates or other animals can discriminate such abstract concepts as attention, intentions or epistemic states in other individuals (Cheney & Seyfarth 1990; Povinelli et al. 1990; Donald 1991; Povinelli & Eddy 1996; Tomasello & Call 1997; Theall & Povinelli 1999; Hauser 2000; Whiten 2000). At the same time, there is little consensus on what might constitute evidence for such discrimination and representation of mental states. On the one hand, failures to demonstrate immediate, first-trial discrimination of manipulations of visual attention are cited in support of the view that the great apes live in states of extreme solipsism, and are oblivious either to the behavioural correlates or the mentalistic implications of visual attention in their social partners (Donald 1991; Nelson 1996; Povinelli & Eddy 1996; Theall & Povinelli 1999). On the other hand, there are several

demonstrations of apes' 'spontaneous' discriminations and apparent tactical uses of the visual attention of others (Menzel & Halperin 1975; Tomasello et al. 1994, 1999; Hare et al. 2000, 2001; Whiten 2000).

To communicate in different modalities as a function of differences in observer visual attention, a signaller must be able to discriminate different states of visual attention in the observer. Recent research into this area has produced mixed results. It is not yet clear which procedural or sample characteristics distinguish studies that fail to elicit discrimination of visual attention in humans by chimpanzees (failed studies) from those that do (successful studies), but there are some obvious differences. First, failed studies attempted to bring under operant control the existing communicative behaviours of the subjects, then transferred the subjects to conditions of changed contingencies (Povinelli & Eddy 1996; Theall & Povinelli 1999), whereas successful studies did not introduce training regimens before presentation of the experimental conditions (Tomasello et al. 1999; Hostetter et al. 2001). Second, failed studies presented subjects with novel objects, without habituation, or unusual experimenter behaviour, also without habituation, during critical transfer trials (Povinelli & Eddy 1996; Theall & Povinelli 1999), thereby confounding object or behavioural novelty with the discriminative cues for transfer, whereas successful studies presented only familiar objects, in subjects' home cages, and eschewed the presentation of unusual human behaviour

Correspondence: W. D. Hopkins, Division of Psychobiology, Yerkes National Primate Research Center, 954 Gatewood Road, NE, Atlanta, GA 30322, U.S.A. (email: whopkins@berry.edu, lrcbh@rmy.emory.edu). D. A. Leavens is at the Department of Psychology, School of Life Sciences, University of Sussex, Falmer, East Sussex BN1 9QH, U.K. A. B. Hostetter is now at the Department of Psychology, University of Wisconsin at Madison, 1202 West Johnson Street, Madison, WI 53706, U.S.A. M. J. Wesley is now at the Division of Pharmacology and Neuroscience, Yerkes National Primate Research Center, 954 Gatewood Road, NE, Atlanta, GA 30329, U.S.A.

(Tomasello et al. 1999; Hostetter et al. 2001). Finally, failed studies tended to use only young animals (Povinelli & Eddy 1996; Theall & Povinelli 1999), whereas successful ones tended to use older animals (Hostetter et al. 2001; Povinelli et al. 2003), although they used some younger animals as well (Tomasello et al. 1999). In a recent, large-scale study of gestural communication by 115 captive chimpanzees from 3 to 56 years of age, significantly fewer juveniles (less than 8 years old) both vocalized and gestured than older chimpanzees did, in the presence of human experimenters (Leavens & Hopkins 1998). For these reasons, we administered only one trial in each of three experimental conditions to 57 adolescent or older chimpanzees, using a protocol designed to be 'naturalistic'; that is, consistent with their captive rearing experiences.

There are numerous reports of audience effects on communication in a single sensory domain in many vertebrate species (reviewed by Hauser 1996), including apes (e.g. Call & Tomasello 1994; Leavens et al. 1996, in press; Wilson et al. 2001). Previous experimental and observational research into multimodal communicative behaviour by chimpanzees is more limited and has produced suggestive evidence consistent with the idea that chimpanzees choose the modality of communication. Tomasello et al. (1994) reported, in an observational study of spontaneous communicative behaviour in a captive group of eight juvenile chimpanzees, that these chimpanzees tended to use tactile displays, such as poking at their conspecifics, when the latter were facing away from the signaller and that no chimpanzee was observed, during 40 h of observation, to use a visual signal when the putative target of the communicative act was facing away from the signaller (similar results have been recently reported for tactile communication by gorillas, *Gorilla gorilla*, by Pika et al. 2003; see also Tanner & Byrne 1996). Tomasello et al. apparently treated gestures as independent data points, so it is unclear to what extent the apparently tactical multimodality of the communicative behaviour of this group was representative of all eight subjects. Although the four observers in that study were trained to 'acceptable levels of agreement' (Tomasello et al. 1994, page 140), no interobserver reliability estimates were reported. These intriguing observations of a small number of juvenile chimpanzees, considered in relation to other published studies, would suggest that chimpanzees in captivity are far more sensitive to the behavioural correlates of visual attention in conspecifics than in their human caregivers, a possibility discussed by, among others, Povinelli & Eddy (1996).

Indirect evidence for tactical use of communication in the visual and auditory domains by a single chimpanzee was reported by Leavens et al. (1996): the chimpanzee appeared to increase his communicative effort in accordance with differences in the apparent attentiveness of different humans, using relatively more vocal behaviour when pointing to unreachable food in the presence of humans who were relatively less attentive than the primary experimenter. Krause & Fouts (1997), in a study of pointing by two sign-language-trained chimpanzees, reported that putative 'attention-getting' behaviours, including cage-banging, 'raspberries' (a bilabial fricative) and signing so vigorously as to be audible, were shown at high frequencies

in an experimental procedure in which an experimenter arrived, sat facing away from the subjects, and then turned to face them only upon hearing an auditory signal. In 100 trials (50 per subject), in only one trial did a chimpanzee point (a visual signal) before the experimenter turned around (see also Bodamer & Gardner 2002).

