Chapter 9
Great Ape Social Attention

Fumihiro Kano and Josep Call

Abstract Recent advances in infrared eye-tracking technology have allowed researchers to examine social attention in great apes in great detail. In this chapter we summarize our recent findings in this area. Great apes, like humans, exhibit spontaneous interest in naturalistic pictures and movies and selectively attend to socially significant elements such as faces, eyes, mouth, and the targets of others’ actions. Additionally, they follow the gaze direction of others and make anticipatory looks to the targets of others’ actions; the expression of these behaviors is adjusted flexibly according to the social contexts, and the viewers’ memories and understandings of others’ goals and intentions. Our studies have also revealed systematic species differences in attention to eyes and gaze following, particularly between bonobos and chimpanzees; several lines of evidence suggest that neural and physiological mechanisms underlying gaze perception, which are related to the individual differences within the human species, are also related to the species differences between bonobos and chimpanzees. Overall, our studies suggest that cognitive, emotional and physiological underpinnings of social attention are well conserved among great apes and humans.

Keywords Action anticipation • Anticipatory look • Eye contact • Eye movement • Eye tracking • Gaze following • Great ape • Memory

F. Kano
Kumamoto Sanctuary, Wildlife Research Center, Kyoto University, Kumamoto, Japan
Department of Developmental and Comparative Psychology, Max-Planck Institute for Evolutionary Anthropology, Leipzig, Germany
e-mail: fkanou@gmail.com

J. Call
Department of Developmental and Comparative Psychology, Max-Planck Institute for Evolutionary Anthropology, Leipzig, Germany
School of Psychology and Neuroscience, University of St. Andrews, St. Andrews, UK
e-mail: call@eva.mpg.de

© Springer Japan KK 2017
Imagine the following situation. While you are walking down the office corridor, a stranger in necktie catches your attention. You are a little surprised because you don’t usually see people wearing necktie in this office. You then notice that the stranger is working at a printer, inspecting the inside of the machine. Now one of your colleagues approaches him and starts talking to him. Although you witnessed only a few events in a short time period, you can probably make a good guess about the identity and the job of the stranger. This person is likely to be a specialist from some other company, and he is here to fix your colleague’s printer.

Events like this are common in our everyday lives and despite the challenge that they pose, we can cope with them almost effortlessly thanks to our cognitive system. One key component of this system is our ability to selectively orient to essential social information in our surroundings, such as the appearance of other people and their focus of attention (Birmingham and Kingstone 2009; Klein et al. 2009). Using this information, we are able to identify people, understand their intentions, and infer their social relations with others. Our ability to spontaneously orient to and decode social information is one of our most fundamental cognitive abilities.

Nonhuman primates also seem to utilize similar skills. For example, juvenile apes and monkeys learn from their close kin members about consumable foods (Ueno and Matsuzawa 2005; van De Waal et al. 2013). Chimpanzees learn from others how to obtain out-of-reach or hard-to-process foods (e.g., termite fishing, nut cracking (Biro et al. 2003; Lonsdorf 2006)). In a food competition context, a subordinate individual carefully avoids taking the foods that are being watched by a dominant (Hare et al. 2000). In a dominance competition, an alpha male keeps watching over his opponent so as to prevent him from making an alliance with the other dominants (De Waal 1982). Previous studies using observation methods to examine their attentional foci revealed an essentially similar nature of social attention in human and nonhuman primates. As in humans, nonhuman primates tend to look at the same foods and tools that the other individuals are handling (i.e., stimulus enhancement, joint attention; (Emery 2000; Tomasello 1995; Whiten 1992). Nonhuman primates also tend to look at the same objects and locations at which others are looking (i.e., gaze following; (Rosati and Hare 2009; Shepherd 2010; Tomasello et al. 1998)). They were also observed to use eye contact to regulate social interactions among individuals (De Waal 1990a; Gomez 1996).

