There is More to Gaze than Meets the Eye

HOW ANIMALS PERCEIVE THE VISUAL BEHAVIOUR OF OTHERS

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There is more to gaze than meets the eye:
How animals perceive the visual behaviour of others

Een blik zegt meer dan duizend woorden:
Hoe dieren het visuele gedrag van anderen waarnemen
(met een samenvatting in het Nederlands)

Ein Blick sagt mehr als tausend Worte:
Wie Tiere das visuelle Verhalten anderer wahrnehmen
(mit einer Zusammenfassung in deutscher Sprache)

Proefschrift

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Aan mijn ouders
Aan Lars

The voyage of discovery is not in seeking new landscapes
but in having new eyes.

– Marcel Proust

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1

General Introduction

Parts of this chapter will appear in an adapted version as: Goossens BMA, Kaminski J Evolutionary roots of gaze following in a Special Edition of the European Journal of Developmental Psychology.

Gaze plays a pivotal role in both human and animal social interactions. In animals, recognizing the focus of others' attention by assessing the direction, the target and the emotional context of gaze may be essential for survival. In humans, gaze cues may provide insight into the emotions or thoughts of the interaction partner and, accordingly, the eyes have been called 'windows to the soul' (Cicero, De Oratore Liber Tertius, 55 BC). The interpretation of others' gaze cues has been proposed to be a crucial element of Theory of Mind (Baron-Cohen 1995), which is the ability to represent and interpret the behaviour of others in terms of mental states (e.g. 'knowing' or 'believing') (Heyes 1998).

Ever since Darwin (1871) proposed that there was a continuity in mental abilities between animals and humans, research effort on non-human animals' cognitive capacities has intensified. Research on advanced cognitive capacities has generally focussed on species phylogenetically closely related to humans, in an attempt to identify evolutionary precursors to human cognition. However, Theory of Mind has been suggested to be uniquely human (e.g. Povinelli et al. 2000), and it has often been associated with the faculty of language (e.g. Malle 2002), thus excluding non-human species. Clear evidence for Theory of Mind in non-human animals has been scarce in spite of extensive research efforts (see e.g. Heyes 1998). Recently chimpanzees, *Pan troglodytes*, were suggested to be sensitive to at least some mental states of others (Hare et al. 2000; 2001), but these conclusions are still under debate (Tomasello et al. 2003a, b; Povinelli and Vonk 2004; Bräuer et al. 2007; Povinelli and Penn 2007). Evidence is beginning to accumulate that Theory of Mind-like abilities may also be present in species phylogenetically remote from humans, such as certain bird species (Emery and Clayton 2004; Vignal et al. 2004; Dally et al. 2006).

Lately, Theory of Mind has been suggested to 'cover a wide range of processes of social cognition' (e.g. Tomasello et al. 2003b), rather than being a unitary phenomenon. Developmental stages of Theory of Mind in human infants, such as gaze following, joint attention and (visual) perspective taking (e.g. Flavell 1999) have been used to assess and study these capacities in animals (Call and Tomasello 2008). In this thesis I focus on a capacity considered central in the development of Theory of Mind, the recognition and interpretation of the visual behaviour of others (Baron-Cohen 1995). I investigated the cognitive mechanisms underlying this capacity in primates (i.e. long-tailed macaques, *Macaca fascicularis*). In addition, I have approached this topic from a comparative perspective by applying similar paradigms to a taxon that is phylogenetically remote to humans, namely fish, in order to address the question of the evolutionary history of this capacity.

EVOLUTION OF COGNITION

Until the end of the nineteenth century animals were generally not granted with having a mind, as the Cartesian view of animals as 'soulless' machines was predominant. However, when Darwin (1871) proposed that cognitive differences between humans and animals were only of degree and not of kind, interest in the abilities of animals and in how cognition may have evolved increased. Research has proceeded by the identification and examination of similarities and differences in the cognitive abilities of a wide range of non-human animals, yielding in essence two different broad schools of thought. The 'general process' view focuses on similarities between species, and argues that general cognitive mechanisms (such as for learning and memory) are not problem- or domain-specific and are widespread across the animal kingdom. That is, the general process view argues for commonality of mechanism (Macphail 1987; Bitterman 2000; Macphail and Bolhuis 2001). In this approach, the performance of diverse animal species (sometimes including humans) is compared employing similar paradigms (Bitterman 2000), in that way scrutinising and emphasizing similarities rather than differences between species in cognitive capacities (Heyes 2000). Animals may differ with respect to their perceptual mechanisms, but not with respect to the mechanisms underlying cognition (e.g. Macphail and Bolhuis 2001; Wynne 2004a).

A different view, that of 'adaptive specialisations', proposes that cognitive mechanisms (like other traits) can evolve in a modular way to meet the requirements of the environment. Animals live in diverse ecological niches that differ in the 'problems' they pose. Natural selection may result in cognitive solutions to these problems, which may lead to specialisations in certain domains, termed 'adaptive specialisations' (e.g. Shettleworth 1998). Studies based on the adaptive specialisation hypothesis have emphasised cognitive differences between species, and have compared the capacities of closely related species living in different ecologies in order to identify these adaptive specialisations and the selection pressures that may have acted on cognition (e.g. Hare et al. 2002). For example, proponents of social intelligence hypotheses argue that social living has been an essential driver of cognitive evolution (Jolly 1966; Humphrey 1976; Whiten 1997), which has resulted in specialisations of cognition for social problem-solving (for alternative or complementary ideas on the drivers of cognitive evolution, such as 'ecological' hypotheses, see e.g.: Parker and Gibson 1977; Milton 1981; Deaner et al. 2000; Reader and Laland 2002). Social life is thought to create cognitive challenges to animals that are different and possibly more complex than those encountered in the physical realm (Humphrey 1976). Animals have to deal with animate conspecifics whose behaviour changes and flexible behavioural strategies are often required to respond adequately in different situations (Tomasello and Call 1997). Advanced cognitive capacities (in for instance primates) may have evolved as adaptations to challenges in the social environment.

Research on complex cognition has traditionally focused on non-human primates, partly because phylogenetically they are human's closest relatives and, from the point of view of common descent, closely related species are expected to be similar in behaviour and cognition. Different behaviours that may indicate advanced cognitive capacities, such as tool use (e.g. McGrew 1992), social learning (e.g. Kawai 1965), or deception (e.g. Whiten and Byrne 1988), have been described in non-human primates. In an attempt to unravel the evolution of human cognitive capacities, researchers have studied the relationship between cognitive capacities of non-human primates and phylogeny (e.g. Byrne 2000), thereby providing hypotheses on when in evolutionary history cognitive changes may have occurred and what capacities were present in common ancestors of contemporary species. Within the primate order, the suggestion of a cognitive divide between the great apes (including humans, see Fig. 1) and other primates (lesser apes, monkeys and prosimians) has been prevailing (Whiten 1997; Byrne 2000), although debated by some (Tomasello and Call 1997). Systematic comparisons of the capacities of a number of different primate species may shed light on this matter.

In general, similarities in cognitive capacities between closely related species are thought to be due to common ancestry. However, students of animal cognition have expanded the range of species studied to social animals from other taxa, such as cetaceans, birds, and carnivores (e.g. De Waal and Tyack 2003), revealing that certain cognitive traits may have evolved several times in different taxa, irrespective of common descent. Similar selection pressures (for instance social lifestyle, see above) in distantly related taxa may result in the evolution of similar cognitive capacities, i.e. convergent evolution (e.g. Emery and Clayton 2004 document similarities in abilities between corvids and apes). Comparative research has extended beyond the primates, but, curiously, mainly to other mammals and birds. As discussed in chapter 4, fish provide an interesting taxon to investigate cognitive evolution. First, some behaviours in both fish and primates show striking similarities at face value, such as social learning, cooperation, deception and punishment (see for review Bshary et al. 2002; Brown et al. 2003). Studying the capacities of distantly as well as closely related species may shed light on the selection pressures that have shaped behaviour and cognition. Second, fish represent an early division in the vertebrate phylogeny (Fig. 1) and the presence of cognitive capacities in fish similar to those in birds and mammals can provide an indication that these characteristics are ancestral, and not convergent, in vertebrates.

ANIMAL SOCIAL COGNITION

Elements of animal social cognition that have been studied in a variety of species include individual recognition (Cheney 1980; Tebbich et al. 2002), the formation and recognition of dominance hierarchies (Dasser 1988; Bergman 2003), deceptive strategies (Whiten and Byrne 1988), mirror-self directed behaviour (Gallup 1970; Plotnik et al. 2006; Prior et al. 2008) and the understanding of other individuals' mental states ('Theory of Mind'). The concept of 'Theory of Mind' was introduced three decades ago by Premack and Woodruff (1978) in their seminal work on the common chimpanzee Sarah. Sarah viewed films depicting a person failing to solve various problems (e.g. human in front of a locked door, trying to open it). Subsequently, she had to choose between photographs depicting solutions and non-solutions to the problems. Sarah selected the correct solutions (e.g. the key picture) more often than would be expected by chance, which led Premack and Woodruff (1978) to argue that she had an understanding of the human's unobservable intentions (i.e. the human's intention to open the door). The validity of this claim has been debated, as alternative explanations may be feasible. Sarah may have used different strategies to solve the task, for instance by assessing the observable goal of the action instead of the actor's mental state (Savage-Rumbaugh et al. 1978). Nevertheless, the theoretical proposition of a Theory of Mind has fuelled research for the past decades in various fields such as animal cognition, developmental psychology, philosophy, and neuroscience (Whiten 1997; Heyes 1998; Call and Tomasello 2008; see also Box 1 on the potential neural basis to Theory of Mind).