In a study specifically designed to test the hypothesis that chimpanzees may use different modalities of communication as a function of an observer's focus of visual attention, Theall & Povinelli (1999) failed to find any evidence that their seven chimpanzees did so (although procedural factors may account for this; see below). In a large-scale experimental study, Hostetter et al. (2001) reported that captive chimpanzees ($N = 49$) were more likely to communicate visually when an experimenter bearing food was facing them and they reported a non-significant trend towards increased propensity to vocalize when an experimenter bearing food was facing away from the chimpanzees. This suggestive pattern of results motivated the present research design. Thus, although some intriguing and suggestive experimental (Hostetter et al. 2001) and observational (Tomasello et al. 1994) findings have been reported, to our knowledge, no previous experimental study has adequately shown that apes communicate in different sensory modalities as a function of observer visual attention.

We asked a relatively more subtle question than has previously been asked of chimpanzee communication: would chimpanzees adjust their communicative behaviour in accordance with whether a human experimenter was offering a banana to them, to one of their cagemates, or to a chimpanzee in an adjacent cage? The primary difference between these three conditions was to which chimpanzee the experimenter was oriented (i.e. visually and posturally). This approach capitalizes on the inherent competitiveness between chimpanzees for food or, in this case, for the experimenter's visual attention and is, therefore, an extension of the approach pioneered to great effect by Hare et al. (2000, 2001). In contrast to Theall & Povinelli (1999), we used only adolescent and adult subjects, we did not require or train the subjects to show communicative behaviour and we used only first-trial data in all analyses.

One additional procedural difference between the present study and that of Theall & Povinelli (1999) regards the timing of our data collection. Theall & Povinelli (1999) required their subjects to place their hands through a specific hole in a Plexiglas screen; this operant response defined the beginning of a 20-s observation interval in each of their experimental conditions. There was, therefore, an unspecified interval on every trial between the time their subjects entered the test chamber and the time at which they placed their hands through the requisite hole, during which no behavioural data were coded. In contrast, we began coding chimpanzees' behaviour immediately upon the arrival of an experimenter bearing desirable food, coding both their first and second responses in the three experimental contexts. Our specific aim in this study was to ask 'Would chimpanzees show communicative behaviours in the visual and auditory domains differentially in accordance with the manipulated visual attention of an experimenter?'

METHODS

Subjects

We used 57 adult chimpanzees (30 males, 27 females) housed at the Yerkes National Primate Research Center (YNRPC), Emory University, Atlanta, Georgia, U.S.A. YNRPC is fully accredited by the American Association for Laboratory Animal Care. Chimpanzees at YNRPC are housed in groups ranging from two to 10 animals, in contiguous cages, comprising both indoor and outdoor sections of equal size. Total living space ranges from 33 m³ (small groups) to 210 m³ (large groups). The chimpanzees' diet consists of commercial primate chow supplemented with vegetables and fruit. They were not food deprived to elicit their cooperation in this study. To our knowledge, they have not been language trained.

The experiments were performed while the chimpanzees occupied the outdoor portions of their home cages. These outdoor enclosures were either 16 m³ (small groups) or 35 m³ (large groups). Adjacent cages were separated by wire mesh, permitting direct visual access to chimpanzees in adjacent cages. Experimenters, standing in corridors outside the cages, were directly visible to the focal subjects in all conditions. The cage walls adjacent to the corridor, through which all human–chimpanzee interactions took place, also comprised wire mesh.

Procedure

We randomly selected focal subjects. In the Focal condition, the first experimenter (E1) knelt 1 m in front of the focal subject's cage and held a banana in front of him, while looking at the subject, calling the subject's name, and engaging in unscripted verbal banter, such as one might use

while interacting with infants or pets, and which is typical of human–ape interactions in captivity. E1 looked directly at the subject throughout the trial. The In-Cage condition was similar to the Focal condition, except that the recipient of the offer was not the focal subject, but a cagemate; hence E1 looked towards the cagemate of the focal subject throughout the trial. In cages in which there were more than two occupants, the most dominant cagemate present was selected to be the recipient of the offer, to minimize aggressive behaviour from the focal subject on food delivery. The Adjacent condition was identical to the Focal and In-Cage conditions, except that the experimenter knelt in front of and offered the banana to a chimpanzee in an adjacent cage. In the Adjacent condition, the nearest apparently attentive chimpanzee was selected to be the recipient of the offer. These conditions were presented in randomized order across subjects.

The first and second behavioural responses of the focal subject in each condition were recorded by a second experimenter (E2) in accordance with the ethogram in Table 1. E2 stood quietly 1 m behind and slightly to one side of E1. Thus, although the banana was being offered to three different chimpanzees in the three conditions, only the behaviour of the focal subject was recorded in each condition. Visual and auditory signals were coded as single occurrences (bouts) if repeated at intervals of less than 1 s. The observation interval was 60 s from the arrival of E1, at the end of which the banana was given to the focal subject (Focal), the cagemate (In-Cage), or the chimpanzee in the adjacent cage (Adjacent). Interference with food delivery was not systematically recorded; in some instances, some chimpanzees attempted to interfere with delivery of food to the recipient of an offer, but the banana was delivered successfully in virtually all trials.

