

Correspondence

Imitation recognition in great apes

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Human infants imitate not only to acquire skill, but also as a fundamental part of social interaction [1–3]. They recognise when they are being imitated by showing increased visual attention to imitators (implicit recognition) and by engaging in so-called testing behaviours (explicit recognition). Implicit recognition affords the ability to recognize structural and temporal contingencies between actions across agents, whereas explicit recognition additionally affords the ability to understand the directional impact of one's own actions on others' actions [1–3]. Imitation recognition is thought to foster understanding of social causality, intentionality in others and the formation of a concept of self as different from other [3–5]. Pigtailed macaques (*Macaca nemestrina*) implicitly recognize being imitated [6], but unlike chimpanzees [7], they show no sign of explicit imitation recognition. We investigated imitation recognition in 11 individuals from the four species of non-human great apes. We replicated results previously found with a chimpanzee [7] and critically, have extended them to the other great ape species. Our results show a general prevalence of imitation recognition in all great apes and thereby demonstrate important differences between great apes and monkeys in their understanding of contingent social interactions.

In phase 1 of the study, the experimenter (E) interacted with non-human great apes (henceforth apes) in four different conditions manipulating the structural and temporal contingency between the apes' and his actions. Testing behaviours are defined as actions, performed to test the contingent relationship between two interacting individuals [1–3]. In human children, these include either deliberately odd behaviours to test form contingencies or odd or repetitive sequences of behaviours to test timing contingencies [2,3,5]. Based on previous work [7], therefore, we coded

testing behaviour in apes as behavioural patterns which were enacted while facing E, if they fell outside of the described repertoire of the species (for example, testing poses; see Figure 1), or were combined in non-standard sequences (testing sequences) or uncharacteristically long bouts of repetitions (behaviour repetitions). Out of 46 coded bouts of testing behaviour, four were testing poses, zero testing sequences and 42 behaviour repetitions (for detailed Supplement Experimental procedures, see the Supplemental data available on-line with this issue).

Apes demonstrated more testing behaviours in conditions in which: E acted synchronous to their actions, compared to a two second delay; E repeated the apes' action, compared to responding with a different action; and E repeated the apes' action at the same time, hence matching timing and form of his actions to the apes' actions

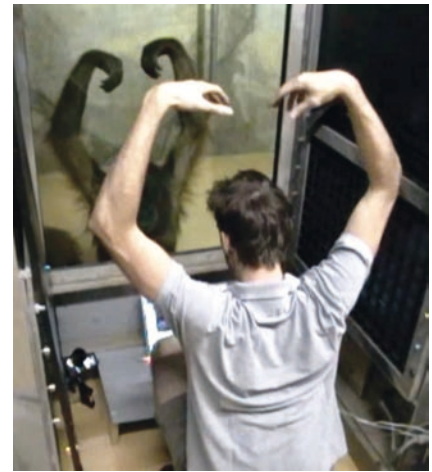


Figure 1. Experimenter and female orangutan (*Pongo pygmaeus*) interacting in the contingent/matching condition showing an example of testing behaviour (testing pose).

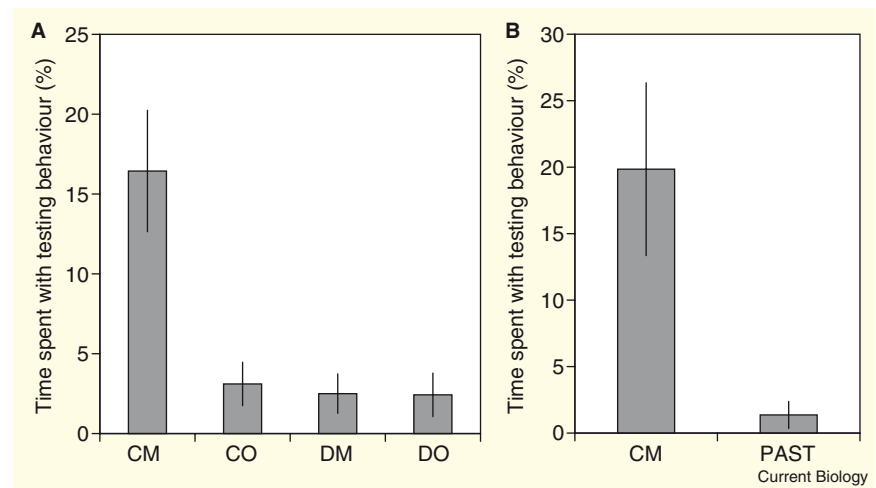


Figure 2. Imitation recognition in great apes.