Within the concept of 'Theory of Mind' (or mental-state attribution), several types of mental states can be distinguished that an individual may be able to attribute to others, for instance goals, intentions, perceptions, knowledge, or beliefs (Call and Tomasello 2008, see for a slightly different distinction Premack and Dasser 1991). Research has begun to uncover which of these mental states animals may be able to assess in others. Chimpanzees, for instance, distinguished between an experimenter who was willing, but unable to pass a food reward, and an experimenter who was able, but unwilling to give the reward (Call et al. 2004), implying sensitivity to the other's *intentions*. Addressing animals' ability to assess what other individuals know, Povinelli and colleagues (1990; 1991) examined whether chimpanzees and rhesus macaques, *Macaca mulatta*,

Box 1: Mirror-neurons: Neural basis of Theory of Mind?

Mirror-neurons are a special group of neurons that fire both when an animal performs an action and when it observes another individual performing the same action. Mirror-neurons were first discovered in pigtailed macaques, *Macaca nemestrina* (Gallese et al. 1996) and have since been described in humans ('mirror-system', Rizolatti and Craighero 2004) and songbirds (Prather et al. 2008). Neuronal activity of area F5 was measured during the monkeys' hand actions, such as breaking a peanut or grasping an object. Researchers noted that exactly the same neurons were active when the animals observed or heard the same or similar actions performed by other individuals (Gallese et al. 1996; Keysers et al. 2003), even when the reached-for object was hidden behind an obstacle and the action had to be inferred (Umilta et al. 2001). This led to the suggestion that mirror-neurons may function in the internal recognition of others' action, by matching the observed action with neurons that fire during the performance of these actions (Gallese et al. 1996).

In humans, although direct experimental evidence on the activity of single neurons is lacking, results of neuro-imaging studies (for review see Rizolatti and Craighero 2004) have suggested the existence of a similar mirror-system (activation of similar brain areas). Corresponding regions are activated both by seeing and experiencing certain actions. Furthermore, overlap between experience and observation of both pain and the emotion disgust has been found in a different brain region (Singer et al. 2004; Wicker et al. 2003). Similarly, the mirror-system is activated only by the sound of certain actions (Gazzola et al. 2006). Also, seeing intentional actions, compared to the same actions without context, seems to activate brain areas that have been associated with the mirror system (Iacoboni et al. 2005). These results suggest that the mirror-system may be the neural basis for experiencing the same actions, emotions or intentions as others, at least in humans. The exact processes through which mirror-neurons acquire their specific responses remain to be investigated (but see Keyzers et al. 2004). The role that mirror-neurons play may be diverse and thus the human mirror system has been associated with imitation (Iacoboni et al. 1999; but see Catmur et al. 2007), language (e.g. Rizolatti and Arbib 1998) and Theory of Mind (e.g. Brune and Brune-Cohrs 2006). However, the mirror-system may be present in species that (probably) lack these advanced cognitive capacities, suggesting that it may be a widespread system for an internal representation of others' emotion or behaviour (Gallese and Goldman 1998).

could discriminate between a knowledgeable and an ignorant (with respect to a hidden food source) experimenter. Rhesus macaques failed this task (Povinelli et al. 1991), and chimpanzees only mastered it after hundreds of trials (Povinelli 1990), suggesting that they may have learned to associate the food reward with the experimenter who had witnessed the food-hiding procedure, rather than understanding the knowledge state of the experimenters (Heyes 1998). More recently, however, Hare et al. (2001) showed that when competing over food, chimpanzees were sensitive to what a dominant conspecific did or did not know. Subordinate chimpanzees showed a preference for food-items that the other had not seen being hidden (or being moved). This was interpreted as evidence that the subordinate responded to the state of knowledge of the dominant competitor. The capacity to assess others' *perceptions* (i.e. what another individual may see or hear) has probably received most attention from students of animal social cognition. At the very basis of the ability to assess others' perceptions lies sensitivity to their visual behaviour, i.e. recognizing the other's gazing direction, recognizing the target of another's gaze and attention (i.e. joint attention), and recognizing the (emotional) context of the other's gaze. Hence gaze following and joint attention are some of the behaviours that have been studied in a variety of animals in this context.

FROM GAZE FOLLOWING TO THEORY OF MIND

Gaze cues may be perceived and interpreted by animals in different ways. In general, researchers have distinguished between gaze following capacities that are based either on learned or simple reflexive responses or on a more sophisticated appreciation that the other may see something (e.g. Povinelli and Eddy 1996a; Tomasello et al. 1999). In the latter case, gaze following may be an essential aspect of Theory of Mind. Several theoretical frameworks have been applied to the study of gaze following in animals. Emery (2000), for instance, distinguished different categories according to the presumed cognitive complexity of the involved capacity, thereby exemplifying the relationship between gaze following and Theory of Mind (Table 1). Butterworth and Jarrett (1991) scrutinised two

Table 1. Categorization of different levels of how gaze cues may be interpreted by an individual. Based on Emery (2000). Lower entries in the table are argued to involve greater cognitive complexity.

Emery's (2000) terminology	Definition of level
Mutual vs. Averted gaze	Individual can recognize whether another individual is looking at it vs. is looking in a different direction.
Gaze following	Individual can follow the direction if the other's gaze (as indicated by eye and/or head direction). (Termed 'ecological gaze following' by Butterworth and Jarrett 1991).
Joint attention	Individual follows other individual's gaze to a specific target (Emery 2000, Butterworth and Jarrett 1991), without being distracted by intervening objects ('geometrical gaze following'), also to locations out of its immediate visual field ('representational gaze following').
Shared attention	Both individuals look (attend) to the same object and also comprehend that the other is looking at that specific object.
Theory of Mind	An individual uses attentional mechanisms (gaze following, joint or shared attention) most likely together with higher-order cognitive strategies such as experience or empathy to predict the intentions, thoughts or goals of another with respect to an attended to object.

of these levels, gaze following and joint attention, and described three developmental stages in these capacities of the human infant (see also Boxes 2 and 3): an 'ecological', a 'geometrical', and a 'representational' stage.

Taking these levels in turn, first, an individual may be able to distinguish **directed (mutual) gaze from averted gaze** (Table 1), potentially based on a simple attentional mechanism. Animals may have a predisposition to detect or attend to socially relevant stimuli like the eyes or eye-like patterns and their direction, which can result in aversion to directed gaze (e.g. an anti-predator strategy) or in a preference to look at the eyes. This sensitivity to the directedness of the eyes (or eye-like stimuli) has been documented in a number of species (see e.g. Emery 2000 for review). Chimpanzees, for instance, preferentially beg from experimenters who are facing them, which has been interpreted as responsiveness to the experimenter's attentional state (Kaminski et al. 2004). Eye sensitivity has also been demonstrated in humans. For example, Bateson and colleagues (2006) reported that people were more generous when donating money in a coffee box when it was decorated with eyes than compared to control stimuli, which has been suggested to be due to an unconscious effect of (pictured) eyes on the perception of being watched.

On the next level, **'ecological' gaze following** (Table 1), an individual attends to another's averted gaze and co-orients in the approximate same direction, without an appreciation that the other's gaze may be directed at something specific. The simplest explanation of this behaviour may be a preference for eyes or eye-like stimuli combined with a reflex-like or learned co-orientation response in the general direction of the other's gaze (following gaze often results in seeing something relevant that may be reinforcing; see also Triesch et al. 2006 for a computational model on gaze following and learning). Next, gaze following at the **'geometrical'** level enables an individual to extrapolate the other's gazing direction to a specific target within its field of vision, also past distracting objects (see Box 2). The gaze following individual must be able to draw an imaginary line of sight between the other's eyes towards the looked-at object. With the **'representational'** level an individual can follow gaze to a location outside its own field of vision (for instance behind itself or behind a barrier, see chapter 2). Note, that Butterworth and Jarrett (1991) use 'representational' in the sense of spatial representations, not in the sense of mentalistic understanding of another's visual behaviour, which would indicate that the gaze follower assesses the other's visual perspective. On the 'geometrical' and 'representational' level, the gaze follower may appreciate that the other's gaze signifies directedness of attention and hence may redirect its own attention to the same object, which signifies **joint attention**, i.e. both individuals are attending to the looked at target.

Box 2: Development of gaze following in human infants

In humans, gaze following has been suggested to be an essential prerequisite and an early manifestation of Theory of Mind (e.g. Baron-Cohen 1995). Human infants show interest in the eyes of others from an early age (two months; Haith et al. 1977). They start to respond to the looking direction of their caregivers at 6-9 months old based on the 'ecological mechanism' (Butterworth and Jarrett 1991). At this stage they follow the approximate direction of the other's gaze until encountering something interesting in the other's line of sight (Scaife and Bruner 1975; Butterworth and Jarrett 1991). Children at 9 months respond similarly to a head-shift with closed eyes (thus irrelevant for seeing) and one with open eyes (Brooks and Meltzoff 2002), implying that they do not yet know about the significance of the eyes in the process of seeing, or alternatively, that the head-turn (as opposed to a shift in direction of the eyes) is a strong trigger to turn in the same direction. Human infants at the age of 12-18 months follow gaze with accuracy to specific targets and past distracting objects, based on the 'geometrical mechanism' (Butterworth and Jarrett 1991). Moreover, they will follow gaze to locations behind them (outside their immediate visual field) and hidden behind barriers, the latter implying an early indication for the understanding of the other's visual perspective (Moll and Tomasello 2004), a more complex socio-cognitive capacity than simple co-orientation.