Table 1. Ethogram: modes of communication

Definitions	
Visual	
Gesture	Extension of one or both hands through or partially through the wire mesh of the cage in an apparent attempt to point to or beg for the food (Goodall 1986; Leavens & Hopkins 1998)
Lip pout	Species-typical facial expression characterized by pronounced lip protrusion (Goodall 1986)
Auditory	
Vocalization	Any noise produced by the subject's mouth or throat during the trial
Clap	Forceful slapping together of palmar surfaces of the hands
Cage bang	Striking any part of the cage with either hands or feet
Bimodal	
Gesture and vocalization	Simultaneous expression of these behaviours
Disengagement	
Depart	Either leaving the cage and testing area, or retreating from the front of the cage without looking at the experimenter
No response	Scored when subjects either showed none of the other behaviours listed here, or had previously left the area and were no longer visible to the observer
Other	
Tactile	Spit or throw
Display	Aggressive display (Goodall 1986)
Rump present	As described in Goodall (1986)
Barter	Apparent attempt to exchange detritus for food (Hyatt & Hopkins 1998)

Larger groups of chimpanzees were housed in multiple adjacent cages; for purposes of the present experiment these multiple cages were treated as a single cage, so that in the Adjacent condition, the offer was made to a chimpanzee in a different cage or set of cages bordering that of the focal subject. In rare cases, the recipient of the offer in multiple-cage housing moved from one cage to another during the trial; when this happened E1 adjusted his position to follow the recipient of the offer, while E2 maintained observation of the focal animal. Occasionally, the focal subject directed communicative behaviour or looked at E2 in the course of the trial; this behaviour was rare and ignored by E2. The focal subject persisted in orienting towards and attempting to communicate with E2, rather than E1, in only one trial, which was omitted from the analysis. Behavioural observation ceased prior to food delivery in all cases; the observer signalled the experimenter to deliver the banana only at the end of each observational interval.

Analysis

First responses

In the first analysis, the chimpanzees were categorized in terms of their first responses: visual (gestures or lip pouts), auditory (vocalizations, cage bangs, or claps), bimodal (simultaneous display of gestures and vocalizations), disengagement (departing or no response) and other behaviours (a 'catchall' category of rare behaviours, such as the tactile responses listed in Table 1). Our research hypothesis was that chimpanzees would apportion their first responses nonrandomly across the three conditions, such that more auditory (putative 'attention-getting' or 'attention-claiming') behaviours (cf. Gómez 1996) would occur when E1 was offering a banana to another individual than when the focal animal was the recipient of the offer and visual behaviours would be shown preferentially when E1 was offering the banana to the focal subject.

We conducted primary analyses with Cochran's Q , a statistic appropriate for nominal data which can be dichotomously characterized over more than two repeated measures in the same or related samples. Post hoc analyses were conducted with McNemar's test for symmetry when $N > 24$ and with binomial tests when $N \leq 24$ in any given pairwise comparison (comparisons with extraordinarily low statistical power are highlighted). Because of the often low statistical power of these pairwise comparisons between conditions, the risk of type II error was high; for this reason, no correction for multiple comparisons was used (i.e. the two-tailed probabilities with $\alpha = 0.05$ are reported in all pairwise comparisons).

Behavioural sequences

In the second analysis, we sought to explore the stability of these patterns over the initial sequences of behaviour of these chimpanzees. The chimpanzees were categorized in terms of their behavioural sequences: visual–visual (a visual response followed by a visual response), auditory–auditory (an auditory response followed by an auditory response), bimodal (either the first or second

response was a simultaneous vocalization and gesture or subjects changed from an auditory first response to a visual second response, or vice versa), disengagement (subjects' first or second responses constituted either departure or no response) and other (subjects' first or second responses constituted one of the category of other responses listed in Table 1). Chimpanzees did not preferentially show sequential visual–auditory or sequential auditory–visual responses in any of the three conditions. In the Focal condition, 13 chimpanzees showed visual, then auditory responses and six auditory, then visual responses (McNemar test for symmetry: $\chi^2_1 = 2.58$, $N = 19$, NS); in the In-Cage condition, no chimpanzee showed a visual, then auditory response, and one showed an auditory, followed by a visual response (a statistical test with only one subject is obviously not meaningful); in the Adjacent condition, six chimpanzees showed a visual, then auditory response, and two showed an auditory, followed by a visual response (McNemar test for symmetry: $\chi^2_1 = 2.00$, $N = 8$, NS). Therefore, because there were no asymmetries in the order of display of sequential bimodal responses in any of the three conditions, we collapsed simultaneous bimodal responses and sequential bimodal responses into a single analytical category, to increase statistical power. Our research hypothesis was that the chimpanzees would show behavioural sequences nonrandomly across the three conditions and in accordance with whether the focal animal or another chimpanzee was the recipient of the offer.

Reliability

Two independent observers simultaneously scored a subset of 20 trials. Agreement as to whether a visual signal was the first response was 100%. Agreement on type of visual signal was Cohen's $\kappa = 0.90$. Agreement as to whether an auditory signal was the first response and on type of auditory signal was 100%.

RESULTS

First Responses

Visual, auditory, bimodal and disengagement behaviours were all nonrandomly distributed across the three conditions (visual, Cochran's Q : $Q_2 = 24.15$, $N = 57$, $P < 0.001$; auditory, Cochran's Q : $Q_2 = 17.29$, $N = 57$, $P < 0.001$; simultaneous visual + auditory, Cochran's Q : $Q_2 = 17.29$, $N = 57$, $P < 0.001$; disengagement, Cochran's Q : $Q_2 = 16.75$, $N = 57$, $P < 0.001$; Fig. 1). Visual and bimodal behaviours were concentrated in the Focal condition, whereas both auditory and disengagement behaviours were concentrated in the In-Cage and Adjacent conditions (the distribution of behaviours in the 'other' category was random across the three conditions; Cochran's Q : $Q_2 = 3.00$, $N = 57$, NS; Fig. 1). Post hoc analyses are presented in Table 2.