Traditional methods have examined social attention indirectly by recording an individual’s body and head orientation as a way to assess their attentional foci, but recent advances in infrared, non-invasive eye-tracking technology have allowed researchers a much more direct and precise analysis of social attention. More specifically, eye-tracking technology offers greater spatial and temporal resolution compared to body and head orientation measures. On the one hand, a greater spatial resolution means that eye tracking can distinguish the individual’s focus of attention with great precision, for instance, whether the viewer is looking at the eyes or the mouth in a face. On the other hand, a greater temporal resolution means that eye tracking can measure for how long individuals maintain focus on certain targets and how they shift attention between them over time, for instance, when the viewer is anticipating the target of an individual’s action.
This method has been commonly used with human adults and infants, but a series of studies by us and our colleagues showed that the same technique can be applied to our closest relatives, the great apes (henceforth apes) who exhibit spontaneous interest in naturalistic pictures and movies. They systematically scan pictures and movies, and their gaze movements inform us about what aspects they perceive as relevant about the depicted objects, actions, and stories. In this chapter we summarize recent studies using eye tracking to examine social attention in apes. The similarities and differences between species will constitute a key aspect for inferring the cognitive and emotional mechanisms of social attention and how they may have evolved over time. The chapter is organized as follows. We first give a brief introduction on the application of this method. In the next section we explore the social elements that apes prefer to attend and its determinants such as the context dependency and the species difference. The third section is devoted to explore how they coordinate their attention with others, and how they adjust these behaviors according to the social contexts, their own memories and understandings of others’ goals. We will close the chapter with a summary of the main findings and future research directions.

9.1 A Method for Tracking the Gaze of Apes

Eye tracking is a method that directly measures the participants’ gaze location with a high temporal and spatial resolution (Duchowski 2007). Figure 9.1 presents our basic experimental setup. Stimuli are presented on a monitor, and a table-mounted remote eye tracker records the ape’s gaze as indicated by the position of her eyes and pupils (corneal and retinal reflections). The eye-tracker and the monitor are placed outside a test booth with a transparent acrylic panel separating them from the ape.

Fig. 9.1 Eye-tracking with great apes. A chimpanzee sitting in front of a computer screen and eye-tracker (left). A juvenile gorilla sipping grape juice while watching movies on a screen (right).
who sits in the booth watching the stimuli presented on the screen. The ape needs to stay roughly in the same position throughout the recording, although their heads do not need to be restrained (unlike a traditional eye-tracking method) because the infrared cameras of the eye tracker can continuously detect both the eye and pupil positions. In order to keep apes as still as possible, we give them access to a dripping nozzle attached to the panel that continuously delivers a small quantity of juice.

Although apes are not rewarded contingent on looking at the stimuli, most of them show spontaneous interests in them. We even observed an occasion when one of the bonobos was so engaged with the presented movie that she stopped drinking the juice and just stared at it. Moreover, we often observe signs of engagement with the stimuli, e.g., bobbing their heads or banging the panel while watching. However, these responses have never been followed by a refusal to participate in subsequent sessions. Therefore, apes seem interested in the pictures and movies, but they do not seem to confuse them with their corresponding referents.

Despite their interest in pictures and videos, the stimuli have to be chosen carefully because they do not view all sorts with the same interest. Here are a few examples that usually fail to keep the apes’ attention: animations made of simple circles and triangles, puppet plays made to entertain human children, and Hollywood-like movies with complex cinematography techniques (including quick transitions of shots and camera works). In contrast, apes maintain their interest when the contents include familiar backgrounds (e.g., home cages), familiar people (e.g., keepers), conspecific primates, simple actions (e.g., eating foods, handling objects and tools), and simple camera angles. Intense social interactions, such as aggression, are also typically successful in keeping apes engaged (Kano and Tomonaga 2010a).

Besides the content, the general pace of the scenes needs to be moderately fast to keep apes’ attention. The reason for this is that compared to humans, apes fixate on one location more briefly (i.e., shorter duration of fixations) and shift their gaze to the next location earlier (i.e., more frequent saccades) (Kano et al. 2011; Kano and Tomonaga 2011). When presented with a still scene, apes typically complete the scanning faster than humans do (and then immediately quit watching). Thus, due to the different basic ape eye-movement characteristics, the transitions of scenes, actions, and events should be kept at a moderately fast pace.