Closely related to joint attention is **shared attention**, with which two individuals perceive that they both are attending to the same object. Joint and shared attention episodes are thought to be central in the development of Theory of Mind in the human infant (Baron-Cohen 1995). The infant may form associations between itself, others, and objects in the environment that others may be attending to (see Table 1). In humans, joint and shared attention skills seem to be particularly impaired in individuals with autism (Box 3).

Finally, based on the attentional mechanisms described above (e.g. following other's direction of attention) and in combination with more advanced cognitive abilities, such as visual perspective taking (the ability to represent what another individual may be seeing from a different perspective) may come the ability to reason about the other's perceptions, intentions, or thoughts concerning the looked at object, i.e. **Theory of Mind**. Research on Theory of Mind in humans has focussed on the developmental trajectory of this capacity in infants (Box 2), on the consequences of impairment in Theory of Mind and related abilities (Box 3) and more recently on the potential neural mechanisms underlying Theory of Mind (Box 1). In animals, stages of human development of elements of Theory of Mind have been used to assess and categorize their abilities.

Box 3: Gaze following and autism

Joint attention skills, such as attending to the gazing direction of others, are essential elements in the social-cognitive development of human infants. The absence or an impairment of these skills is thought to be the earliest behavioural symptom of autism (Baron-Cohen 1995; Bruinsma et al. 2004). There is abundant evidence that autistic children have severe problems in attending to the gazing direction of others during social interactions (Leekam et al. 1997; 1998). However, not all elements of gaze following appear to be affected. Reflexive attentional cueing by social stimuli (eyes or faces) seems to be intact in both children and adults with autism as diverse studies employing a spatial cueing paradigm report (e.g. Chawarska et al. 2003; Swettenham et al. 2003; Kylliaeinen et al. 2006). In this paradigm, subjects are presented with a directional cueing stimulus on a screen (e.g. moving/static eyes directed at one side) and a successively appearing target. In general, targets are detected and identified faster if the preceding directional cue matches the location of the target ('validity effect'), implying that directional information can be acquired from directional social stimuli, such as moving eyes or faces.

Leekam et al. (1997) addressed the geometric component of gaze following, i.e. the ability to determine where another individual is looking and what target he might be seeing, by comparing the performance of children with autism and a normal developing control group in a visual perspective taking task and a spontaneous gaze following task. Autistic children could assess where another person was looking, but only when explicitly asked to do so. The same children, however, failed to follow the gaze of an experimenter who suddenly turned her head and eyes, indicating that they did not employ their geometric capacities to monitor the other's gaze during social interactions. Surprisingly enough, the children with autism were quicker in determining where exactly another person was looking. Some of them also used an explicit strategy to assess the target of the other's attention by drawing a line from the other's eyes to the looked-at target with their fingers, which made their responses more accurate than those of the control children. The authors concluded that, although the geometric mechanism of attending to others' gazing direction (Butterworth and Jarrett 1991) seems to be intact in autistic children, the ecological mechanism (preceding the geometric mechanism in typically developing children; Butterworth and Jarrett 1991) seems to be impaired in children with autism. This suggests that Butterworth and Jarrett's (1991) simpler mechanisms are not essential for more advanced capacities to develop.

Taken together results on gaze following in autistic individuals are mixed. Although responses in natural spontaneous interactions seem to be impaired, related capacities such as reflexive co-orientation or geometric capacities seem to be intact. This disparity may be a result of different cognitive mechanisms underlying gaze following in autism and typical development (Leekam et al. 1997). Support for this hypothesis stems from the finding that the development of social cognitive capacities in autistic children follows a different trajectory than in typically developing children (Carpenter et al. 2002). However, it is currently unclear which developmental, cognitive or motivational aspects impair gaze following in people with autism. A more developmental approach of gaze following in autistic children (Nation and Penny 2008) may uncover why exactly children with autism fail in attending to other's gazing direction and how early deficits affect later behaviour.

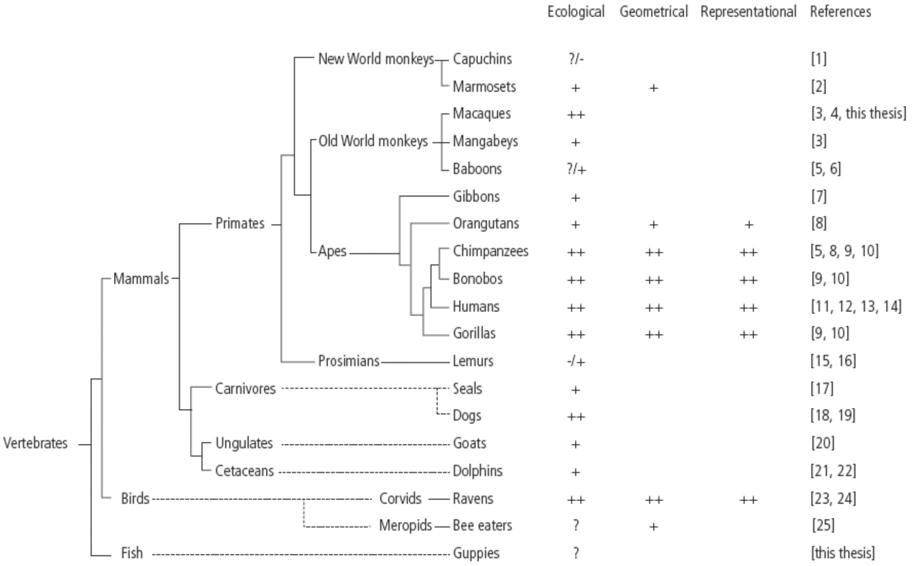
GAZE FOLLOWING AND JOINT ATTENTION SKILLS IN ANIMALS

Animals' ability to attend to the visual cues of other individuals has been documented in a wide range of species (Emery 2000). Here, I review the current evidence on gaze following and joint attention abilities in non-human animals in the framework of Butterworth and Jarrett's (1991) different levels of gaze interpretation.

'Ecological' gaze following in animals

Various primate species have been shown to follow the gaze direction of other individuals. In a series of experiments, Povinelli and Eddy (1996a) demonstrated that chimpanzees are able to follow the looking direction (indicated by head- or eye-cues) of a human experimenter. A similar result (attending to head-direction) was found in the other great apes (bonobo *Pan paniscus*, gorilla *Gorilla gorilla*, orang-utan *Pongo pygmaeus*; Bräuer et al. 2005). The ability to follow others' gaze is not only present in the apes, but also in various monkey species, that are more distantly related to humans (Fig. 1). Emery and colleagues (1997) showed in a computerized task that rhesus macaques can locate an object according to the gazing direction of a stimulus animal depicted on the computer-screen. In a different study with live conspecific demonstrators, individuals of five primate species (chimpanzees, sooty mangabeys *Cercocebus atys torquatus*, rhesus macaques, stumptail macaques *Macaca arctoides*, and pigtailed macaques) followed the gaze direction of a conspecific (Tomasello et al. 1998). Attention of one animal, the demonstrator, was drawn by an experimenter, who was located out of the subject's sight in an observation tower. Once the demonstrator had shifted gaze towards the experimenter, it was recorded whether the nearby subject responded with head turns towards the same location. Animals of all the species reliably attended to the conspecific's gazing direction. Gaze following has also been studied in prosimians, the extant group of primates most distantly related to apes (see Fig. 1), with mainly negative results (Itakura 1996; Anderson and Mitchell 1999). However, a recent study demonstrated that ring-tailed lemurs, *Lemur catta*, are sensitive to the gazing direction of group-members when moving freely in a social group. In this study, a telemetric gaze-tracking system was used that allowed studying the visual behaviour from the perspective of the animal (Shepherd and Platt 2008). This is an example of how methodology may determine the outcome of a study, suggesting that applying a standard test to a wide range of species may not always provide a fair comparison of capacities.

Outside the primate order, there is also abundant evidence for 'ecological' gaze following. Some marine mammals, such as dolphins, *Tursiops truncatus*,



	Ecological	Geometrical	Representational	References
Capuchins	?/-			[1]
Marmosets	+	+		[2]
Macaques	++			[3, 4, this thesis]
Mangabeys	+			[3]
Baboons	?/+			[5, 6]
Gibbons	+			[7]
Orangutans	+	+	+	[8]
Chimpanzees	++	++	++	[5, 8, 9, 10]
Bonobos	++	++	++	[9, 10]
Humans	++	++	++	[11, 12, 13, 14]
Gorillas	++	++	++	[9, 10]
Lemurs	-/+			[15, 16]
Seals	+			[17]
Dogs	++			[18, 19]
Goats	+			[20]
Dolphins	+			[21, 22]
Ravens	++	++	++	[23, 24]
Bee eaters	?	+		[25]
Guppies	?			[this thesis]

Figure 1. Phylogeny of species that have been tested on their gaze following capacities
+ indicate evidence from one study, ++ indicate evidence from multiple studies, - indicate negative results, and ? equivocal evidence. Blanks indicate that, to my knowledge, no study has been conducted in this species. References: 1 = Anderson et al. 1995, 2 = Burkart and Heschl 2006, 3 = Tomasello et al. 1998, 4 = Ferrari et al. 2000, 5 = Vick et al. 2001, 6 = Vick and Anderson 2003, 7 = Horton and Caldwell 2006, 8 = Bräuer et al. 2005, 9 = Tomasello et al. 1999, 10 = Okamoto-Barth et al. 2007, 11 = Butterworth and Jarrett 1991, 12 = Moll and Tomasello, 13 = Brooks and Meltzoff 2002, 14 = Caron et. al 2002, 15 = Itakura 1996, 16 = Shepherd and Platt 2008, 17 = Scheumann and Call 2004, 18 = Miklosi et al. 1998, 19 = Hare and Tomasello 1999, 20 = Kaminski et al. 2005, 21 = Pack and Herman 2004, 22 = Tschudin et al. 2001, 23 = Bugnyar et al. 2004, 24 = Schloegl et al. 2007, 25 = Watve et al. 2005

and seals, *Arctocephalus pusillus*, spontaneously attend to the gaze direction of humans (indicated by head-direction; Tschudin et al. 2001; Pack and Herman 2004; Scheumann and Call 2004). Dogs, *Canis familiaris*, and goats, *Carpa hircus*, respond to pointing or gazing (as indicated by head movement) directions of humans and/or conspecifics (Miklosi et al. 1998; Hare and Tomasello 1999; Kaminski et al. 2005). Also members of more distantly related taxa have been tested for their gaze following abilities. Ravens, *Corvus corax*, for example, have been shown to co-orient with the gaze (head and eye direction) of a human experimenter from an early age (Bugnyar et al. 2004; Schloegl et al. 2007). In this test, a human experimenter shifted gaze (head- and eye-direction) to a distant location to which the hand-raised subjects responded with immediate co-orientation. Taken together there is compelling evidence that 'ecological' gaze following to different kind of visual cues (such as eye-, head- or body-direction) is a widespread capacity among vertebrates (see Fig. 1). However, the majority of animals that have been tested for gaze following capacities are mammals or birds (Emery 2000).

