The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*

MICHAEL TOMASELLO*, BRIAN HARE† & TARA FOGLEMAN‡

*Max Planck Institute for Evolutionary Anthropology
†Department of Anthropology, Harvard University
‡Yerkes Regional Primate Research Center, Emory University

(Received 4 May 2000; initial acceptance 5 June 2000; final acceptance 12 September 2000; MS. number: 6575R)

Primates follow the gaze direction of conspecifics to outside objects. We followed the ontogeny of this social-cognitive skill for two species: rhesus macaques and chimpanzees. In the first two experiments, using both a cross-sectional and a longitudinal design, we exposed individuals of different ages to a human looking in a specified direction. Rhesus infants first began reliably to follow the direction of this gaze at the end of the early infancy period, at about 5.5 months of age. Chimpanzees did not reliably follow human gaze until 3–4 years; this corresponds to the latter part of the late infancy period for this species. In the third experiment we exposed individuals of the same two species to a human repeatedly looking to the same location (with no special object at that location) to see if subjects would learn to ignore the looks. Only adults of the two species diminished their gaze-following behaviour over trials. This suggests that in the period between infancy and adulthood individuals of both species come to integrate their gaze-following skills with their more general social-cognitive knowledge about other animate beings and their behaviour, and so become able to deploy their gaze-following skills in a more flexible manner.

A variety of primate species visually track the gaze direction of conspecifics to outside entities. There is solid experimental evidence for chimpanzees, sooty mangabeys, *Cercocebus torquatus*, and three species of macaque (*Macaca mulatta*, *M. nemestrina*, *M. arctoides*; Emery et al. 1997; Tomasello et al. 1998).

In terms of function, following the gaze of conspecifics is useful because it allows individuals to take advantage of the visual experience of groupmates that spy some interesting or important phenomenon, such as food, predators, or significant social interactions. Gaze following is thus closely akin to social learning (the individual learns something about the world by first attending to the behaviour of conspecifics) and so its function and fitness consequences presumably derive from the extra information about the environment that this social behaviour makes available (for discussion, see papers in Heyes & Galef 1996). In terms of phylogeny, very little is known about the evolutionary history of gaze following in primates, but it is relevant that at least some other mammalian species seem to track conspecific gaze as well, for example, domestic dogs, *Canis familiaris*, in some situations (Hare & Tomasello 1998) and mountain goats, *Capra aegagrus* (M. Tomasello, unpublished data). This suggests that gaze following has an evolutionary history that extends back prior to the origins of the order Primates.

In terms of mechanism, the physiological bases of primate gaze following have not been identified specifically, but some progress has been made, as Perret & Mifflin (1990) have identified some of the neural mechanisms by which rhesus macaques orient to the eyes of conspecifics. In addition, a number of recent studies have revealed some surprising new information about the psychological mechanisms underlying the gaze-following behaviour of chimpanzees. First, chimpanzees follow not just conspecific, but also human, gaze. They do this on the basis of eye direction alone independent of head direction (Povinelli & Eddy 1996a), even when the target is located above or behind them (Itakura 1996; Povinelli & Eddy 1997). Call et al. (1998) also found that when a chimpanzee tracked the gaze of another individual to a location and found nothing interesting there, they often looked back to the individual's face and tracked the gaze.
direction a second time (so-called ‘checking back’). Second, after a suggestive finding of Povinelli & Eddy (1996b), Tomasello et al. (1999) found that chimpanzees do not just follow human gaze in a generic directional manner, but rather they track the other’s gaze to a specific target, even if that means moving their body so they can see behind a barrier or passing by an attractive distractor. Together, these studies thus disconfirm the generic ‘orienting response’ model of chimpanzee gaze-following, supporting instead the hypothesis that chimpanzees follow the gaze direction of other animate beings geometrically to specific locations. Third, Hare et al. (2000, 2001) have found that chimpanzees know what conspecifics can and cannot see (and, indeed, what they have and have not seen in the immediate past), as subordinates preferentially pursue food items that a dominant cannot see (or has not seen) because of various strategically placed occluders.