9.2 Apes’ Attentional Focus and Its Determinants

9.2.1 Focal Elements of Interest

Figure 9.2 presents the gaze locations of 14 bonobos looking at the face and full body pictures of conspecific (Kano et al. 2015). Similarities between humans and apes can be seen clearly here. Apes attend to the face, especially the eyes. In addition, upon stimulus presentation their first fixation is typically directed to the face and eyes. This may be due to the fact that, like humans, apes’ social perception is also specialized
for faces (Parr et al. 2009; Tomonaga and Imura 2009), and their initial fixation in an area around eyes is used for face recognition (Guo 2007; Hsiao and Cottrell 2008).

The similarities between humans and apes are not only about the attentional foci but also about the flexibility in the shift of attentional foci based on the scene contents. When the pictures include simply the face and the body, or the eyes and the mouth, without particular postures or expressions, they mostly look at the face and the eyes. When the pictures include facial expressions (Fig. 9.2, top-right), they look longer at the mouth than the eyes. When the individual in the pictures holds an object (Fig. 9.2, bottom-left), they look longer at the objects than the face. Not surprisingly, when ano-genital areas are visible (Fig. 9.2, bottom-right), these areas also attract more attention than the face.

Figure 9.3 depicts another example showing the apes’ ability to shift attention based on an agent’s action (Kano and Call, unpublished data). In the presented video, an actor ape faced an out-of-reach grape; he then got a stick and used it to rake in the grape. When the chimpanzees were presented with this video, they initially focused on the actor ape, but once the action started they shifted their focus of attention to the grape and sustained it there until the whole action completed. This means that apes do not merely focus on basic scene elements, but they can dynamically shift their attention to different elements of the scene as the action unfolds.
Like in humans, the focus of attention is sensitive to the ongoing contexts in great apes. Context-dependent gaze requires a viewer to flexibly adjust her focus of attention depending on the context, which in turn offers a glimpse of the viewer’s understanding about a particular event. For instance, at the zoo, we have often observed that apes usually do not pay much attention to unfamiliar (regular) visitors in the public areas. However, when those same unfamiliar visitors enter the service areas behind the scenes, apes suddenly become interested in them; some apes may even tease them by spitting a mouthful of water. Likewise, when apes spot a familiar person in the visitor areas, they might greet them enthusiastically or tease them by throwing a branch at them.

Kano and Tomonaga (2013) examined a chimpanzee’s eye movement in a context-rich real-life environment depicted in Fig. 9.4. For several days, the chimpanzee participant saw a different experimenter coming into the test room to play a simple gesture game on each day. The experimenter was either a familiar experimenter that the chimpanzee saw in the particular test room regularly (familiar, regular experimenter), a familiar experimenter that the chimpanzee did not see in that test room regularly (familiar, irregular experimenter), or a completely unfamiliar experimenter that the chimpanzee had never seen anywhere (unfamiliar, irregular experimenter). The results showed that the chimpanzee looked at the unfamiliar-irregular experimenter the longest and the familiar-regular the shortest (the familiar-irregular experimenter somewhere between). This pattern could indicate a degree of surprise in the chimpanzee. In addition, when the experimenter started a simple gesture game, the chimpanzee shifted her attention from the experimenter’s face to the task-relevant elements, i.e., the experimenter’s hands and the rewards. Thus, the chimpanzee’s gaze was task-dependent. This study exemplified a remarkably strong context-dependency of gaze when the chimpanzee was tested in a context-rich real-life environment, where (potential) interaction with the social partner matters.
9.3.1 Species Uniqueness of Gaze