Species from other taxa may also rely on visual behaviours of others. Some fish species, for example, have been shown to use visual cues to recognize conspecific individuals (Warburton and Lees 1996) or learn about predators and escape routes by observing the behaviour of conspecifics (e.g. Reader et al. 2003). Young jewel fish, *Hemichromis bimaculatus*, have been shown to flee eye-like stimuli as compared to other spot patterns, suggesting that they have a predisposition to recognize eyes or eye-like stimuli (Coss 1979), but this may be due to the conspicuousness of the eye-like stimuli instead of the similarity to actual eyes (Stevens et al. 2008). In addition, it has been suggested that fish species living in shallow water reefs have evolved specialized perceptive and cognitive skills in the context of visual processing (Kotrschal et al. 1998). These studies indicate that fish can also be sensitive to eye-like stimuli and use visual information in their behaviour. However, so far there is no evidence for gaze following in vertebrates outside mammals and birds (see Fig. 1).

'Geometrical' gaze following in animals

Following Butterworth and Jarrett (1991), the next level of interpreting others' gazing behaviour is 'geometrical' gaze following, which enables an individual to track the other's line of sight to the exact location and past distracting objects, implying that both individuals direct their attention to the same target, i.e. joint attention (see Table 1). This capacity has been demonstrated in chimpanzees that followed the gaze of a human experimenter to the exact location while distracting items were displayed within the experimenter's approximate looking direction (Tomasello et al. 1999). This capacity has also been documented in common marmosets, *Callithrix jacchus*, with subjects choosing the correct looked-at object out of several possible objects within their visual field (Burkart and Heschl 2006). For non-primate species, there is some evidence in birds for geometrical gaze following. Bee-eaters, *Merops orientalis*, recognized whether the gaze of a potential predator (i.e. a human experimenter) was directed at them, at their nest or elsewhere. This indicates that they tracked the other's line of sight in a geometrical way to the exact location of the other's attention (Watve et al. 2002). Similar to 'ecological' gaze following, there is evidence for geometric skills in different vertebrate taxa, although it has been investigated in fewer species (see Fig. 1).

'Representational' gaze following in animals

Finally, representational gaze following enables an individual to track another individual's gaze to locations outside its own immediate field of vision. Chimpanzees have been shown to follow gaze to locations behind them, which human infants do at the age of 18 months (Butterworth and Jarrett 1991; Povinelli and Eddy 1996a; see also Box 2), and which indicates the individual's representation of unseen space. Another way of addressing this level of gaze following has been by the use of visual barriers that may block the subject's line of sight, thereby creating space outside the subjects' field of vision. In this task, the experimenter, instead of looking at something within the subject's visual field, directs his/her attention to something behind an occluder such that the subject cannot see what the experimenter is looking at. If an individual interprets gaze as an indicator of another individual's perspective and is sensitive to the geometrical properties of the experimenter's line of sight, it should relocate to a position allowing visual access to what the other is looking at. There is evidence that all great ape species and also ravens follow the gaze of a human experimenter to a location behind a barrier that obstructs their view (Tomasello et al. 1999; Bugnyar et al. 2004; Bräuer et al. 2005). All species tested relocate to a position from which they can see where the human experimenter is looking and they do so more often than in a control condition in which the human is not looking to a location behind the barrier (Tomasello et al. 1999; Bräuer et al. 2005). In a recent study modelled after Caron et al. (2002), Okamoto-Barth et al. (2007) showed that some ape species also modify their gaze following behaviour based on the nature of the obstacle blocking the experimenter's (instead of the animals') view (e.g., obstacle with or without a window). Animals relocated more often to the correct location when the barrier contained a window through which the experimenter actually could see something, than when there was no window in the barrier and the experimenter's line of sight was terminated at the barrier (Povinelli and Eddy 1996a).

In summary, extant data suggest that gaze following based on the more advanced 'geometrical' and 'representational' levels seems to be restricted to a number of species, mainly to great apes and ravens (see Fig. 1). However, it remains matter of further research whether this implies a restriction of these capacities to large-brained animals such as primates and corvids, or whether it reflects lack of studies on species from other taxa. This issue is addressed in chapter 3 and 4.

AIMS AND OVERVIEW OF THESIS

'Ecological' gaze following is present in a wide range of species, such as certain non-human primates, domesticated mammals, marine mammals, and some birds. The wide range of species responding to others' looking behaviour raises questions concerning the evolution of this capacity and the underlying mechanisms in the different species. In humans, there is abundant evidence and consensus on the significance of the eyes and the capacity for joint attention in the development of Theory of Mind (Baron-Cohen 1995; Flavell 1999; for review Flom et al. 2007). Yet for many animal species it remains to be investigated whether the behaviour is based on such a sophisticated understanding of the other's visual behaviour, and may as such be used to evaluate Theory of Mind-related capacities in these species. It is thus essential for the study of animal social cognition to (a) examine the cognitive mechanisms that may underlie animal gaze following, i.e. whether the behaviour in the different species is based on basic attentional mechanisms or on more sophisticated capacities that are relevant in the development of the ability to attribute mental states, (b) study primate species outside the great apes to address phylogenetic questions concerning primate cognitive evolution, and (c) from a comparative perspective to identify species from various taxa with similar capacities in order to address the evolutionary history of this particular capacity. The main objective of this thesis was thus to examine how animals, in particular long-tailed macaques, *Macaca fascicularis*, and guppy fish, *Poecilia reticulata*, perceive and interpret the visual behaviour of others. First, I examined the cognitive mechanisms underlying gaze following behaviour in long-tailed macaques (chapters 2 and 3). Second, from a comparative perspective, I investigated how widespread the behaviour is and therefore explored beyond the borders of the mammals and birds, that had been studied so far, taking a closer look at another vertebrate species, the guppy (chapter 4).

In **chapter 2** I describe an experiment on gaze following capacities in long-tailed macaques. Prior to this study a number of primate species had already been shown to be sensitive to the gazing direction of both conspecific and heterospecific individuals (Tomasello et al. 1998; Ferrari et al. 2000). First, it had to be established whether long-tailed macaques, like other macaque species, would attend to the gazing behaviour of a human experimenter. Second, animals supposedly derive information from the visual behaviour of others. So far there has been no evidence on how social information during gaze-shift affects the response of a gaze following individual. Social facial expressions may be used to gain information on the nature of the target, for instance, observing an individual directing facial threats elsewhere, may lead to the gaze follower's expectation on the nature of the target in the direction of the other's gaze. Therefore, I investigated whether long-tailed macaques respond to social information provided by the demonstrator during gazing.

In **chapter 3** I examine whether long-tailed macaques are able to follow the gaze of a conspecific to a location hidden behind a physical obstacle, a barrier (e.g. Tomasello et al. 1999). Passing this test indicates the ability to extrapolate a vector from the other's gazing direction to a location outside one's own view, a more advanced capacity than simple co-orientation, suggesting 'geometrical' and 'representational' gaze following. For this purpose, the visual attention of a conspecific demonstrator was drawn by a suddenly appearing mirror to a location a subject could not see without relocating. The use of a conspecific demonstrator in this experiment complied with the call for more ecologically valid experiments in the study of animal cognition.

In order to address questions on the evolution of a certain skill, the taxonomic range needs to be determined. As studies on gaze following have so far been restricted to birds and mammals, I extended the range of species to another vertebrate taxon, namely fish. In **chapter 4** I investigate the capacities to attend to the visual behaviour of conspecifics in a poecilid fish, the guppy. Guppies are a highly visual species. They live in groups with numerous individuals and have been shown to be good social learners. In a series of experiments, I investigated whether fish would (a) respond to a directional cue (indicated by the body- and swimming direction) given by familiar conspecifics, and (b) would be able to use a competitors' perspective or behaviour in order to obtain food in a visual perspective taking task.

In the **final chapter** of this thesis, I summarize the results and discuss the implications for future research. The ability to respond to the visual behaviour of others has been argued to lie at the basis of more complex social-cognitive capacities such as visual perspective taking, deception or mental state understanding. Future research needs to show which cognitive mechanisms underlie gaze following and joint attention, in order to investigate whether and how these abilities are linked to the ability to assess others' perceptions (part of Theory of Mind). Moreover, as the capacity of 'ecological' gaze following is found in different taxa, future research must establish how widespread this and the more advanced joint attention levels of gaze following are. Only in this way can the evolutionary history of these capacities and the selection pressures favouring them be revealed, selection pressures that may have driven the evolution of more advanced cognitive capacities such as Theory of Mind.