We have thus begun to make some progress, for at least some primate species, on questions of the function, phylogeny and mechanism of gaze following. We have basically no information, however, on Tinbergen’s (1951) fourth key explanatory perspective: ontogeny. The study of ontogeny is important in its own right as an explanation of a behavioural skill in terms of its history in the individual; but, in addition, information on ontogeny often has important implications for questions of mechanism, for example, with respect to questions concerning the kinds of environmental interactions that might be necessary for the development and use of a skill. We therefore followed the ontogenetic trajectory of the skills of two primate species, rhesus macaques and chimpanzees, in following the gaze direction of human beings. We then investigated the degree to which individuals of different ages in these two species habituate to repeated instances of gaze when it leads to no interesting outcomes, as a measure of the role of learning in the development of gaze-following skills.

**EXPERIMENT 1: RHESUS ONTOGENY**

There is no demonstration to date that rhesus macaques will follow the gaze direction of human beings. Itakura (1996) reported negative results for four macaque individuals (but see Anderson & Mitchell 1999, for positive results in four of five stump-tailed macaques, *M. arctoides*). We investigated this behaviour first in a cross-sectional sample of individuals, and then in a longitudinal follow-up of the youngest subjects from that sample.

**Methods**

**Subjects**

Our subjects were from 10 groups of rhesus macaques housed in large outdoor, open-air, enclosures (ca. 25 m², wire mesh) at the Yerkes Primate Center. The enclosures contained various enrichment structures such as climbing bars, conduit pipes and metal barriers. All animals were fed twice daily, once with monkey chow and once with fruit. The groups ranged in size from 51 to 121, with an average size of 84.6 individuals. All groups were composed of a mix of ages and sexes. When the experiment began, the birthing season had just ended and the new cohort of infants was 2–5 months old. No special feeding or housing regimes were imposed during testing.

**Cross-sectional procedure**

Each group was tested in its outdoor enclosure on each of 3 days. In each of these sessions the group received two experimental trials and two control trials, for a total of six experimental and six control trials per group overall (60 of each type of trial totalled across the 10 groups and 3 days). Experimental and control trials were administered in alternating order, with the type of first trial counterbalanced both across groups and across sessions within groups.

One day’s testing went as follows. The human experimenter (T.F.) watched from a distance until several individuals were near the side of the fence. At that point she approached the side of the enclosure (to within 2–3 m) and administered four trials of 10 s each in succession. There were two types of trials. In experimental trials, the experimenter looked straight up into the air for 10 s, moving both head and eyes but with her body remaining facing the monkeys. In control trials, she looked directly at the monkeys (although at no particular one and with her body remaining facing the monkeys). There was no pause between trials, and so the four trials for a given day lasted exactly 40 s. A second experimenter videotaped all trials (excluding the first experimenter from the picture so the tapes could be coded blind).

All scoring was done from the videotapes. A coder (T.F.) blind to experimental condition viewed each session. Each individual who was present and facing the experimenter for all four trials of a session (i.e. all 40 s) was identified and considered a subject. Each subject was then evaluated on each trial, with the number of subjects varying from one to five per session. The coder classified each of these subjects by age: infant (current cohort, 2–5 months); yearling (previous year’s cohort); 2–3 year olds; and adults (4 years or more); and whether each individual did or did not look up into the air during each trial, the criterion being any look (however brief) in which the subject clearly oriented its head and eyes above the experimenter’s head towards the sky. An independent coder (B.H.), also blind to experimental condition, then coded a randomly selected 20% of the sessions. Inter-observer reliability was 95% for age of subject and 94% for whether an individual looked up on a given trial.

Because of the large number of monkeys involved (846), individuals could not be recognized. However, subjects were sampled from 10 compounds on three occasions, and during a single test individuals could be reliably distinguished on the videotapes. We used these facts to construct a sample of 51 clearly distinct individuals. We did this by using only the data from a single test (i.e. day) for each age group for each compound. For each age group in each compound we used the data from the test at which the most individuals of that age were present. This resulted in a ‘restricted sample’ of 10 infants, 13 yearlings, 9 juveniles, and 19 adults, all
clearly distinct individuals. Because of this restriction of sampling to one test per compound, each subject was scored on only two experimental and two control trials.