Despite their basic similarities, apes and humans also show significant differences in their gaze patterns. Yarbus’s (1967) classic study showed that when presented with facial pictures, the trajectory of eye movement (i.e. scan paths) in humans tends to describe an inverted triangle, with its angles on each of the eyes and the mouth. In contrast, chimpanzees, orangutans, and gorillas tend to look shorter to the eye region and longer to the mouth region than humans do (Kano et al. 2012; Kano and Tomonaga 2010b). Thus their scan paths tend to describe lines connecting the eye and mouth, with the connection between the eyes being less pronounced (but see bonobos below). This is a robust pattern since such a difference in scan path pattern can be observed relatively independently from the stimulus variation. For example, when presented with the pictures of facial expressions instead of neutral faces (Fig. 9.2 top-right), apes looked longer at the mouth, while humans still devoted some time to looking at the eyes (Kano and Tomonaga 2010b).

However, interestingly, bonobos are somewhat exceptional among non-human great ape species. In an experiment, we presented the two species with a series of pictures containing the images of both species (Kano et al. 2015).
Figure 9.5 illustrates the main viewing differences that we observed between them. In general, bonobos viewed longer the face and the eyes compared to chimpanzees, whereas chimpanzees viewed longer the mouth, the ano-genital region, and the objects manipulated by the models than bonobos. A discriminant analysis clearly distinguished the two species (Fig. 9.5): 29 out of 34 participant apes were correctly classified into their own species.

One plausible explanation for the species differences between bonobos and chimpanzees may be related to their species-typical temperaments. In humans, looking into another individual’s eyes—eye contacts—predicts the viewer’s
temperament and the interpersonal relationships (Argyle and Dean 1965; Kleinke 1986); people with a higher need for affiliation showed an increased level of eye contact. In the case of bonobos and chimpanzees, they are known for their differences in the patterns of aggression and affiliation. Bonobos exhibit a larger repertoire of affiliative behaviors toward conspecifics than chimpanzees do, such as non-conceptive sexual behaviors, frequent play among adults, and non-aggressive encounters with strangers (De Waal 1990b; Furuichi 2011; Palagi 2006; Tan and Hare 2013). It has been hypothesized that these species-typical behaviors of bonobos have evolved in part as a response to the relaxation of intra-group competition and the selection against male aggression (Furuichi 2011; Hare et al. 2012). As a result, bonobos may have developed more relaxed attitudes toward others, and such temperamental characteristics may allow them to look into the eyes of others without experiencing as much a social stress as chimpanzees do.

Several lines of evidence suggest that the differences in gaze perception between bonobos and chimpanzees are related to their neural and physiological differences. First, although the general brain structure is largely conserved across the species, the local gray matter in the amygdala and the anterior insula differ between bonobos and chimpanzees (Rilling et al. 2012). As a region related to social interaction and stress, the amygdala was found to respond to the eyes selectively, when the viewers were fixating on the eyes of stimulus faces (Dalton et al. 2005; Mosher et al. 2014). Second, the oxytocin-receptor gene is also reported to be different between bonobos and chimpanzees (Staes et al. 2014). Oxytocin is found to be related to attention to the eyes. Oxytocin administration increased eye orientation in humans and macaques (Ebitz et al. 2013; Guastella et al. 2008). Third, it has been hypothesized that prenatal androgens may be higher in chimpanzees than bonobos, as suggested by their differences in a 2D-4D (digit) ratio (McIntyre et al. 2009). The level of prenatal androgens has been associated to the level of eye contact: in human children, a higher level of prenatal androgens is associated with a decreased level of eye contact (Lutchmaya et al. 2002). These studies suggest that neural and physiological mechanisms underlying gaze perception, which are related to the individual differences within the human species, are also related to the species differences between bonobos and chimpanzees.