Behavioural Sequences

As for first responses the behavioural sequences visual–visual, auditory–auditory, bimodal and disengagement

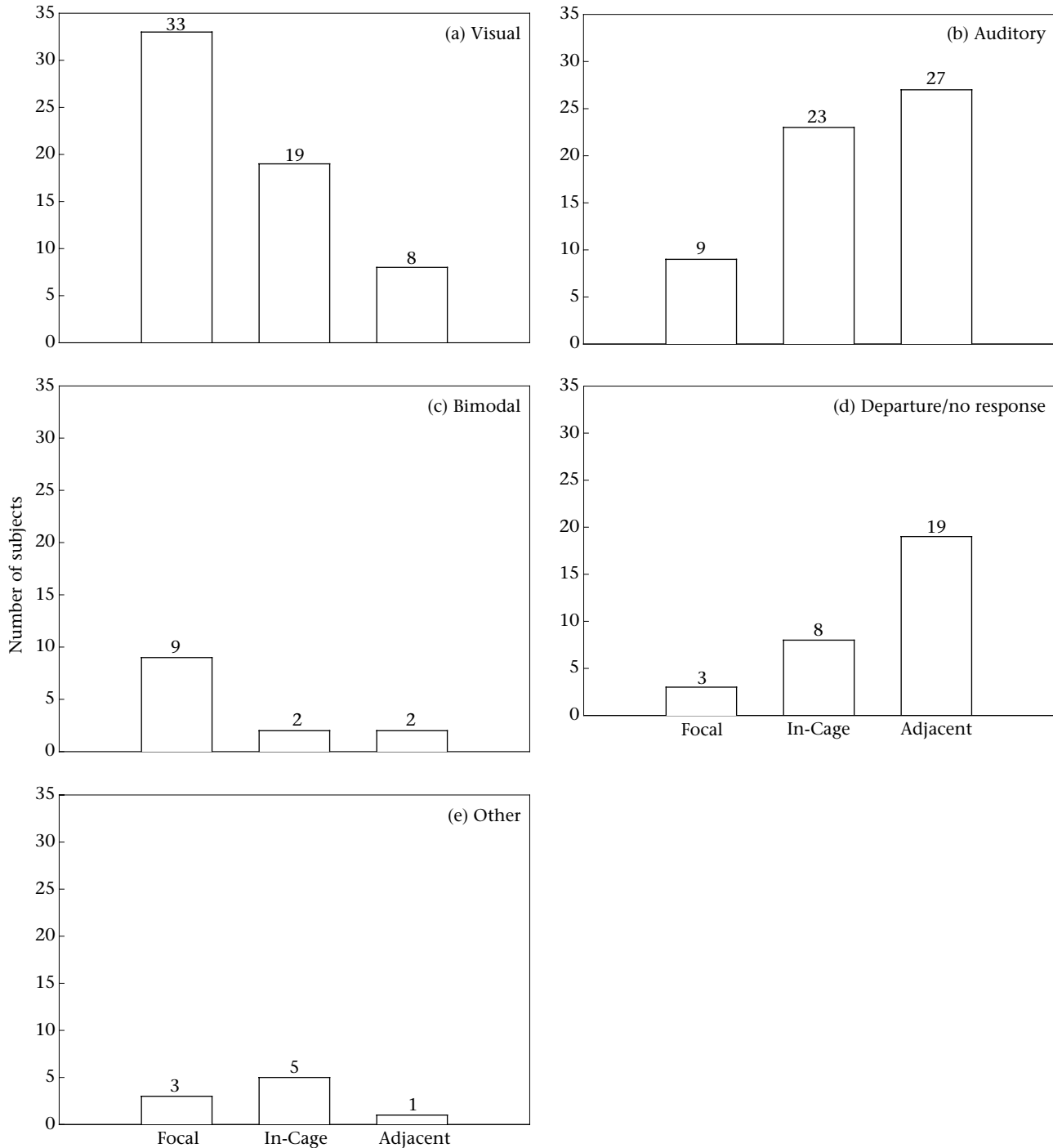


Figure 1. Frequency distribution of the first communicative behaviours of the 57 chimpanzees in each of the three experimental conditions, Focal (a banana was given to the focal subject), In-Cage (a banana was given to its cagemate) and Adjacent (a banana was given to a chimpanzee in an adjacent cage). (a) Visual responses, (b) auditory responses, (c) bimodal responses (simultaneous gestures with vocalizations), (d) departures or no responses and (e) other responses. Sample sizes are given above the bars. See Table 2 for post hoc analyses.

were nonrandomly distributed across the conditions (visual–visual, Cochran’s Q : $Q_2 = 10.00$, $N = 57$, $P = 0.007$; auditory–auditory, Cochran’s Q : $Q_2 = 6.00$, $N = 57$, $P = 0.05$; bimodal, Cochran’s Q : $Q_2 = 13.28$, $N = 57$, $P = 0.001$; disengagement, Cochran’s Q : $Q_2 = 15.44$, $N = 57$, $P < 0.001$). Visual–visual sequences were

shown exclusively during the Focal condition, bimodal sequences mainly during the Focal condition, and auditory–auditory and disengagement sequences were concentrated in the conditions in which the banana was being offered to another chimpanzee (sequences that included responses categorized as ‘other’ were randomly

Table 2. Post hoc analyses for first responses and behavioural sequences

	Pairwise comparison	Test statistic*	N†	P
First responses (see Fig. 1)				
Visual	Focal > In-Cage	$\chi^2_1 = 5.63$	30	0.018
	Focal > Adjacent	$\chi^2_1 = 19.86$	29	<0.001
	In-Cage > Adjacent	Binomial test	19	0.019
Auditory	Focal < In-Cage	Binomial test	18	<0.001
	Focal < Adjacent	Binomial test	24	<0.001
	In-Cage = Adjacent	Binomial test	20	NS
Bimodal	Focal > In-Cage	Binomial test	9	0.039
	Focal > Adjacent	Binomial test	9	0.039
	In-Cage = Adjacent	Binomial test	2‡	NS
Disengagement	Focal = In-Cage	Binomial test	4‡	NS
	Focal < Adjacent	Binomial test	11	0.001
	In-Cage < Adjacent	Binomial test	13	0.022
Other responses§	—	—	—	—
Behavioural sequences (see Fig. 2)				
Visual–visual	Focal > In-Cage	Binomial test	5‡	<0.063
	Focal > Adjacent	Binomial test	5‡	<0.063
	(In-Cage & Adjacent)**	—	—	—
Auditory–auditory	Focal < In-Cage	Binomial test	5‡	<0.063
	Focal < Adjacent	Binomial test	9	0.039
	In-Cage = Adjacent	Binomial test	12	NS
Bimodal	Focal > In-Cage	$\chi^2_1 = 4.65$	31	0.039
	Focal > Adjacent	$\chi^2_1 = 10.32$	28	0.001
	In-Cage = Adjacent	Binomial test	19	NS
Disengagement	Focal < In-Cage	$\chi^2_1 = 7.26$	27	0.007
	Focal < Adjacent	$\chi^2_1 = 12.00$	27	0.001
	In-Cage = Adjacent	Binomial test	24	NS
Other responses§	—	—	—	—

*McNemar's test for symmetry was used when $N > 24$ and binomial tests were used when $N \leq 24$.