**Longitudinal procedure**

To determine in more detail the exact age at which rhesus monkeys begin to follow human gaze reliably we followed the infant cohort (2–5 months of age) longitudinally until they were ca. 1 year of age. The cohort was composed of 219 infants, with 13–30 infants in each of the 10 compounds.

Once per month (approximately every 30–40 days) for 7 months after the cross-sectional study, the same human experimenter tested one infant individual from each of the 10 compounds. The testing was done in the same basic manner as in the cross-sectional study, except it was done on individuals rather than small groups. The experimenter waited until an infant was alone and close to the fence (away from its mother), at which point she approached and administered two experimental and two control trials (counterbalanced for order across groups). This meant that there were 10 subjects with two experimental and two control trials each (a total of 20 trials of each type) at each monthly interval. Because individuals could not be recognized, we do not know whether the same individuals were observed across the 7 months within a group.

Again, all trials were videotaped by a second experimenter and all scoring was done from the videotapes first by the primary coder and then by a secondary coder (both blind). Agreement on the infants’ behaviour of looking up or not looking up was 96.4%.

**Results**

**Figure 1a** presents the results for the restricted sample of observations for the cross-sectional study (containing 51 clearly distinct individuals, each of whom could score either 0, 1, or 2 in both the experimental and control conditions). Few of the 10 infants looked up at all in either condition (two looked up more in the experimental than in the control condition and none in the opposite direction; Wilcoxon matched-pairs signed-ranks test: Z=1.34, NS). Of the 13 yearlings, nine looked up more in the experimental than in the control condition, whereas only two looked up more in the control than in the experimental condition (Wilcoxon: Z=2.29, P<0.02). Of the nine juveniles, five looked up more in the experimental than in the control condition, whereas none looked up more in the control than in the experimental condition (Wilcoxon: Z=2.24, P<0.02). Finally, of the 19 adults, 11 looked up more in the experimental than in the control condition, whereas only one looked up more in the control than in the experimental condition (Wilcoxon: Z=2.22, P<0.02).

Given the large number of individuals in each compound, the likelihood that any one individual would be sampled more than once across test administrations was quite low, and so, as a secondary analysis we also analysed the data from all three tests. (We felt this was necessary because the sample of infants in the primary analysis was so small that the negative result might be due to a lack of power.) The results duplicated those of the primary analysis. The majority of infants did not look up at all, with only two looking up more in the experimental than in the control condition (Wilcoxon: Z=1.34, N=12, NS), and comparisons in all of the other age groups remained significant (Wilcoxon tests: P<0.02).

**Figure 1b** presents the results of the seven longitudinal follow ups with the infant cohort. The first longitudinal test, when infants were 4.5 months of age, yielded no significant difference between experimental and control conditions (six looked up more in experimental, three in control). This confirmed the negative findings for these same infants at 3.5 months of age in the cross-sectional study. For all other ages, however, subjects looked up more often in the experimental than in the control condition (Wilcoxon matched-pairs signed-ranks tests): 5.5 months: 4 looked up more in experimental, 0 in control; Z=2.00, P<0.03; 6.5 months: 6 looked up more in experimental, 0 in control; Z=2.25, P<0.02; 7.5 months: 6 looked up more in experimental, 1 in control; Z=1.90, P<0.03; 8.5 months: 7 looked up more in experimental, 0 in control; Z=2.53, P<0.01; 9.5 months: 7 looked up...
more in experimental, 0 in control; Z=2.46, P<0.01; 10.5 months: 9 looked up more in experimental, 0 in control; Z=2.74, P<0.01.