### 9.4 Co-orienting Attention with Others

Now let’s turn our attention from simple orienting behavior to a more dynamic aspect of social attention. Social attention is not only about how long one looks at each social element but also about how well one coordinates attention with others. Imagine one simple reaching action performed by an agent (Fig. 9.6). When an agent is performing an action, the action sequence can be divided into several small sub-actions (Land et al. 1999). The agent first looks at the target object, moves his/her hand toward the object, and then grabs the object. If the viewer follows the action of
an agent, the viewer could anticipate the action goals and look to the target objects before the final grabbing action happens. Co-orientation often constitutes a first crucial step for engaging in joint activities with the agent and gauging the agent’s perception, goals and intentions. The viewer’s gaze responses in Fig. 9.6b (agent looking at the object) and c (agent reaching toward the object) are typically referred respectively as gaze following and action anticipation. The following three sections discuss our studies investigating apes’ abilities on gaze following and action anticipation including the social context and the viewers’ memories and understandings of others’ goals and intentions that modulate the expression of these behaviors.

### 9.5 Anticipating the Actions of Others

An anticipatory look is defined as looking at the target objects of an ongoing action before the action sequence is completed. Only recently did researchers start to examine this behavior, thanks to the advance in eye-tracking technology that allows researchers to capture the subtle eye movement happening in just a fraction of a second. Like humans (Cannon and Woodward 2012; Falck-Ytter et al. 2006; Flanagan and Johansson 2003), apes also make reliable anticipatory looks in response to an agent’s action (Kano and Call 2014b; Myowa-Yamakoshi et al. 2012).

The anticipatory looks made by humans are cognitively sophisticated; they attend to a reaching action based on the agent’s goals and intentions (Cannon and Woodward 2012; Senju et al. 2011; Southgate et al. 2007; Woodward 1998). We conducted a study to examine whether apes’ anticipatory looks could also be based on an agent’s current action goal. In this study, we tested bonobos, chimpanzees, and orangutans using a paradigm designed by Cannon and Woodward (2012) (see Fig. 9.7). In the original paradigm, human infant participants first saw a human
agent’s hand repeatedly reaching toward and grabbing the same one of two objects. Then the locations of the two objects were switched, and this time, the hand made an incomplete reach action toward the objects stopping halfway between the two objects. In the control condition, human infant participants saw instead an inanimate mechanical claw performing the same actions. Infants presented with the incomplete hand reach made anticipatory looks to the familiar object (the object that had been grabbed before) instead of the familiar location (where the object used to be). In contrast, such a result was not found in the control condition with the claw. Our apes performed just like human infants: they directed more looks at the familiar object in the hand condition but not in the claw condition. Thus, we confirmed that, like in humans, anticipatory looks in great apes are based on an agent’s action goals, rather than mere location or direction of the agent’s hand movements.

We found no significant species differences in this study. Bonobos and chimpanzees, and orangutans displayed a similar frequency and pattern of anticipatory looks. Thus, it is possible that species differences are only limited to gaze perception and do not extend to action perception or goal understanding. Relatedly, autistic children, known to differ from typical developing children in attention to eyes and gaze following, did not display a different pattern of anticipatory looks to an agent’s reaching action from typically developing children (Falck-Ytter 2010).

9.6 The Role of Memory in Anticipatory Looking

Goal-based anticipatory looks in apes possess a memory component; after apes learned the agent’s goal in the familiarization trials (see Fig. 9.7), they used that memory to anticipate the reaching goal in the test trial. This memory is most likely to be a short-term memory or possibly a procedural memory that has been learned.
through repeated presentations of the same actions. Can apes also make anticipatory looks based on a long-term memory of a single-trial experience? Traditionally, it has been considered that nonhuman animals lack the ability to remember single events for a long time period, except in very limited contexts [e.g., taste aversion, (Garcia et al. 1955)]. However, recent studies on episodic-like memory in nonhuman animals (Babb and Crystal 2006; Clayton et al. 2003; Kart-Teke et al. 2006; Martin-Ordas et al. 2010) revealed that it is not necessarily the case. Thus it is possible that apes’ anticipatory looks to an agent’s action could also be based on long-term memory after a single-trial exposure of that action.