2

Gaze following in monkeys is modulated by observed facial expressions

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ABSTRACT

Gaze following and the ability to understand that another individual sees something different from oneself are widely considered important components of animal social cognition. Recent studies suggest that gaze following is taxonomically widespread, yet for many species there is no evidence that gaze following is employed in a flexible manner and is more than a simple so-called 'orienting reflex'. Here, we measured the effect of social facial expressions, mimicking responses to social events, on gaze following in long-tailed macaques, *Macaca fascicularis*, using a human demonstrator. Gaze-shifts accompanied by a socially meaningful facial expression (the Bare Teeth display) elicited stronger gaze-following responses than neutral gaze-shifts. Subjects also 'check-looked', that is, looked back and forth between the experimenter's face and their gaze direction, which has been proposed to indicate that a subject understands that another individual is looking at a specific stimulus. Monkeys' gaze following is thus modulated by the facial emotional expressions of the demonstrator, providing evidence that their gaze following is more flexible than was previously thought. This modulation may be due to a specific arousal- or attention-based mechanism or may be based on the subject understanding that the demonstrator is attending to something the subject cannot see.

INTRODUCTION

Gaze following, the ability to track the gaze direction of other individuals, has been proposed to be an important component of animal social cognition because it may be based on an individual's understanding that the perceptions of others can differ from its own. In human infants this understanding has been proposed to be a precursor to Theory of Mind (Baron-Cohen 1995), the capacity to understand another individual as a different mental agent with its own intentions, emotions and goals (Premack and Woodruff 1978). In addition, the observation and interpretation of another's gaze may play a key role in the development of a Theory of Mind in the life of an infant (Baron-Cohen 1995). However, for nonhuman primates the 'cognitive' interpretation of gaze following has been challenged (Povinelli and Eddy 1996a,b). Animals from various taxa (chimpanzees, *Pan troglodytes*; rhesus macaques, *Macaca mulatta*; ravens, *Corvus corax*; goats, *Capra hircus*; dogs, *Canis familiaris*; and seals, *Arctocephalus pusillus*; Miklosi et al. 1998; Tomasello et al. 2001; Bugnyar et al. 2004; Scheumann and Call 2004; Kaminski et al. 2005) attend to the gazing direction of others, but for many species it remains unclear whether gaze following is flexibly employed rather than a fixed response to another individual's sudden change of visual orientation (Emery 2000). It is also not known to what extent the social context in which an individual shifts gaze influences gaze following. We investigated whether gaze following in long-tailed macaques, *Macaca fascicularis*, is flexibly employed by displaying facial expressions with social and emotional meanings during gaze-shifts. In this way, we could analyse whether subjects would take a mimicked social event into account as indicated by a change in their gaze-following response, potentially shedding light on their level of gaze interpretation.

Among primates, there is substantial evidence for gaze following (or visual co-orientation) of both conspecifics and heterospecifics (Tomasello et al. 1998; Anderson and Mitchell 1999; Lorincz et al. 1999; Emery 2000; Bräuer et al. 2005). Chimpanzees and rhesus macaques can follow human gaze from an early age (Tomasello et al. 2001), even solely eye direction, irrespective of head and body posture (Ferrari et al. 2000). However, without extensive training, chimpanzees, rhesus macaques and capuchin monkeys, *Cebus apella*, do not appear to use human gaze as a cue to locate hidden food (Anderson et al. 1995; 1996; Call et al. 1998; Burkart and Heschl 2006 for evidence in common marmosets, *Callithrix jacchus*). This limited extent of gaze interpretation may indicate what has been termed an 'orienting reflex' or 'low-level' understanding (Povinelli and Eddy 1996a). A co-orienting response to an individual's gaze-shift may be conditioned by means of conspicuous objects or events in the line of sight that can act as reinforcers. The individual learns to attend and respond to the visual cue of another's gaze-shift. In this interpretation, the gaze-following individual does not necessarily know exactly where the other individual is looking nor does it have an expectation of what the other is seeing. Instead, it simply looks in the direction another looks, as a result of a reflex or conditioned response. This response may, however, be influenced by the context in which the other individual shifts its gaze. Such context-specific responses may also be learned, but would none the less indicate a more flexible interpretation of gaze following than the low-level explanation currently allows.

A cognitively more demanding interpretation of gaze following is that the gaze following individual understands that the other's attention is directed at something, for instance a conspecific. This explanation suggests that the gaze follower has the knowledge that the other individual is seeing something different from itself, which in turn is a prerequisite to understand that the other has different knowledge (Tomasello et al. 1999). The gaze-following individual matches another's looking direction, expecting to see the target the first individual is observing, possibly with an expectation about the nature of the target.

Recent evidence indicates that some animals may have some understanding of another's visual perception while or after following gaze. Chimpanzees, rhesus macaques, and orang-utans, *Pongo pygmaeus*, can judge whether another individual at a different location can see a food item they see (Hare et al. 2000; Flombaum and Santos 2005; Shillito et al. 2005), which indicates an appreciation of the other's visual perspective. Great apes, like humans, look back and forth between the experimenter's face and the experimenter's gaze direction (Scaife and Bruner 1975; Call et al. 1998; Bräuer et al. 2005; see also Scerif et al. 2004). This check-looking behaviour has been proposed to indicate an individual's understanding that another is looking at something (Scaife and Bruner 1975; but see Corkum and Moore 1995). In addition, chimpanzees and ravens follow the gaze of a human experimenter around physical barriers (Tomasello et al. 1999; Bugnyar et al. 2004), even when temporarily distracted by a conspicuous object in the line of sight (Tomasello et al. 1999). Thus, instead of merely turning their head in the correct direction, the animals relocate themselves to a position from where they can see what the other is seeing (Tomasello et al. 2005). These results suggest that chimpanzees and ravens can determine the location of the target to which another individual is attending and that their gaze following is more than a mere co-orienting reflex (Tomasello et al. 1999; Bugnyar et al. 2004). Although these results shed light on individuals' knowledge of the location of the targets others are looking at, it remains unclear whether and how the animals' gaze following is also influenced by the knowledge, intentions or emotions of another.

Primates are experts in recognizing facial expressions (Nahm et al. 1997; Gauthier and Logothetis 2000; Parr et al. 2000; Gothard et al. 2004) and in determining the direction another individual is looking (Keating and Keating 1982; Perrett and Mistlin 1991). Social interactions are a prominent part of primate life (Tomasello and Call 1997). The social context in which an individual shifts its gaze may therefore provide a naturalistic way to study gaze following and the flexibility with which this behaviour may be employed. In the present study, a human experimenter displayed social facial expressions during gaze-shifts, thereby mimicking a response to a social event. We assumed that animals would perceive facial expressions displayed by a human experimenter similarly to conspecific facial expressions (Paukner et al. 2007). We compared responses to gaze-shifts with a social expression to gaze-shifts with a neutral facial expression. By employing meaningful social expressions we took advantage of their important role in social interactions (Cheney and Seyfarth 1990) and consequent likely salience for the subjects. We also investigated the response to a novel facial expression not displayed in macaques to control for the possibility that social expressions were more salient than a neutral facial signal because they involved more muscular activity, rather than because they mimicked a species-specific signal. We predicted that long-tailed macaques, like other primates, would follow the gaze of an experimenter. Furthermore, we predicted that gaze-shifts accompanied by a socially meaningful facial expression would elicit a stronger gaze-following response than a neutral gaze-shift or a meaningless face if the animals took into account the transmitted information of the facial expression.

METHODS

Subjects

Subjects were 13 captive adult long-tailed macaques housed at the Ethology Station of Utrecht University. All subjects belonged to the same stable social group of 19 animals living in an 18-m^3 inside enclosure with access to a 160-m^3 outside compound. They were fed commercially available monkey chow daily and received additional fruits and vegetables weekly. Water was available ad libitum throughout. One animal (Pu) died of natural causes before starting experiment 3. The dominance hierarchy was established before experiments began using ad libitum observations of a unidirectional submissive behaviour (i.e. the silent Bare Teeth display). Subsequently the linearity-index *h*' was calculated using

Table 1. The study group, excluding infants. M = Male, F = Female. Me and Ic stopped entering the test cage after completing the first experiment. Pu died from natural causes before the start of the experiment involving the meaningless face. Ch (rank 12) did not participate in the experiments as she became highly stressed during pilot separations.

Subject	Sex	Age (years)	Rank/ Category
Cl	M	9	1 / high
Er	F	18	2 / high
Vi	M	6	3 / high
Li	F	7	4 / high
Co	F	9	5 / mid
Ic	F	10	6 / mid
Su	F	10	7 / mid
Ro	F	22	8 / mid
Se	F	11	9 / low
Ni	F	7	10 / low
Lo	F	8	11 / low
Me	F	7	13 / low
Pu	F	10	14 / low

the program MatMan 1.1 (Noldus Technology; de Vries 1998). This resulted in a linear hierarchy ($h' = 0.59$, directional consistency index = 0.92, $P < 0.001$). Since hierarchies in this species generally remain stable throughout prolonged periods (Veenema et al. 1997), we assumed that the ranks we assigned beforehand did not change during the course of the three experiments. We divided the group into low-, mid- and high-ranking individuals (Table 1). Subjects had participated in earlier studies on mate choice (Nikitopoulos et al. 2005) and neophobia (unpublished data) but had no experience with tasks similar to ours. Experiments were approved by the Ethical Committee of Utrecht University (DEC 04/197).