One obvious issue in this study is habituation, since the human look was essentially to nothing, which might lead to some learning over time. In each session in both the cross-sectional and longitudinal studies, subjects received two experimental trials relatively close together. To look for habituation effects, we compared the first and second experimental trials for each subject in each session. There were no significant differences for the infant cross-sectional sample, or for these same youngsters across all their development during the first year, or for the yearlings from the cross-sectional sample (note that this is an entirely different group of individuals). However, there were significant differences between the first and second experimental trials within a session for both the juveniles and the adults: 2–3 year olds: Z=5.44, P<0.05; adults: Z=5.18, P<0.01.

Discussion

Rhesus monkeys began to follow human gaze, upwards into the air, reliably from about 5.5 months of age. The negative results for the youngest infants (at 3.5 months, during the cross-sectional study) were based on very few data, since infants mostly did not look up in either the experimental or control condition. However, when these same infants were seen 1 month later, at 4.5 months, the majority did look up, but they did so just as often in the control condition as in the experimental condition. At 5.5 months of age and at all subsequent monthly intervals, rhesus individuals followed gaze reliably.

The rhesus were especially likely to follow human gaze from about the first to the second birthday. From 2 years and into adulthood, they still followed human gaze reliably, although at levels about two-thirds that of the yearlings. At about 1 year of age something may make attending to the visual gaze direction of others especially important, perhaps their special vulnerability to predation (Cheney & Wrangham 1987). This ontogenetic pattern may also have something to do with the fact that it was human gaze they were following; perhaps in this captive setting 1-year-old infants begin to display their gaze-following skills indiscriminately, and after that they learn to restrict them more particularly to conspecifics. Finally, as rhesus monkeys mature they must begin to monitor more seriously happenings other than the gaze direction of others, perhaps especially humans outside their compounds, when they are in their natural social groups (as they were when tested in this study). They therefore have no time for others who look at nothing, and so they learn very quickly not to follow the gaze of these individuals (and so they begin to ignore it, as the older individuals did on trial 2).

One other interpretative issue is important. Given our experimental design, rather than the experimental manipulation of looking into the air eliciting looking behaviour, our control condition might have suppressed it. Therefore, another possible control condition (which would have presented its own interpretative problems, of course) could have been to have no human present. Although we did not have such a condition in this study (indeed we think our control condition is, on balance, the better one), in Tomasello et al. (1998) there was a control baseline condition in which we simply measured the likelihood that a rhesus monkey (sitting within its compound) would look up to the tower where humans were located within a 10-s interval. That value was 17%, which is almost identical to the percentage of trials in which individuals looked up in the current experiment’s control conditions (20%). There is thus no evidence that our control condition produced artificially low levels of the target behaviour.

**EXPERIMENT 2: CHIMPANzee ONTOGENY**

In contrast to rhesus macaques, there are a number of studies showing that adult chimpanzees follow human gaze (e.g. Povinelli & Eddy 1996a; Call et al. 1998; Tomasello et al. 1999). There is no information on the ontogeny of this skill, however, and so establishing an ontogenetic sequence was our primary aim.

**Methods**

**Subjects**

Subjects for this study were eight infant and juvenile chimpanzees who lived in one of two seminatural social groups at the Yerkes Primate Center. Environmental enrichment and feeding were the same as for the rhesus macaques. Table 1 lists the individuals and their ages (1–5 years) as well as other pertinent information about their life histories. Each social group contained ca. 18 individuals of various ages and genders and lived in its own outdoor open-air, corral (ca. 25 m²), which had adjacent to it some indoor areas, where testing took place. No special feeding or housing regimes were imposed during testing.

**Cross-sectional procedure**

Each infant was tested in its indoor area with only its mother present on each of 2 separate days within a 2-week period. In each of these sessions the infant received three experimental trials and three control trials, for a total of six experimental and six control trials overall. Experimental and control trials were administered in alternating order, with the type of first trial counterbalanced both across groups and across sessions within groups.