Kano and Hirata (2015) tested this possibility in bonobos and chimpanzees by presenting them movies twice with one-day delay and measuring their anticipatory gaze patterns (Fig. 9.8). The movie story started with an ape-like character attacking a human agent. The agent then reached ambiguously toward two different objects (weapons for revenge) for a few seconds, grabbed one of them, and then hit the ape-like character with it. Apes watched this movie only once on the first day, and on the second day (24 h later), they watched the same movie again except one change; the location of objects was switched. This change, the same technique applied to the study mentioned above, enabled us to examine whether or not they remembered the content rather than the location of the objects. As apes are typically engaged in and encode better an intense social interaction such as aggression than they do to neutral events (Kano et al. 2008), the original agent’s reaching events were enhanced with aggression events in this study. In addition, to create a novel event in a familiar situation that could best engage ape participants, the study used the background and a human actor that were familiar to the participant apes, in combination with objects (weapons) and an antagonist (the ape-like character) unfamiliar to the apes. If the ape participants remembered which objects the agent chose, they should anticipate the target object on the second but not on the first day of watching. Our results con-
firmed this prediction. Importantly, their anticipatory looks to the target object were observed only just before the agent grabbed the object but not throughout the second presentation, suggesting that apes remembered the timing of event occurrence, or the relation between the agent’s action and object (rather than the object per se).

9.7 Following Gaze of Others

Gaze following is defined as looking in the same direction as other individuals after seeing their gaze direction. Gaze following is probably the best studied aspect of social attention in both human and nonhuman primates. Previous studies have shown that humans, apes, monkeys, and lemurs (Ruiz et al. 2009; Sandel et al. 2011; Shepherd and Platt 2008) as well as other non-primate animals [e.g., dogs, ravens, red-footed tortoises; (Bugnyar et al. 2004; Téglás et al. 2012; Wilkinson et al. 2010)] follow the gaze of others in a real-life situation. When the situation was presented in pictures and movies, humans, apes, monkeys, and dogs still reliably follow the gaze of the models (Deaner and Platt 2003; Hattori et al. 2010; Kano and Call 2014a; Téglás et al. 2012). In humans and monkeys, gaze following occurs reflexively within a fraction of a second and relatively independently of any task demand (Deaner and Platt 2003; Shepherd 2010). Gaze following could also occur non-reflexively under a sophisticated cognitive modulation. For example, when a model’s line of sight was blocked by a barrier, humans, apes, monkeys, and ravens looked around the barrier rather than simply followed the model’s gaze (Amici et al. 2009; Bräuer et al. 2005; Bugnyar et al. 2004; Moll and Tomasello 2004).

Although all primates tested follow gaze, species differences emerge depending on the experimental conditions. In a study, bonobos more frequently followed the gaze of human models than chimpanzees did (Herrmann et al. 2010); stump-tail macaques followed the gaze of conspecific models more than rhesus macaques did (Tomasello et al. 1998); and human children followed the gaze of human models more than apes did (Herrmann et al. 2007). In an eye-tracking experiment, chimpanzees followed the gaze of only conspecific model but not that of human model, while human participants followed the gaze of both models (Hattori et al. 2010). Most previous studies used a pairwise comparison of species and/or a human experimenter as a model, leaving it unclear whether the reported species differences reflected particular responses to the conspecifics or general sensitivity to the gaze signals.

We thus conducted an experiment using a crossed experimental design with participant species and depicted species, in which bonobos, chimpanzees, orangutans, human adults, and infants (1-year-olds) were presented with both conspecific and allospecific models (Fig. 9.9). Movies depicted a model, either a conspecific or an allospecific, turning his/her head to one of two identical objects repeatedly. Our results showed a species difference in both conspecific preference and the general gaze sensitivity. Consistent with the previous study (Hattori et al. 2010), chimpanzees followed the gaze of a conspecific chimpanzee but not that of allospecifics
Bonobos also followed the gaze of both conspecific and allospecific models, and overall more frequently, with shorter latencies, than chimpanzees did. Orangutans showed somewhat intermediate responses: they followed the gaze of conspecifics and bonobos but not the gaze of humans, with overall intermediate frequencies among the ape species. Human adults followed the gaze of both conspecific and allospecific models, and overall more frequently than the ape species. Human infants, unlike human adults, followed the gaze of a human model (as frequently as bonobos did) but not the gaze of allospecific ape models.