†Because statistical comparisons ignored individuals who did not change their behaviour across conditions, this number is less than the total sample of 57 chimpanzees.

‡N is too small for confident statistical comparison.

§Because the omnibus test for Other responses was not significant, no post hoc analyses were performed.

**Because no visual–visual sequences were recorded in the In-Cage and Adjacent conditions, no post hoc analysis was performed (see Fig. 2a).

distributed across the conditions; Cochran's Q : $Q_2 = 1.17$, $N = 57$, NS; Fig. 2). Of the 15 chimpanzees who showed two successive responses in the auditory domain, only one did so in the Focal condition (Fig. 2b). Post hoc analyses are presented in Table 2.

Vocal Production

Could the patterns of auditory responses be accounted for by the utterance of 'complaint' vocalizations by these chimpanzees? In other words, might focal subjects, upon seeing an experimenter offer a banana to another chimpanzee, express dismay, rather than try to obtain the visual attention of the experimenter? This would still constitute evidence for the discrimination of intentional states in human experimenters, but is a plausible alternative interpretation for a nonrandom distribution of auditory responses. We reasoned as follows: if the chimpanzees are expressing vocal dismay at the impending delivery of a banana to another chimpanzee, they ought to be as dismayed during their first response as they are during their second response. If, on the other hand, their behaviour was part of an attention-getting tactic, then

we would expect them to express a different response after an initial vocalization fails to affect the behaviour of the experimenter. No chimpanzee who initially vocalized in any of the conditions vocalized as its second response; rather, second responses tended to be auditory or disengagement (Table 3). Comparable numbers of chimpanzees first vocalized then made some other communicative bid (9, 10, 12, in the Focal, In-Cage and Adjacent conditions, respectively). For the few subjects who showed two successive auditory responses (1, 4, 8 in the Focal, In-Cage and Adjacent conditions, respectively) the result is statistically significant (Cochran's Q : $Q_2 = 6.73$, $N = 57$, $P = 0.035$). Post hoc binomial tests revealed that Focal < Adjacent ($N = 9$, $P = 0.039$), In-Cage = Adjacent ($N = 10$, NS) and Focal = In-Cage ($N = 3$, NS, note that low statistical power renders this comparison equivocal). Thus, the data are distributed in accordance with the tactical communication hypothesis.

DISCUSSION

Our results demonstrate the tactical use of communicative behaviours by chimpanzees in the presence of an