Test Procedure

Testing took place in a cage (1.00 x 0.90 x 1.00 m, height x width x depth) connected to the animals' inside home enclosure by a tunnel. Sliding doors were used to separate the subjects from the group. The test cage was elevated 1.80 m above the ground. Between the top of the cage and the ceiling there was a space of 1.40 m. During testing the experimenter was on eye level with the subject. Animals were trained to voluntarily separate from the group and enter the test cage. In the test cage the animals had no visual access to the social group, but limited auditory contact was possible. Two subjects (Ro, Ic) had infants, which they took with them into the test cage in most of the test sessions. The infants did not appear to affect the subjects' performance.

Experiment 1: Gaze Following with Neutral Facial Expression

Thirteen subjects were tested individually for their ability to follow the gaze of a human experimenter with a neutral facial expression using a design similar to that employed with apes (Call et al. 1998; Bräuer et al. 2005). We compared reactions in two different conditions. In the gaze-shift condition the experimenter suddenly shifted her gaze to a predefined location on the ceiling. In the look-straight condition she kept on looking at the subject's chest. The look was directed at the chest since long-tailed macaques can perceive direct eye contact as a threat. Each subject received six trials, each lasting 10 s in both conditions, spread out over two sessions in a 3-week period. The order of conditions was pseudo-randomized with the restriction that one condition (either gaze shift or look-straight) could be administered only twice in succession. One-half of the subjects received the gaze-shift condition as first trial, the other individuals the look-straight condition.

After separation from the group the experimenter captured the attention of the animal by feeding small treats (fruit or bread) and talking quietly to the animal. A trial would start only after the animal was attending to the experimenter. In the gaze-shift condition, the experimenter began a trial by shifting her gaze to a predefined location on the ceiling outside the cage while still offering a treat out of reach of the animal. In the look-straight condition, the experimenter announced the start of a trial to give a clear onset ('Start'). Since the experimenter was talking to the subject continuously between trials, we do not expect the acoustic signal ('Start'), uttered in the same soft tone of voice, to have influenced the subject's behaviour. A second experimenter videotaped the behaviour of the subject with a Sony Hi8 Handycam CCDTR825E and timed the trials. After 10 s, the completion of the trial was indicated by the same experimenter ('Stop'). In both conditions the subjects received the food item that the first experimenter had offered during the trial. After reestablishment of the subject's attention the next trial started.

Experiment 2: Gaze Following with Social Facial Expression

We tested 11 animals in the experiment involving social facial expressions. Two animals that had participated in the previous experiment did not complete all sessions of this experiment because they were unwilling to enter the test cage. They were excluded from the analysis. There were three experimental conditions and one control condition. In all conditions the experimenter shifted her gaze to the same predefined location on the ceiling as in experiment 1. During experimental trials the experimenter displayed one of three facial expressions while looking up (Fig. 1), whereas the control condition was a gaze-shift at the ceiling with a neutral facial expression. The distinct experimental conditions consisted of three 'meaningful' faces, that is, part of the long-tailed macaques' facial repertoire (Fig. 1). The expressions we used cover several domains of social life in macaques, namely aggression (Open Mouth), submission (Bare Teeth) and affiliation (Lip Smack) (Angst 1974). Two of these facial expressions are important for the establishment and maintenance of the dominance hierarchy (Open Mouth and Bare Teeth).

The general procedure was the same as that in experiment 1 except for the intertrial intervals of at least 30 s in which the subject could eat the reward. Each subject was tested individually in six sessions spread out over a 7-month period. The sequence of the three meaningful facial expressions as well as the order of conditions was pseudo-randomized and counterbalanced across the animals. During a single session only one of the three facial expressions was tested in two experimental and two neutral-face control trials. This design was chosen to prevent confusion of the subjects due to the experimenter directing facial expressions with different social meanings to the ceiling within one single session.

Figure 1. Emotional facial expressions. From left to right: Bare Teeth, the signal for fear and submission is shown from subordinate to dominant animals in both provoked and unprovoked situations. The Lip Smack shows affiliation between interaction partners. In contrast, the Open Mouth is mostly used in aggressive encounters to intimidate the opponent. Pilot experiments revealed that the animals would respond in a comparable way to the facial expressions when displayed by a human experimenter as they would to a conspecific.

Experiment 3: Gaze Following with Meaningless Facial Expression

To control for the possible effect of any extraordinary human face involving random contractions of the facial muscles we subsequently tested the animals' reaction to a fourth facial expression. We used a facial expression that was not part of the monkeys' or the human facial repertoire and thus most likely did not convey any meaning. Ten subjects received a total of four control and four experimental trials in a pseudo-randomized order spread out over two sessions. The procedure was otherwise the same as that for experiment 2.

Facial Expressions

Four facial expressions were displayed by the experimenter during the gaze-shift in experimental trials. The first three facial expressions are part of the animals' behavioural repertoire (Angst 1974) whereas the fourth was artificial and created by us for the purpose of this study. Facial expressions in long-tailed macaques are very characteristic and stereotyped (Angst 1974, Fig. 1). We assumed that animals would perceive facial expressions displayed by a human experimenter similarly to those displayed by conspecifics. It has been shown that monkeys look at human and conspecific faces in a similar way when a facial expression is displayed (Nahm et al. 1997). In addition, during pilot experiments we had observed that the animals would respond appropriately to species-specific facial expressions when performed by a human experimenter. In general, animals responded to human lip smacking with affiliative behaviour (lip smacking or lifting of the eyebrows), whereas human Open Mouth threats resulted in escape and gaze avoidance or return of the threat, depending on the individual. Baring teeth to a threatening individual would often result in ceasing of the threat.

(1) Bare Teeth: Eyebrows are lifted and lips are pulled up, so that teeth and gums are visible. The Bare Teeth display is a submissive and fearful behaviour exclusively shown by a subordinate to a dominant animal, even when not provoked.
(2) Lip Smack: The mouth is opened fast and repeatedly while looking at the interaction partner with raised eyebrows. The signal is mostly used in a friendly, affiliative context.
(3) Open Mouth: Eyes are wide open, sometimes with lifted eyebrows, and fixed at interaction partner. The mouth is open with lips covering the teeth. This display is used in aggressive encounters to threaten the interaction partner.
(4) Meaningless Face: Cheeks are blown up in an extreme way. The mouth is closed. To our knowledge, this expression is meaningless to macaques and humans. This facial expression was matched with the other facial expressions in

the degree and area of facial movement involved, since it involves movement of the mouth that also affects the area around the eyes.

Data Analysis

Two observers, blind to the experimental conditions, recorded the total number of looks up and down per trial. If a subject ceased its earlier gaze up, returned to the face of the experimenter and gazed up again immediately, we defined this as a check-look. All occurrences within every trial were scored. Because long-tailed macaques, like various other primates, can monitor their surroundings by inconspicuous glancing (Emery 2000), we also included subtle looks or eye-only looks. Therefore, to record the looks in a systematic way, we defined a look up as a deviation of head and/or eyes with an angle of at least 45° above an estimated horizontal line between the eyes of the experimenter and the subject. The minimum duration of a look was set at 20 ms. In few trials, some of the subjects climbed up to the cage ceiling (perhaps to get a better view of the experimenter's face). While climbing, they mostly looked up straight in the direction of climbing. In those cases it was difficult to distinguish whether the gaze was due to the direction of movement or to the cue provided by the experimenter. We therefore defined a relevant look as a deviation of head and/or eyes towards the spot the experimenter was focusing compared to the direction the individual was climbing. As a measure of general gazing activity the number of looks down was recorded. We scored a look down as any deviation downwards from (1) the estimated horizontal line between the experimenter's and the subject's eyes or (2) the estimated line between the subject's eye and the food the experimenter was presenting, whichever was lowest. In addition, the scratching rate, defined as the number of quick repeated movements of hand and/or foot through the fur per trial, was scored because it indicates current levels of stress and anxiety (Schino et al. 1988; Pavani et al. 1991; Maestripieri et al. 1992). Interobserver reliability was high with 83% agreement on the number of looks per trial and a Cohen's kappa of 0.75 ($P < 0.001$).

Data were analysed with SPSS 12.1. Where data met the requirements of parametric tests paired t tests and repeated-measures ANOVA were applied; otherwise exact Wilcoxon signed-ranks test and exact Friedman's ANOVA were used (Mundry and Fischer 1998). In experiment 2 Bonferroni corrections were applied to the pairwise comparisons of the number of looks, and thus P values below 0.017 should be considered statistically significant. In the same experiment, one-tailed tests were used for the pairwise comparison of the different facial expressions with the respective controls and with the average control because we had a clear prior prediction, whereas all other tests were two tailed.

RESULTS

Experiment 1: Monkeys follow the gaze of a human experimenter

Subjects directed significantly more looks up during the gaze-shift condition than during the look-straight condition (Fig. 2A; Paired t test: $t_{12} = 8.78$, $P < 0.001$). The animals followed the experimenter's gaze direction (i.e. looked up) in 90% of the gaze-shift trials, compared to 40% of the control trials. The response to gaze-shifts did not differ significantly between the two sessions (Paired t test: $t_{12} = 1.83$, $P > 0.2$), providing no evidence that animals habituated to the experimental procedure. In addition, there were more 'check-looks' (for definition see Material & Methods) in the gaze-shift condition than in the look-straight condition (Fig. 2B; Exact Wilcoxon signed-rank test: $T = 0$, $N = 13$, $P < 0.01$). Eight of 13 individuals engaged in check-looking during at least one gaze-shift trial.