Thus, our results showed that these species differed in both general sensitivity to the gaze signals and particular responses to the conspecifics. It is particularly interesting to find that, among the tested participants, only chimpanzees and human infants followed the gaze of only conspecifics. One interpretation of this result is that chimpanzees and human infants are more motivated to follow the gaze of the most relevant others, the conspecifics. They may preferentially acquire information from only the most relevant others to learn about the environment efficiently. In this regard, our results may be consistent with the previous report of selective social referencing and behavioral copying by chimpanzees and human children (Dindo et al. 2009; Haun et al. 2012; van De Waal et al. 2013). The bonobo-chimpanzee difference in gaze following is again remarkable. We found that both bonobos and chimpanzees followed the gaze of conspecifics, but bonobos, but not chimpanzees, followed the gaze of allospecifics. Bonobos followed the gaze of both conspecific

![Fig. 9.9 A study on gaze following using a cross experimental design. For each participant species (left), both conspecific and allospecific models (right) were presented. Participants observed the model repeatedly looking at one of two identical objects](image-url)
and allospecific models overall more frequently and with shorter latencies than chimpanzees did.

The observed bonobo-chimpanzee differences may be related to their differences in temperaments and neural and physiological mechanisms, and the associated differences in gaze perception. In support of this idea, previous studies suggested that, in macaques and humans, the relative strength of reflexive and voluntary components in gaze following may be modulated by androgen-related mechanisms (Shepherd 2010). For example, subordinate monkeys followed the gaze more reflexively than dominant monkeys (Shepherd et al. 2006); human females followed the gaze of a familiar person more reflexively than males (Deaner et al. 2007). In the case of bonobos and chimpanzees, previous studies have shown that they are different in the levels of prenatal and adulthood androgen (Sannen et al. 2003; McIntyre et al. 2009). Thus, in bonobos, gaze following may be modulated by a reflexive (nonselective) rather than voluntary (selective) process to a larger extent than in chimpanzees; that is, bonobos may have followed the gaze of both conspecific and allospecific models more reflexively and therefore less selectively than chimpanzees did in our study.

One remaining puzzle is that, although we showed that chimpanzees do not follow the gaze of human models in our experiment, chimpanzees do follow the gaze of human experimenter in real-life behavioral experiments (Bräuer et al. 2005; MacLean and Hare 2012). It is conceivable that the context-rich real-life environment may better motivate the chimpanzees to follow human gaze. For example, when a chimpanzee faces a human experimenter in such situations, she may be more likely to attend to the human because he could provide some food. Besides, humans tend to add ostensive cues to the gaze cues during interaction (Csibra and Gergely 2009), making an eye contact and calling the chimpanzee’s name before looking at the target object. Such ostensive cues increase the likelihood that human infants will follow the adult’s gaze (Senju and Csibra 2008). In this regard, the ostensive cues might better motivate the chimpanzee to follow the experimenter’s gaze as well. Our recent study partly replicated the effect of human ostensive cues on gaze following in chimpanzees (Kano, Moore, Krupenye, Tomonaga, Call, in prep).

9.8 Conclusions and Future Directions

In this chapter, we have discussed the characteristics of apes’ social attention. We have described both similarities and differences between the species and discussed the possible mechanism underlying them. Consistent with the previous studies using observational (non-eye-tracking) methods, we found a number of similarities in the expression of social attention between apes and humans. All species attend to the same social elements including the face, eyes, and mouth of others as well as the targets of others’ actions. They follow the gaze direction of others, and they make anticipatory looks to the targets of others’ actions. In addition, they flexibly adjust
these behaviors according to the social contexts, and the viewers’ memories and understandings about others’ goals and intentions. We also found significant differences between the species. Bonobos (and humans) look longer the eyes of others than chimpanzees. Bonobos may follow the gaze direction of others more reflexively and less selectively than chimpanzees do. These species differences seem to be derived from each species’ unique temperaments. Several lines of evidence suggest that neural and physiological mechanisms underlying gaze perception, which are related to the individual differences within the human species, are also related to the species differences between bonobos and chimpanzees. Therefore, overall, the current data suggest that the cognitive, emotional and physiological underpinnings of social attention are well conserved across humans and all great ape species.