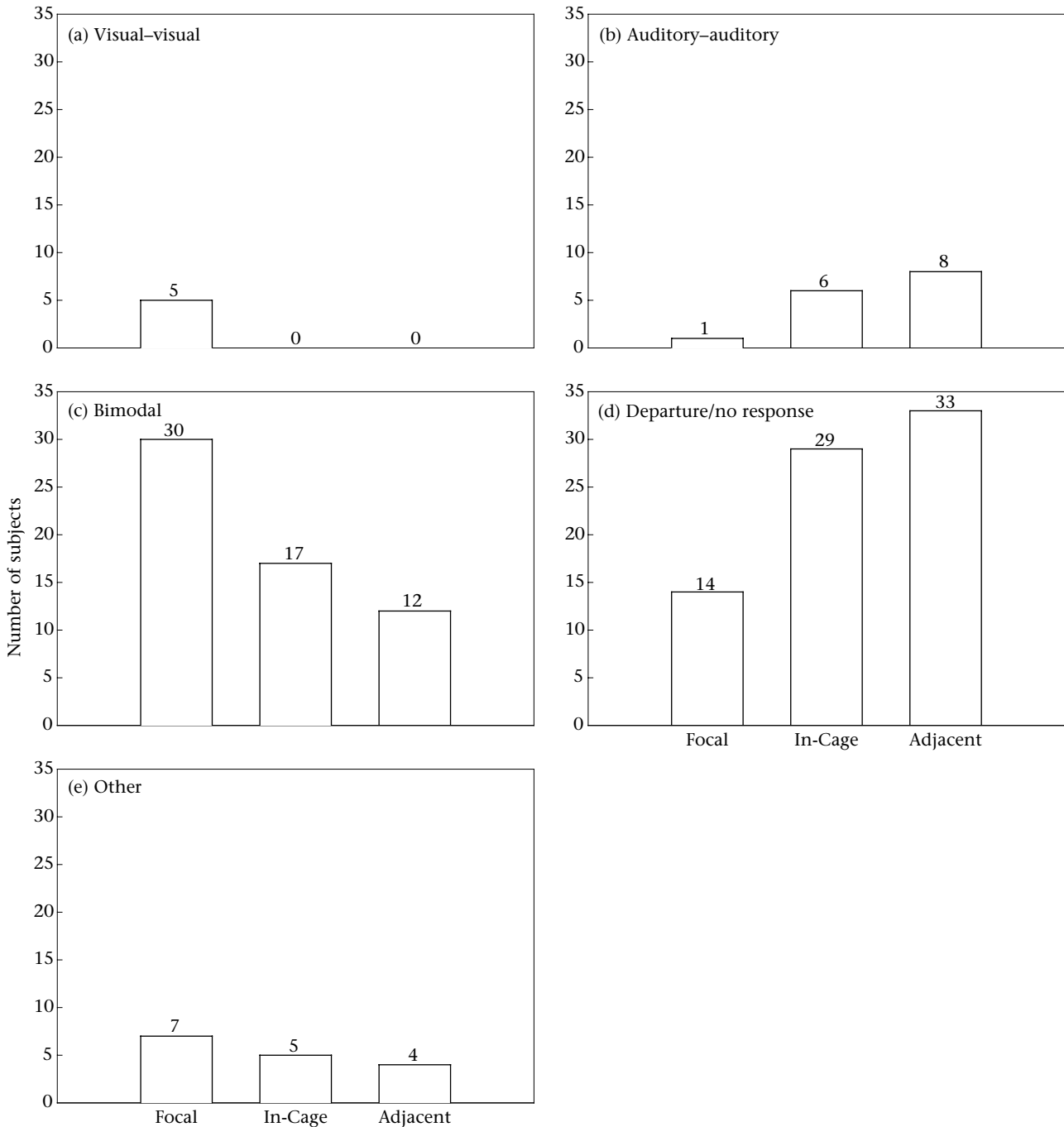


Figure 2. Frequency distribution of behavioural sequences of the 57 chimpanzees in each of the three experimental conditions, Focal, In-Cage and Adjacent (see Fig. 1 for details). (a) Unimodal visual-visual sequences, constituting the first and second responses, (b) unimodal auditory-auditory sequences, (c) bimodal sequences, including simultaneous bimodal responses as either the first or second response and sequential bimodal (auditory-visual or visual-auditory) responses as the first and second response, (d) sequences that included disengagement (either departure or no response) as either the first or second response and (e) other responses. Sample sizes are given above the bars. See Table 2 for post hoc analyses.

experimenter offering desirable food to themselves and to other chimpanzees. It is important to emphasize that in our use of the word, 'tactical', we do not imply any mental state attribution by any party concerned with this study (chimpanzees, experimenters or authors); to note that these behaviours were used tactically is to comment upon

the manifest skill involved (Figs 1, 2), which is all the more striking because these skills could not have been acquired during the experiment, because every subject received only one trial in each experimental condition. Hence, the discriminative competence of these chimpanzees was acquired without explicit training before the experiment.

Table 3. Sequelae of initial vocal responses

	Focal	In-Cage	Adjacent
Auditory elaboration			
Vocal	0	0	0
Other auditory (cage bang)	1	4	6
Auditory/tactile (display)	0	0	2
Switch to visual			
Visual	6	2	1
Vocal + gesture	2	3	2
Tactile (spit)	0	0	1
Other response	0	1	0
Disengaged	0	8	7

Because it is impossible, in principle, to design an experiment in which a change in attention, intention or knowledge state is not confounded with a change in the physical context, or more specifically, the media or content of information transfer (Vanderwolf 1998), most experimental enquiries into the discrimination and representation of mental states involve training of operant responses to the behavioural correlates of attention, intentions or epistemic states, with subsequent transfer to novel conditions in which these behavioural correlates are altered (Call & Tomasello 1994, 1999; Povinelli & Eddy 1996; Theall & Povinelli 1999). High performance on transfer to a condition in which the behavioural cues to attention, intentions or epistemic states have been manipulated in a communicative partner constitutes evidence for the discrimination of the experimental conditions, but cannot, in principle, serve to demonstrate unambiguously the discrimination or representation of mental states, even where performance on the initial trials of transfer is high. This is, again, because it is axiomatic that, for any signalling organism to discern changes in the attentional, intentional or epistemic states of a receiver, they must discriminate between the physical indices of the hypothetical mental states in question, and therefore all mental state attribution must be predicated upon these discriminations of observable events (MacCorquodale & Meehl 1948; Leavens 2002). It is worth noting that these publicly observable events may constitute the putative mental states in question; that is, it may be the case that to invoke a mental state as being causal in behaviour is to confuse a description of mentality with its explanation (Thompson 1997). Under the by no means unassailable assumption that it is meaningful to speak of unobservable mental states as being causal in behaviour, to the limits of current technology, it will be ambiguous whether organisms that do apparently discriminate between different mental states or intentions are responding on the basis of (1) changes in the physical conditions or (2) these physical changes plus the hypothetical mental states of a social partner (Vanderwolf 1998). This limitation in the study of comparative social cognition will ensue until such time as it may become possible to measure directly psychological processes such as mental state attribution independent of overt behaviour (MacCorquodale & Meehl 1948; Bergmann 1962; Vanderwolf 1998). This inherent

ambiguity in the interpretation of experimental results which obtains when organisms do rapidly discriminate between experimental conditions (as in the present study) can only be amplified when organisms either acquire a particular discriminative response after some experience in the critical transfer conditions (suggesting that they are learning the discrimination during transfer, rather than transferring an acquired discrimination) or fail to acquire a discrimination at all (Hauser 1996, page 593; Povinelli & Eddy 1996; Call & Tomasello 1999).

The procedure we used was deliberately designed to be consistent with the life experiences of these chimpanzees. Our results show that the chimpanzees discriminated between the experimental conditions with no explicit training, but first-trial data can never isolate a particular learning mechanism (Leavens et al. 1996, in press; Leavens & Hopkins 1998). Thus, what we can say with confidence is that these chimpanzees have generalized their pre-experimental learning experiences to the present experimental circumstances. What we cannot definitively answer (for reasons given above) is whether they acquired the discrimination through incidental operant conditioning, insight learning, or application of a higher-order inferential or representational process. For comparison, consider the evidence for the transition to intentional communication in human infancy. Although most infants begin to point at about a year of age, it is not until about 18 months of age that infants who point to distal objects also reliably look to their social partners prior to pointing, as though they are monitoring the attentional status of the recipient of their gestures before gesturing (Franco & Butterworth 1996). Have they learned, as some would argue, that their social partners are intentional beings with visual perspectives that differ from their own, or has this behaviour emerged through incidental operant conditioning during their previous life experience of pointing in the presence of others, in which only pointing that has been visually attended to has been reinforced? We simply do not know. As Tomasello (1999, pp. 88–89) recently pointed out, ‘empirically, we do not know whether infants learn to point via ontogenetic ritualization [i.e. incidental operant conditioning] or imitative learning ...’ (see Reddy 2001 and Thompson 1997 for related discussion in developmental and ethological perspectives, respectively). Indirect evidence suggesting that the development of communicative competence in human infancy is dependent upon pre-experimental learning is provided by studies of atypically developing populations. Infants of mothers suffering from mental illness, for example, display a developmental delay in intentional communication as do children who have suffered serious deprivations in their early social environments (reviewed in, among others, Hobson 2002). Taken together, the evidence strongly suggests that pre-experimental experience is crucial to the spontaneous expression of many aspects of intentional communication in humans. Thus, we can assert that human infants after about 18 months of age appear ‘spontaneously’ to take into account the attentional status of their social partners when they point to distal objects, but we cannot yet isolate a particular learning pathway to that pattern of

behaviour. The question about whether humans or chimpanzees acquire their communicative competence through incidental operant conditioning or some other learning process remains open.