Experiment 2: Gaze following is modulated by facial expression

Subjects looked up significantly more often when the experimenter displayed a facial expression than when she looked up with a neutral face (Repeated Measures ANOVA: $F_{1,10} = 6.80$, $P < 0.03$). Gaze following was significantly more frequent in response to a signal of fear/submission (Bare Teeth: Fig. 3; Paired t test: $t_{10} = 2.54$, $P = 0.014$, one-tailed), while gaze-shifts with two other facial expressions did not have a significant effect (Fig. 1, Open Mouth and Lip Smacking). The response to Bare Teeth was also significantly greater than the average response during the combined controls (Paired t test: $t_{10} = 2.57$, $P = 0.014$, one-tailed, Average Control: $\overline{X} \pm SE = 1.09 \pm 0.13$, Bare Teeth: $\overline{X} \pm SE = 1.38 \pm 0.16$), suggesting that

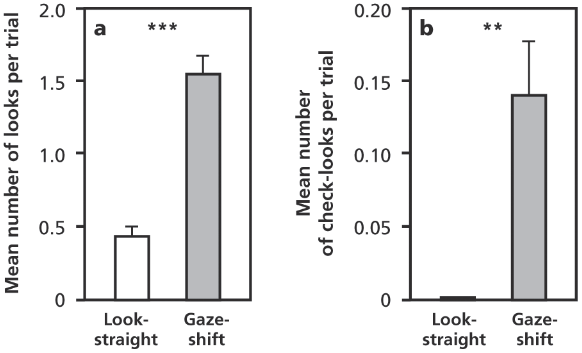

Figure 2. (a) Mean number of looks up per trial (±SE) in the look-straight and the gaze-shift condition. Subjects followed gaze significantly more often when the experimenter shifted her gaze to the ceiling compared to when she looked straight ahead (*** indicates $P < 0.001$). (b) Mean number of check-looks per trial (±SE) in the look-straight and the gaze-shift condition. Subjects performed significantly more check-looks in the gaze-shift than in the look-straight condition, that is, they directed significantly more looks back at the experimenter after having followed her gaze and subsequently looked up again (** indicates $P < 0.01$).

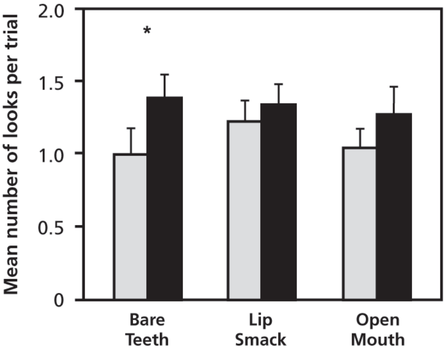

Figure 3. Mean number of looks up per trial with (±SE) when the experimenter shifted her gaze with a meaningful or a neutral facial expression. Black bars illustrate the response to a gaze shift accompanied with one of the facial expressions, grey bars indicate the levels of response to the neutral face. The subjects directed significantly more looks up when the experimenter's gaze shift was accompanied by a social facial expression. Post-hoc analysis revealed that the gaze following response to one of the expressions was significantly different from its respective control, namely the Bare Teeth display, which communicates fear and submission of the signaller (* indicates $P < 0.02$).

the effect was not due to an especially low response in the Bare Teeth control trials. Subjects had a tendency to check-look more often during gaze-shifts accompanied by a social facial expression than when the experimenter looked up with a neutral face (Exact Wilcoxon signed-ranks test: $T = 0$, $N = 11$, $P = 0.12$). There was no decrease in response to the neutral facial expression between the sessions (Repeated Measures ANOVA, $F_{5,50} = 0.841$, $P > 0.5$). The number of looks down, recorded as a measure of general gazing activity, did not differ significantly between a gaze-shift accompanied by a facial expression compared to a neutral face (Repeated Measures ANOVA: $F_{1,10} = 0.03$, $P > 0.8$), nor did it significantly differ between the three different facial expressions (Repeated Measures ANOVA: $F_{2,20} = 0.48$, $P > 0.6$). We did not find significant differences in scratching rate between any of the social versus neutral faces (Exact Friedman's ANOVA: $\chi^2_5 = 3.81$, $P > 0.7$).

Experiment 3: No differential responsiveness to neutral and meaningless facial expressions

There was no significant difference between the number of looks up in response to the gaze-shift accompanied by a meaningless or a neutral facial expression (Fig. 4; $t_9 = 1.00$, $P > 0.3$). In addition, there was no difference in response to the neutral facial expression between the two sessions (Paired t test: $t_9 = 0.017$, $P > 0.8$).

Change in responsiveness between experiments

Over the course of the experiments there was a change in response towards the neutral gaze-shift (Repeated Measures ANOVA: $F_{2,18} = 22.40$, $P < 0.001$).

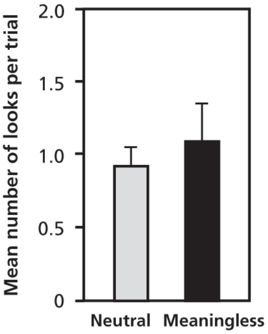

Figure 4. Mean number of looks per trial (±SE) when the experimenter displayed a neutral versus a meaningless facial expression. No significant difference was found between these conditions.

Pairwise comparisons revealed that this was due to a decrease in response to the neutral gaze-shift between experiments 1 and 2 ($P < 0.01$). However, and of particular relevance to the interpretation of the results, there was no decrease in the number of looks up between experiments 2 and 3 ($P > 0.5$).

DISCUSSION

The monkeys in this study followed the gaze of a human experimenter with frequent check-looks, compared to a control condition in which there was no gaze-shift. In addition, the animals showed stronger gaze-following responses when the human's gaze-shift was accompanied by a social facial expression. Gaze following was significantly more frequent in response to a signal of fear and submission than to a neutral facial expression, whereas gaze-shifts accompanied by two other social expressions or a meaningless facial expression did not have this effect. Thus, gaze following in monkeys was modulated by the outward expression of the emotional state of the signalling individual. Our findings suggest that gaze following is flexibly employed according to the facial expression that is observed.

Additionally, we found that the monkeys frequently looked back at the signalling individual and looked up again (check-looks) during experimenter's gaze-shifts, thereby confirming earlier results on the presence of check-looking in human infants and some nonhuman primate species (Scaife and Bruner 1975; Call et al. 1998; Scerif et al. 2004; Bräuer et al. 2005). Moreover, check-looking responses seemed to be stronger during gaze-shifts accompanied with facial expressions. Check-looking has been proposed to indicate that the gaze-following individual understands that the signaller is seeing something different from itself (Scaife and Bruner 1975; Butterworth and Cochran 1980). Although there are alternative explanations for this behaviour (for instance, a repeatedly triggered gaze-following response) (e.g. Corkum and Moore 1995), it suggests that the gaze-following individual checks back on the demonstrator because it fails to see what the other is seeing (Scaife and Bruner 1975; Butterworth and Cochran 1980).

The effect of a social facial expression on gaze following indicates that the animals may have responded based on the understanding that the experimenter was reacting to something socially relevant and meaningful that the subjects could not see themselves. However, the greater responsiveness to the experimenter's gaze-shift when accompanied by a facial expression (displayed by a human) could also be explained by an elevated general level of attention or arousal. That is, the level of attention or arousal caused by the movement involved in displaying Bare Teeth or the emotional content of this facial expression might have been greater than that for the other facial expressions. However, there are several arguments against this interpretation. First, although pilot studies revealed that monkeys respond appropriately to a human displaying species-specific facial expressions it remains possible that the animals are not able to read the meaning of the facial expression and respond only to the facial movement involved. In that case, Lip Smacking may be expected to elicit the strongest response since it involves repeated lip movements and sounds. We found no indication that this was the case. Second, assuming that the animals recognize the meaning of the facial expression, the highest level of emotional arousal would be expected in response to the aggressive signal (Open Mouth display), which often precedes a physical attack. Although the signal is not directed at the subject, it still indicates a physical conflict in which the subject may become involved. Contrary to this expectation, the gaze-following response to the Open Mouth display was the lowest of all three social expressions. Third, an elevated emotional arousal may result in increased scanning behaviour. As a measure of general gazing and scanning activity we counted the looks down during experimental and control conditions. The number of looks down did not differ significantly between conditions. Moreover, emotional arousal will likely result in elevated anxiety, which can be measured by scratching rates (Pavani et al. 1991; Maestripieri et al. 1992). We found no evidence for differences in anxiety between conditions because scratching rates did not differ between conditions or facial expressions. Fourth, the animals did not respond more strongly to the meaningless facial expression than to the neutral face. Although conclusions drawn from this comparison should be treated with caution because of the low statistical power, the result suggests that the animals do not respond to a face with a random muscular contraction as strongly as they do to a face that mimics a facial expression with which they are familiar and which in this case signals fear and submission of the sender. Together, these arguments suggest that elevated general arousal is unlikely to cause the modulating effect of the Bare Teeth display on gaze-following responses.

Our results conflict with findings in human infants (Flom and Pick 2005). Seven-month old infants followed gaze less when a facial expression conveying a certain emotion (such as happy or sad) was displayed: infants seemed to pay more attention to the facial expression than to the gazing direction, which the authors interpreted as the infants' inability to understand the referential nature of the mothers' signal (Flom and Pick 2005). Studies on human adults are consistent with our results because adults' responses to averted gazes are stronger with accompanying fearful or angry faces than neutral faces (Holmes et al. 2006; Putman et al. 2006). Yet the response of the macaques in our study contrasts with other findings in macaques that did not show stronger gaze-following responses to displays of affiliation and greeting than to a neutral facial expression (Paukner et al. 2007). This difference may be due to the wider range of emotional facial expressions we employed in this study, including expressions that communicate fear and threat. Our results may suggest that the macaques were responding to the significance of a social event that the experimenter was signalling, in particular during the Bare Teeth display. In interactions with conspecifics, only fearful and threatening events or dominant individuals evoke this display. It seems plausible that the Bare Teeth signal, which indicates a potentially threatening stimulus, elicits stronger responses than affiliative signals, which do not indicate a potential threat (Parr and Hopkins 2000).