There are at least two important future research directions. The first is a more detailed examination of species and individual variation in social attention. We found that the pattern of social orienting is highly species-specific and related to each species’ unique temperaments. We could thus predict further diversity of social orienting in primate phylogeny, including non-ape species, such as Old-World monkeys (e.g., rhesus and stumptail macaques) and New-World monkeys (e.g., capuchin and spider monkeys). Those closely related species may differ in their social systems and temperaments, similarly as bonobos and chimpanzees do. In addition, it is also important to examine how individuals’ unique experiences affect the pattern of social attention, as the differences in early social experiences are known to affect the social and cognitive abilities of great apes (e.g. “encultured” chimpanzees reared by humans in human environment, Carpenter and Tomasello, 1995). Such an examination of species and individual variation should further help us to understand the mechanism and evolution of social attention in primates.

The other research direction is a more detailed examination of cognitive functions, such as a theory of mind and memory, in apes. We believe that an anticipatory looking paradigm could be particularly useful to reveal the cognitive underpinnings of social responses. Whether or not apes make anticipatory looks based on an agent’s intention is a goal worth pursuing. To show that one truly understands not only the current action goals of an agent but also the intentions of an agent, ultimately we need to find an evidence of false-belief understanding in the participant (Gergely and Csibra 2003). If apes are able to make correct anticipatory looks based on agent’s intention even when the agent carries a false belief about the location of the desired object, then we can be confident that apes do make anticipatory looks based on agent’s intentions. Such results have already been found with infants as young as 2 years old by measuring their anticipatory looking (Senju et al. 2011; Southgate et al. 2007). The use of an appropriate eye-tracking version for apes may offer a possibility that apes possess at least certain implicit form of false-belief representation (see Krupenye, Kano, et al., 2017 for the update).

Anticipatory looks are, by definition, based on the participant’s knowledge, memory, or understanding about the regularities of events and agents’ actions. In this sense they differ fundamentally from simple orienting responses which are likely under the control of both low-level perceptual and high-level cognitive functions. We believe that these findings from our studies will open up further possibilities to explore the unrevealed cognitive potentials as well as the diversity of individual minds in nonhuman animals.
Acknowledgments  We thank Drs. Masaki Tomonaga and Satoshi Hirata for their invaluable supports in conducting the studies presented here. Financial support came from Ministry of Education, Culture, Sports, Science and Technology (K-CONNEX to FK), Japan Society for Promotion of Science (KAKENHI 26885040, 16 K21108 to FK) and European Research Council (Synergy grant 609819 SOMICS to JC).

References

Argyle M, Dean J (1965) Eye-contact, distance and affiliation. Sociometry 28(3):289–304
De Waal FBM (1990b) Sociosexual behavior used for tension regulation in all age and sex combinations among bonobos Pedophilia. Springer, New York, pp 378–393
Hare B, Wobber V, Wrangham R (2012) The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. Anim Behav 83(3):573
Great Ape Social Attention

Kleinke CL (1986) Gaze and eye contact: a research review. Psychol Bull 100(1):78–100
MacLean EL, Hare B (2012) Bonobos and chimpanzees infer the target of another’s attention. Anim Behav 83(2):345–353
Sandell AA, MacLean EL, Hare B (2011) Evidence from four lemur species that ringtailed lemur social cognition converges with that of haplorhine primates. Anim Behav 81(5):925–931
Shepherd SV (2010) Following gaze: gaze-following behavior as a window into social cognition. Front Integr Neurosci 4:e5