One day’s testing went as follows. The human experimenter waited beside the cage (within 2 m) until the infant was relatively close and looking in her general direction. She then administered six trials of 10 s each in succession. There were two types of trials. In experimental trials the experimenter looked straight up into the air for 10 s, moving both head and eyes but with her body remaining facing the subject. In control trials the experimenter looked directly at the subject. There was no pause between trials, and so the six trials for a given day lasted exactly 60 s (unless the subject had to be coaxed back to
the test area). A second experimenter videotaped all trials (excluding the first experimenter from the picture).

All scoring was done from the videotapes. An independent coder (T.F.) blind to experimental condition viewed each session. For each trial the coder classified whether each individual did or did not look up into the air during each trial, the criterion being any look (however brief) in which the subject clearly oriented its head and eyes above the experimenter’s head towards the sky. A second coder, also blind to the experimental trial, then coded a randomly selected 20% of the sessions. Interobserver reliability for whether an individual looked up on a given trial was 100%.

### Longitudinal procedure

To determine in more detail the exact age at which chimpanzees begin to follow human gaze reliably, we followed the youngest infants (and one slightly older individual who performed poorly in the cross-sectional study) longitudinally until they were ca. 1 year old. These were Dover, Abbey, Tara and Azalea (see Table 1; Juliette was also tested on one occasion, see below).

Once every 2 months (ca. every 60 days) for 10 months after the cross-sectional study, the same human experimenter tested each of the four infant chimpanzees. The testing was done as in the cross-sectional study (also in the indoor area, with the mother present). The experimenter waited until an infant was close to the fence and attentive, at which point she approached and administered three experimental and three control trials (counterbalanced for order across groups). This was then repeated after a 30-min break. This meant that each subject had six experimental and six control trials at each of the bimonthly test periods. At the last testing session, an additional infant had become old enough to test, and so was tested on one occasion (Juliette).

The majority of trials were videotaped by a second experimenter and most scoring was done from the videotapes first by the primary coder and then by a secondary coder (both blind). Agreement on the infants’ behaviour of looking up or not was 95%. Owing to lack of personnel on some test days, a few trials were scored live by the experimenter.

### Results

Table 2 presents the results for the cross-sectional study. Two of the 1–2-year-old infants (Azalea, Tara) did not look up at all in either the experimental or control trials (there were six trials of each type). In contrast, the

<table>
<thead>
<tr>
<th>Subject</th>
<th>Age</th>
<th>Experimental</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stewart</td>
<td>4 years 10 months</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Dover</td>
<td>4 years 4 months</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Liza</td>
<td>4 years 3 months</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Kerri</td>
<td>3 years 6 months</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Jamie</td>
<td>3 years 2 months</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Abbey</td>
<td>3 years 2 months</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Tara</td>
<td>2 years 10 months</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Juliette</td>
<td>1 year 8 months</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Azalea</td>
<td>1 year 4 months</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
three 3 year olds (Abbey, Jamie, Kerri) looked up 83% of the time in the experimental trials, but only 22% of the time in the control trials. The three 4 year olds (Liza, Dover, Stewart) looked up 78% of the time in the experimental trials, but only 11% of the time in the control trials. With only three subjects at each age, statistical comparisons within age are impossible, but if the two older ages are combined we find a strong difference between experimental and control trials ($t_s=8.03$, $P<0.001$) and numerically the two ages are almost identical.

Figure 2 presents the results for each of the five infants in the longitudinal study. Plotted in this figure for each subject at each time is the number of looks up in the experimental condition minus the number of looks up in the control condition (the value could thus potentially go from $-6$ to $+6$). The two youngest infants, Juliette and Azalea, did not look up significantly more in experimental than control trials at any time ($\chi^2=0.93$ and 0.17, respectively, NS). On the other hand, the three oldest subjects all looked up more in the experimental than in the control trials over the 10-month observation period. Tara gradually began to follow gaze more and more after her third birthday, and for the 10-month period as a whole she looked up in eight experimental and only one control trial ($\chi^2=6.22$, $P<0.02$). Three-year-old Abbey was more inconsistent over the 10 months (she actually seemed to go down), but still showed significant gaze following for the entire period; six looks in experimental and only one in control ($\chi^2=3.96$, $P<0.05$). Finally, the oldest subject Dover, between 4 and 5 years, clearly became skilful (after having not been skilful in the cross-sectional study) by the middle of the observation period and then stayed that way, with 17 looks in the experimental and only two in the control condition ($\chi^2=16.09$, $P<0.001$).