We could find no evidence that the striking patterns observed in the auditory domain could be attributed to 'complaint' vocalizations expressed upon seeing an experimenter posturally express the apparent intention to give a banana to another chimpanzee. The chimpanzees who initially vocalized adjusted their behaviour, mostly within the auditory domain, consistent with an attention-getting interpretation and inconsistent with a 'complaint' hypothesis (Table 3). However, this finding does not constitute a contrast between a 'rational' and an 'emotional' interpretation: during these experimental episodes the chimpanzees were highly animated.

Chimpanzee communicative signals in both auditory and visual domains are highly variable both in context of use and form of signal (e.g. Goodall 1986; Tomasello et al. 1994; Tomasello & Call 1997). Goodall (1986, page 145), for example, commented on the 'inventiveness, plasticity of behavior, [and] social awareness' that characterizes chimpanzee communication in the wild. In a series of studies of communication in groups of captive chimpanzees, Tomasello and his colleagues emphasized the flexible nature of the use of conventionalized signals between communicative interactants (e.g. Tomasello et al. 1994). In this sense, these signals are, to varying degrees, conventionalized through interactions. It is therefore difficult to compare captive sites or captive and wild populations of chimpanzees in terms of the display of specific gestures and vocalizations. However, essentially all of the signals that chimpanzees used in our study have been described either in other captive populations, in feral chimpanzees, or both. For example, extending the hand towards the experimenter with the palm supinated and hand cupped (a begging gesture) is commonly described among both captive and wild populations (see references in Table 1), as is the extension of the hand towards an observer with the palm in a more pronated position. Although we did not attempt to categorize vocalizations, those most frequently observed were (1) raspberries (described in feral orang-utans, *Pongo pygmaeus*, by van Schaik et al. 2003; also known as a 'Bronx cheer'), (2) food barks (described in feral chimpanzees by Goodall 1986, and common in captive populations) and (3) extended grunts (described in feral chimpanzees by Goodall 1986). A raspberry is produced by expelling air forcefully, usually in a repetitive fashion, through closed, somewhat protruded lips (a bilabial fricative). Raspberries seem to be a relatively prominent part of the vocal repertoires of chimpanzees in captivity, usually in apparently 'attention-getting' contexts (e.g. Krause & Fouts 1997; Leavens & Hopkins 1998; R. Wrangham, personal communication; see also Marshall et al. 1999), but we are unaware of any systematic analyses of these vocalizations and their contexts in wild chimpanzees. In summary, the gestural and vocal repertoires of the chimpanzees in our sample are similar to the kinds of visual and vocal signals used by chimpanzees in the wild (with the exception of the raspberry) and in other captive facilities.

The chimpanzees in the present study showed an immediate, first-trial discrimination of three different experimental conditions characterized by complex, dynamic behaviour patterns on the part of the experimenters. For this reason, it is not possible to isolate particular features of the stimulus array (experimenters' posture, head orientation, vocal behaviour, etc.) to which the chimpanzees were responding. Nevertheless, these chimpanzees clearly discriminated between the experimental conditions in which the experimenter's posture, and head and eye orientation varied systematically across conditions. Thus, the chimpanzees discriminated between conditions that differed in the chimpanzee to which the experimenter was oriented. These postural and visual orientations were not statically maintained, but dynamically followed the movements, if any, of the recipient of the food offer in each condition and were, therefore, more naturalistic than in some previous studies (e.g. Povinelli & Eddy 1996; Theall & Povinelli 1999) but also less amenable to precise characterization. To the degree that kneeling in front of, leaning towards, looking at and extending a banana towards, while calling out the name of, a chimpanzee constitutes an operational definition of an 'offer to a recipient' of food, then we conclude that these chimpanzees clearly discriminated the intended recipient of the food in their communicative behaviour. It necessarily follows, for reasons given above, that if any individual organism can discriminate different attentional, intentional or epistemic states in other organisms, this must depend upon the discrimination of perceptible (physical) changes in the stimulus array that index these changes (Menzel & Halperin 1975). The present experiment, in which a large sample of chimpanzees showed immediate, first-trial tactical choice over the mode of communication in accordance with the manipulated intentions of a human experimenter, constitutes the first such demonstration of this prerequisite capacity in a large sample of chimpanzees, in ape-human interactions typical of captive circumstances.

Acknowledgments

We thank Frans B. M. de Waal and Darren Long at Living Links who provided logistical support, Kim A. Bard, University of Portsmouth, for helpful commentary and critique and Janette Wallis, Marc Hauser, Richard Wrangham, John Mitani and Andrew Whiten for their helpful discussions of chimpanzee raspberries. We also thank the anonymous referees for insightful and authoritative comments that have improved the manuscript. D.A.L. thanks the former School of Cognitive and Computing Sciences, University of Sussex for generous support. The study was supported by NIH grants NS-42867, NS-36605, HD-38051 and RR-00165 to the Yerkes National Primate Research Center, and the Living Links Center for the Advanced Study of Ape and Human Evolution.

References

- Bergmann, G. 1962. Purpose, function, scientific explanation. *Acta Sociologica*, 5, 225–238.