(A) Mean percentage (+SE) of total time (four trials x 30 seconds) apes spent engaged in testing behaviour in each of the four conditions of phase 1. Contingent/matching (CM), the experimenter (E) replicated all actions as the ape exhibited them; contingent/other (CO), as the ape performed an action, E performed a different action synchronously; delayed/matching (DM), E replicated all actions two seconds after the ape exhibited them; delayed/other (DO), two seconds after the ape performed an action, E performed a different action (CM: M = 16.49, SE = 3.82; CO: M = 3.15, SE = 1.40; DM: M = 2.50, SE = 1.24; DO: M = 2.47, SE = 1.40). A mixed ANOVA with the within-subject factors contingency (contingent/delayed) and match (matching/other) and species as a between-subject factor revealed significant effects of contingency ($F_{(1,7)} = 11.45$; $p = .012$; partial $\eta^2 = .62$), match ($F_{(1,7)} = 8.94$; $p = .020$; partial $\eta^2 = .46$) and contingency x match ($F_{(1,7)} = 8.60$; $p = .022$; partial $\eta^2 = .55$). There were no significant differences between species and no other interactions. In the CM condition 9 of 11 animals exhibited testing behaviour at least once. In the CO, DM and DO conditions, only 5/11, 3/11 and 4/11 animals showed testing behaviour at least once. (B) Mean percentage (+SE) of total time (four trials x 30 seconds) apes spent engaged in testing behaviour in each of the two conditions of phase 2. CM (see Figure 2A); PAST: E observed the videotapes of the CM condition of phase 1, and replicated all actions as the apes (and E) had exhibited them eight weeks earlier (CM: M = 19.85, SE = 6.50; PAST: M = 1.36, SE = 1.02). A repeated-measures ANOVA with the within-subject factor condition (CM/PAST) revealed a significant main effects of condition ($F_{(1,7)} = 7.74$; $p = 0.019$; partial $\eta^2 = .44$). In the CM condition 7 of 11 animals exhibited testing behaviour at least once, while in the PAST condition only 2/11 animals showed any testing behaviour at all.

(Figure 2A). Apes never displayed testing sequences.

Based on previous work [7], we administered an additional test (phase 2) to assess whether apes responded to the imitative nature of E's actions or to some behavioural peculiarity unconsciously exhibited by E. In this case, E either imitated the ape, or, observing the videotapes of phase 1, replicated all actions as the ape had exhibited them eight weeks earlier. Apes demonstrated more testing behaviours when E imitated their current- than their past actions (Figure 2B). Of a total of 26 coded bouts of testing behaviour, five were testing poses, zero were testing sequences and 21 behaviour repetitions. These results replicated those of phase 1 and showed that testing behaviour was indeed caused by the imitative quality of the interaction and not by inadvertently peculiar behaviour of E.

We found that, in response to being imitated, apes reliably displayed behaviours more closely aligned to the behaviours observed in human infants than to those observed in monkeys. The observed behaviours are interpreted as testing the structural and temporal contingencies of an interaction. Apes displayed odd behaviours testing form contingencies and repetitive sequences of behaviours testing timing contingencies. Unlike children, however, apes never exhibited testing sequences. Our data replicated previous results with a chimpanzee [7] and are consistent with the hypotheses that apes have the ability to explicitly recognize the contingency between actions in a social interaction and the directional impact of their own actions on others' actions.

Our data reveal an important difference between great apes and monkeys in understanding contingent social interactions. Further, the absence of testing sequences in our ape sample contrasts starkly with their abundance in human children [1–3,5], suggesting a potential species difference within the great apes. Taking a phylogenetic perspective [8,9], we infer that the competences for contingent social interactions increased around the time of the common ancestor of great apes, approximately 15 million years ago, and possibly again in the hominid line. The increased social competence in great apes relative to monkeys fits with theories arguing that dispersed social systems, common in great ape but not

monkey societies, caused selection pressures favouring advanced social cognitive abilities [10].

Supplemental data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/18/7/Rxxx/DC1>

Acknowledgements

We are indebted to the keepers at Zoo Leipzig for their support and to Bridget Waller and Katja Liebal for helpful comments. This research was supported by the Max Planck Society for the Advancement of Science and the European Commission (SEDSU Project #012-984 NEST- Pathfinder). The authors declare no competing financial interest. Correspondence and requests for materials should be addressed to D.B.M.H. (daniel.haun@port.ac.uk).

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