In terms of habituation effects, when the first and second experimental trials of the cross-sectional study were compared, no differences were found: the chimpanzee infants looked equally often in the first and second trials.

**Discussion**

Chimpanzees began to follow human gaze, upwards into the air, reliably from ca. 3–4 years of age. The poor performance of the youngest chimpanzees must be viewed with some caution, of course, given the small number of subjects involved. However, if we look at all of the youngest subjects at all of their longitudinal time points before 3 years of age, there were 48 trials of each type (given to three different individuals), and there were eight looks up in the experimental trials and five in the control trials, a nonsignificant difference. From 3 to 3.5 years, there were also 48 trials of each type given to three individuals, but in this case there were 18 looks up in the experimental and four in the control. (The likelihood of looking up spontaneously in Tomasello et al.’s (1998) study, 16% of 10 second trials, was about the same as in our control condition, 19% of 10 second trials. As in the rhesus experiment, this provides a kind of second control comparison for the experimental condition.)

For this group of chimpanzees, therefore, infants did not begin to follow human gaze reliably until after their third birthday. This is a much older age, in absolute terms, than the rhesus monkeys in experiment 1. But chimpanzee life expectancy is close to twice that of rhesus, and conventionally chimpanzee infancy lasts for 4–5 years whereas rhesus infancy lasts for only 1 year. Nevertheless, even in ontogenetically calibrated terms, the gaze-following skills of chimpanzees emerged only at the very end of the infancy period, whereas those of rhesus monkeys emerged in the middle of this period.

Four of our subjects participated in Tomasello et al.’s (1999) study some months beforehand. In that study they were given the opportunity to follow human gaze around an opaque barrier. The two who did well in our study (Jamie and Stewart, 3–4 years old, who both looked in every experimental trial) were also skilful in that study, as skilful as the adults, in fact. The two subjects who did less well in the current study (Dover and Abbey, also 3–4 years old, who only looked in about half of the experimental trials) were less skilful in the previous study. One possible interpretation of this result is that as soon as chimpanzees begin to follow gaze reliably, they do so in a very sophisticated way (i.e. geometrically to specific targets).

**EXPERIMENT 3: RHESUS AND CHIMPANZEE HABITUATION**

There was some evidence from the first two experiments that rhesus juveniles and adults habituated to our looking procedures, whereas none of the rhesus or chimpanzee infants did so. However, two trials is not enough to test habituation systematically; even if a looker seems to be looking at nothing on one occasion, following their gaze a second time would still seem reasonable, but perhaps not after five or more trials. In experiment 3, therefore, we exposed both rhesus monkeys and chimpanzees of different ages to human looks into the air (no interesting objects available) for many trials in succession. The main question was whether gaze following is a relatively fixed and unmodifiable response in these two species, or whether at some developmental point it is subject to modification by learning; that is to say, the question is at
what developmental point, if any, individuals will learn to ignore a human who keeps looking at nothing.

Methods

Subjects

Subjects for this study were 23 rhesus monkeys and 14 chimpanzees from the Yerkes Primate Center. Rhesus monkeys were individuals from the same social groups as in experiment 1 (and a few others), but who were being individually housed for various brief periods in the Center’s veterinary clinic. For testing, subjects were therefore individually housed (after their treatments, they were returned to their social groups). No veterinary treatments, feeding, or any other scheduled activities were interrupted for purposes of testing. Subjects were in three age groups: seven 1 year olds; eight 2–3 year olds; and eight adults (4–14 years of age). Average age was 7.8 years.

Chimpanzees were from the same two social groups as in experiment 2 and five individuals participated in that experiment (see Table 1). There were eight adults with an average age of 22 years, and six infants with an average age of 4 years. Subjects were individually tested, as in experiment 2, in their indoor enclosures.