- Bodamer, M. D. & Gardner, R. A.** 2002. How cross-fostered chimpanzees (*Pan troglodytes*) initiate and maintain conversations. *Journal of Comparative Psychology*, **116**, 12–26.
- 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.** 1999. A nonverbal false belief task: the performance of children and great apes. *Child Development*, **70**, 381–395.
- Cheney, D. L. & Seyfarth, R. M.** 1990. *How Monkeys See the World*. Chicago: University of Chicago Press.
- Donald, M.** 1991. *Origins of the Modern Mind: Three Stages in the Evolution of Culture and Cognition*. Cambridge, Massachusetts: Harvard University Press.
- Franco, F. & Butterworth, G.** 1996. Pointing and social awareness: declaring and requesting in the second year. *Journal of Child Language*, **23**, 307–336.
- Gómez, J.-C.** 1996. Ostensive behavior in great apes: the role of eye gaze. In: *Reaching into Thought: The Minds of the Great Apes* (Ed. by A. E. Russon, K. A. Bard & S. T. Parker), pp. 131–151. Cambridge: Cambridge University Press.
- Goodall, J.** 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Belknap Press.
- Hare, B., Call, J., Agnetta, B. & Tomasello, M.** 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, **59**, 771–785.
- Hare, B., Call, J. & Tomasello, M.** 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour*, **61**, 139–151.
- Hauser, M.** 1996. *The Evolution of Communication*. Cambridge, Massachusetts: MIT Press.
- Hauser, M.** 2000. *Wild Minds: What Animals Really Think*. London: Allen Lane.
- Hobson, P.** 2002. *The Cradle of Thought: Exploring the Origins of Thinking*. London: Macmillan.
- Hostetter, A. B., Cantero, M. & Hopkins, W. D.** 2001. Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology*, **115**, 337–343.
- Hyatt, C. W. & Hopkins, W. D.** 1998. Interspecies object exchange: bartering in apes? *Behavioural Processes*, **42**, 177–187.
- Krause, M. A. & Fouts, R. S.** 1997. Chimpanzee (*Pan troglodytes*) pointing: hand shapes, accuracy, and the role of eye gaze. *Journal of Comparative Psychology*, **111**, 330–336.
- Leavens, D. A.** 2002. On the public nature of communication. *Behavioral and Brain Sciences*, **25**, 630–631.
- Leavens, D. A. & Hopkins, W. D.** 1998. Intentional communication by chimpanzees: a cross-sectional study of the use of referential gestures. *Developmental Psychology*, **34**, 813–22.
- Leavens, D. A., Hopkins, W. D. & Bard, K. A.** 1996. Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **110**, 346–353.
- Leavens, D. A., Hopkins, W. D. & Thomas, R. K.** In press. Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*.
- MacCorquodale, K. & Meehl, P. E.** 1948. On a distinction between hypothetical constructs and intervening variables. *Psychological Review*, **55**, 95–107.
- Marshall, A. J., Wrangham, R. W. & Arcadi, A. C.** 1999. Does learning affect the structure of vocalizations in chimpanzees? *Animal Behaviour*, **58**, 825–830.
- Menzel, E. W. & Halperin, S.** 1975. Purposive behavior as a basis for objective communication between chimpanzees. *Science*, **189**, 652–654.
- Nelson, K.** 1996. Four-year-old humans are different. Why? *Behavioral and Brain Sciences*, **19**, 134.
- Pika, S., Leibal, K. & Tomasello, M.** 2003. Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning, and use. *American Journal of Primatology*, **60**, 95–111.
- Povinelli, D. J. & Eddy, T.** 1996. *What Young Chimpanzees Know about Seeing*. Chicago: Society for Research in Child Development.
- Povinelli, D. J., Nelson, K. E. & Boysen, S.** 1990. Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **104**, 203–210.
- Povinelli, D. J., Theall, L. A., Reaux, J. E. & Dunphy-Lelii, S.** 2003. Chimpanzees spontaneously alter the location of their gestures to match the attentional orientation of others. *Animal Behaviour*, **66**, 71–79.
- Reddy, V.** 2001. Mind knowledge in the first year: understanding attention and intention. In: *Blackwell Handbook of Infant Development* (Ed. by J. G. Bremner & A. Fogel), pp. 241–264. Hove: Blackwell.
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M.** 2003. Orangutan cultures and the evolution of material culture. *Science*, **299**, 102–105.
- Tanner, J. E. & Byrne, R. W.** 1996. Representation of action through iconic gesture in a captive lowland gorilla. *Current Anthropology*, **37**, 162–173.
- Theall, L. A. & Povinelli, D. J.** 1999. Do chimpanzees tailor their gestural signals to fit the attentional states of others? *Animal Cognition*, **2**, 207–214.
- Thompson, N. S.** 1997. Communication and natural design. In: *Perspectives in Ethology. Vol. 12* (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 391–415. New York: Plenum.
- Tomasello, M.** 1999. *The Cultural Origins of Human Cognition*. Cambridge, Massachusetts: Harvard University Press.
- Tomasello, M. & Call, J.** 1997. *Primate Cognition*. Oxford: Oxford University Press.
- Tomasello, M., Call, J., Nagell, K., Olguin, K. & Carpenter, M.** 1994. The learning and use of gestural signals by young chimpanzees: a trans-generational study. *Primates*, **35**, 137–154.
- Tomasello, M., Hare, B. & Agnetta, B.** 1999. Chimpanzees, *Pan troglodytes*, follow eye gaze geometrically. *Animal Behaviour*, **58**, 769–777.
- Vanderwolf, C. H.** 1998. Brain, behavior, and mind: what do we know and what can we know? *Neuroscience and Biobehavioral Reviews*, **22**, 125–142.
- Whiten, A.** 2000. Chimpanzee cognition and the question of mental re-representation. In: *Metarepresentation: A Multidisciplinary Perspective* (Ed. by D. Sperber), pp. 139–167. Oxford: Oxford University Press.
- Wilson, M. L., Hauser, M. D. & Wrangham, R. W.** 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behaviour*, **61**, 1203–1216.