Procedure

The procedure was identical for the two species. The experimenter sat in front of the subject’s cage and waited for them to come close and to look in her direction. She then began a series of 30 consecutive trials with that individual. In each trial, the experimenter simply looked up to the ceiling for 10 s. There was then a 30–60 s pause (depending on how long it took for the subject to become correctly positioned again), at which point the next trial was initiated. All trials were videotaped.

The experimenter (T.F.) then coded all trials for looks to the ceiling. A second coder (B.H.) then coded the first five trials of every subject (20%). Agreement for the rhesus monkeys was 92% and for the chimpanzees 85%.

Results

The two infant groups never habituated to the procedure, whereas the two adult groups habituated quickly (Fig. 3). There was no drop in performance (no habituation) for the two rhesus infant groups and the one infant chimpanzee group from the first block of five trials to the second block of five trials. On the other hand, six of the adult rhesus monkeys looked up less in the second five trials than in the first, two looked an equal number of times in the two blocks, and no subject looked more in the second five trials (Wilcoxon matched-pairs signed-ranks test: \( Z = 2.27, P < 0.05 \)). All eight of the adult chimpanzees looked up more often in the first than in the second block of five trials (Wilcoxon matched-pairs signed-ranks test: \( Z = 2.56, P < 0.01 \)). After the first 10 trials all groups levelled off, with some variation but with no further significant habituation observed.

Discussion

Rhesus and chimpanzee infants and juveniles continued to follow a human’s gaze to a blank ceiling across 10 consecutive trials, whereas adult rhesus and chimpanzees habituated to this procedure relatively quickly. Perhaps the most striking finding is the similarity of the ontogenetic pattern between the two species. In both cases it was only adults who consistently began to ignore the human who kept looking to an empty ceiling. Even though rhesus consistently looked up more often than chimpanzees in this experiment, absolute comparison between the two species is not warranted because they may have engaged in spontaneous looking behaviour in this situation to differing degrees.

Comparison of these results with those from experiments 1 and 2 reveals that the older rhesus monkeys, especially the adults, seemed to follow gaze more often in this experiment than in experiment 1. Undoubtedly part of the explanation is that in experiment 1 subjects were tested in small groups in their natural enclosures, whereas in experiment 3 individuals were tested in isolation, in the veterinary facilities, which might have made them more nervous than normal. The adult chimpanzees in experiment 3 looked up only 50% of the time in the first five trials, which is less often than the 3–4 year olds in experiment 2, but this is because the former were habituating from trial 1. Six of the eight adults in experiment 3 (75%) looked up on the first trial, a value comparable with that shown by the 3–4 year olds in experiment 2.

Because the chimpanzee infants in experiment 3 had previously experienced six trials of human gaze in experiment 2, we must be cautious in interpreting the observed age difference in habituation. Perhaps the chimpanzee infants began to habituate to the procedure in experiment 2 and then levelled off in experiment 3. However, in experiment 2 there was no evidence of chimpanzee infant habituation: when the infants’ first and second trials were compared, there was no difference (values identical). Second, experiment 3 was conducted several months after the end of experiment 2, seemingly sufficient time to recover from any possible habituation.
effects. Third, there was no evidence of habituation for the infants in experiment 3; they were identical in the first and second set of trial blocks. Finally, the one chimpanzee infant who did not participate in experiment 2 (Reid), and so who had no chance to be affected by it, did not look in any way different from the other infants. Some of the adult chimpanzees in experiment 3 were reared by humans in a nursery whereas this was not true of any of the infants. Given that the looker in experiment 3 was a human, this may explain the quicker habituation of the adults. However, the same was not true of the rhesus subjects, all of whom had very similar rearing histories in their social groups, and they showed exactly the same age difference.

Our conclusion is thus that for both rhesus monkeys and chimpanzees in experiment 3 the observed age effect in habituation is a real one. Learning comes to play a more important role in rhesus and chimpanzee gaze following over time, specifically between the infancy and adulthood periods.

**GENERAL DISCUSSION**

Both rhesus macaques and chimpanzees began to follow gaze reliably during infancy. However, for rhesus macaques this was middle infancy, the middle of the first year, whereas for chimpanzees it was late infancy, 3–4 years. When this skill first emerged it was relatively inflexible and impervious to learning; that is, the individual continued to follow the gaze direction of another no matter how many times that other looked into space at nothing. But by adulthood, individuals began to ignore a looker who continued to look at nothing. This presumably means that in the period between infancy and adulthood individuals of both species come to integrate their gaze-following skills with their more general social-cognitive knowledge about other animate beings and their behaviour, and thereby become more skilled at deploying these skills flexibly, in a manner adapted to the exigencies of particular social circumstances. The first reliable gaze-following skills in human infants emerge at ca. 10 months of age (Butterworth & Jarrett 1991; Corkum & Moore 1995; Carpenter et al. 1998). This is considerably younger as a proportion of life span than for either rhesus or chimpanzees, suggesting some kind of heterochronic change in the ontogeny of gaze following in the human species (and perhaps the greater area of exposed white sclera in the human eye is associated with this change; Kobayasgi & Koshima 1997).

We must of course remain cautious about the generality of our findings given that in all cases the looker-experimenter was a human being. But comparison of the overall rates of gaze following in our study with those of Tomasello et al. (1998), in which these two species followed the gaze of conspecifics while in their social groups, yields generally comparable figures. In addition, in Tomasello et al.’s (1999) study chimpanzees followed human gaze around barriers and past distractors to locate the looker’s specific visual target. This would seem to indicate that when interacting with humans chimpanzees are not deploying some impoverished version of their gaze-following skills, but rather using some of their most sophisticated skills, presumably the same ones they are using in their daily interactions with conspecifics.

Although we have very little information on how rhesus monkeys understand the gaze of others, a number of recent studies have shown that chimpanzees track the gaze of others to specific targets, and that they know when a conspecific competitor can and cannot see the object of competition (see Call & Tomasello, in press, for a review). In the study of following gaze around barriers and past distractors (Tomasello et al. 1999), some subjects were older infants and they did as well as adults, suggesting that following gaze geometrically to a target characterizes chimpanzee gaze following from its ontogenetic origins. In the studies in which subjects needed to judge what a competitor could and could not see (Hare et al. 2000, 2001), no infants participated, and so we know nothing about the age of emergence of this skill. All we can conclude at the moment, therefore, is that at least some of the more complex cognitive processes that accompany gaze following in chimpanzees are a part of the skill from early in its ontogeny. Future research should attempt to determine if this is also true of the other more complex aspects of chimpanzee gaze following as well, and it would be useful to know if rhesus monkeys, or any other primate species, are able to interpret the gaze of others in the same way as chimpanzees.

Virtually all previous studies of primate cognitive ontogeny have investigated aspects of physical cognition only, for example, knowledge of objects and their properties (see Tomasello & Call 1997, for a review). We tracked the ontogeny of a fundamental social-cognitive skill, which is perhaps of special importance since primates seem to use their cognitive skills more in social than in physical interactions. In general, ontogenetic studies of cognition and social cognition are an important source of information for such things as: when a skill typically emerges in relation to other skills; how much individual variation is normally observed in a skill; and what kinds of modifications a skill may undergo if individuals have different personal experiences. Information of this type is crucial in characterizing the precise nature of a particular cognitive skill and the ways in which different species are able to acquire, modify and use this skill adaptively.

**Acknowledgments**

This investigation was supported in part by a grant from the National Science Foundation to M.T. (IBN-9507418) and in part by NIH grant RR-00165 from the National Centre for Research Resources to the Yerkes Regional Primate Research Center. The Yerkes Center is fully accredited by the American Association of Laboratory Animal Care. We thank Malinda Carpenter and Nancy Megna for help with data collection, and Josep Call for statistical advice.
References