Surprising, however, was the finding that the Open Mouth display did not elicit an increase in the gaze-following response because this signal can also indicate a social event that may affect the subject. Signals communicating fear may be more important to an individual than aggressive displays since fear clearly and unmistakably communicates a threat (e.g. the presence of a dominant conspecific) in close proximity. Accordingly, fear in others is a highly salient stimulus facilitating acquisition of knowledge about fearful objects (Olsson and Phelps 2007). A threatening display on the other hand may not directly concern the gaze-following individual itself because it is obviously meant for someone else, most likely a subordinate individual. Therefore the message of this signal may be more ambiguous. Alternatively, individuals of different ranks might be affected differently by facial expressions of aggression and submission, which are used in the establishment and maintenance of the dominance hierarchy. To address this we conducted an exploratory analysis by examining the effect of social dominance rank (categories: high - mid - low; Table 1) on gaze following. Although the small number of subjects limited the possibilities for statistical analysis, we did note apparent differences in responsiveness to gaze-shift with expression according to subject's social rank, particularly in the Open Mouth condition, where high-ranking animals were least responsive and mid-ranking animals most responsive. For high-ranking individuals it may not be relevant whether and to whom subordinate individuals (or individuals outside the hierarchy such as a human) direct an aggressive display. It may, however, be of more interest to mid- or low-ranking individuals because for instance the approach of a threatening animal could have severe consequences for them. The differential response to an agonistic facial expression other than the Bare Teeth display is in line with the recent finding that gaze following is dependent on the social rank of the gazing individual (Shepherd et al. 2006) and moreover strengthens the interpretation that gaze following is flexible and is more than a simple reflex. Further research on social facial expressions, the identity of the signaller and its relationships to the observing individual is required to better understand the influence of rank on the response to a gaze-shift accompanied by facial expressions.

Our findings suggest that long-tailed macaques exhibit gaze following in a flexible way. Two possible explanations may account for this: (1) the behaviour may be based on a specific arousal- or attention-based mechanism that enhances gaze-following responses only during the most salient facial expressions (one of which may be Bare Teeth) but does not affect our measures of general visual scanning or anxiety or (2) the behaviour may be based on a voluntary response. The second explanation implies that the monkeys took into account the social event indicated by the experimenter's facial expressions and that gaze-following responses were guided by the knowledge that the other individual was attending to a feared stimulus. Evidence is emerging that monkeys know more about the perceptions of others than previously thought, such as the significance of the eyes in the process of seeing (Perrett and Mistlin 1991; Ferrari et al. 2000) or whether another individual can see or hear them (Flombaum and Santos 2005; Santos et al. 2006). Adding social facial expressions to the study of gaze following may shed light on how animals respond to gazes that convey a meaning, that is, that indicate social events, highly relevant in animal groups with complex relationships. The question of whether gaze following in monkeys is based on a mentalistic understanding of the observing animal about the other's visual target still remains open. None the less, we show that gaze following can be adjusted to the social context in which the gaze-shift takes place. This suggests that gaze following in monkeys is flexibly employed, which, combined with other recent findings, indicates that monkeys' abilities regarding social cognition have been underestimated.

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Long-tailed macaques, *Macaca fascicularis*, follow conspecific gaze to a hidden location

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ABSTRACT

Gaze following, the ability to track the direction of another's gaze, is thought to be an important component of human and animal social cognition. Several animal species attend to the gaze direction of others, but it remains unclear whether the behaviour is based on a simple co-orientation mechanism or on a more sophisticated perception of the other's visual behaviour. The capacity to follow another's gaze to a location hidden behind a physical obstacle has been argued to indicate refined skills in determining the exact direction of the other's gaze ('geometrical gaze following') and a representation of space outside one's own visual field. This capacity has been shown in human infants, great apes, and ravens, *Corvus corax*. We tested whether long-tailed macaques, *Macaca fascicularis*, follow a conspecific's gaze to a hidden location. When a conspecific demonstrator gazed at a mirror hidden behind a barrier, subjects relocated to a position where they could see the mirror location and directed significantly more focussed looks behind the barrier than in a situation where there was no conspicuous gaze cue by the demonstrator. Thus long-tailed macaques follow gaze to a hidden location, suggesting that this capacity may be widespread across the non-human primates, rather than restricted to the great apes.

INTRODUCTION

Gaze following is the capacity to track the looking direction of other individuals to a different location (Scaife and Bruner 1975). This capacity has received considerable interest, both in animal and human behaviour research (Gomez 2005), as it is considered to be important in processes such as social learning and language acquisition (Baldwin and Moses 1994). Moreover, the ability to follow another individual's gaze may form the basis of cognitive capacities that relate to mental state understanding (Baron-Cohen 1995). In human infants, gaze following develops from a general sensitivity to eyes an eye-direction to the cognitively more complex knowledge that the other is seeing something when shifting gaze (e.g. D'Entremont et al. 2007). These latter stages are proposed to be essential in the development of a Theory of Mind (Baron-Cohen 1995), i.e. the ability to understand that other individuals have emotions, thoughts and intentions different to one's own. In non-human animals, there is growing evidence for gaze following in a wide range of species, such as primates, birds, marine mammals and some domesticated species (Miklosi et al. 1998; Emery 2000; Bugnyar et al. 2004; Kaminski et al. 2005; Pack and Herman 2007). Functionally, attending to another individual's gazing direction is important for any group-living animal, since it can provide information on social events, predators or food locations (e.g. Tomasello et al. 1998). However, for many species little is known concerning the cognitive mechanisms underlying gaze following.

Butterworth and Jarrett (1991) proposed three consecutive mechanisms in the development of gaze following in human infants. First, on the most basic level, the child responds to the approximate direction of the other's look, without tracking the line of sight to a specific target. Second, with the 'geometrical' mechanism the child tracks an imaginary line of sight to a specific object within his/her field of vision, past distracting objects. On the third level, with the 'representational' mechanism the child follows gaze to a location outside his/her field of vision (for instance behind his/herself). Butterworth and Jarrett (1991) use 'representational' in the sense of spatial representations, not in the sense of mentalistic understanding of another's visual behaviour.

A task proposed to indicate advanced gaze following capacities tests whether animals can track another's looking direction to a location hidden behind a physical obstacle (Tomasello et al. 1999; Bugnyar et al. 2004; Bräuer et al. 2005). In this task an experimenter shifts gaze to a location behind an obstacle that obstructs the subject's view of the location at which the gaze is focussed. If merely responding to the direction of the other's gaze, the observing individual will follow gaze and co-orient in approximately the same direction as the experimenter.

Alternatively, the observing animal may recognize that the experimenter's gaze is directed to a location behind the barrier (Tomasello et al. 1999; 2005) and will subsequently attempt to see what the other is looking at. To achieve this, the animal has to extrapolate gaze in a geometrical way. In addition, it must have some representation of the space behind the barrier (sensu Butterworth and Jarrett 1991) that it cannot visually access from its current perspective.

Human infants (aged 12-18 months), great apes and ravens will respond to an experimenter's gaze to a hidden location behind a barrier by relocating themselves to a position where they can see this location (Tomasello et al. 1999; Bugnyar et al. 2004; Moll and Tomasello 2004; Bräuer et al. 2005). Whether other species can follow gaze to a hidden location has not yet been shown. This raises the possibility that within the non-human primates this capacity may be restricted to the great apes, and thus an analysis of gaze following capabilities in monkeys will contribute to the understanding of the evolution of such capacities. We investigated whether long-tailed macaques, *Macaca fascicularis*, are able to track a conspecific's looking direction to a hidden location, as this could indicate refined perception of the other's visual behaviour. In the present study, attention of a conspecific individual (demonstrator) was suddenly drawn to a location not visible to the subject, by the appearance of a mirror (see Tomasello et al. 1999; Bräuer et al. 2005, for similar methodologies). We predicted that if the subject was able to track the conspecific's gaze direction to a location outside its own visual field, hidden behind the barrier, it would move to a suitable viewing area and actively orient to see what the other was looking at.

METHODS

Subjects

Subjects were 13 adult long-tailed macaques (6 males, 7 females; mean age: 8.7 years) from a single social group of 27 animals at the macaque colony of Utrecht University. Animals were housed in an indoor enclosure (235 m3) with access to an outdoor compound (800 m3). Water was available ad libitum throughout. The animals received commercially available monkey chow and grains daily and fruit twice a week. Prior to testing, the dominance hierarchy was determined by analysing submissive and aggressive behaviours that were observed ad libitum (linearity index: $h' = 0.45$, $P < 0.001$). The animals did not have previous experience with cognitive tests or other experiments.

Apparatus

A wooden barrier (h: 128 x w: 52 cm) attached vertically to the demonstrator's compartment (Fig. 1) created an area that only the demonstrator could see when the demonstrator and subject were at their starting locations. To attract the demonstrator's attention towards this area, we designed an experimental device that could be remotely controlled and would elicit a response from the demonstrator towards the location hidden for the subject. On a tray we fixed a mirror (15 cm x 15 cm) alongside a wood panel of the same size (Fig. 1: 'P' & 'M'). The hinged wood panel and mirror could be independently and silently pulled upright by concealed nylon strings from an adjacent room. When flat, both looked similar and did not attract the attention of the animals, since the reflecting side of the mirror was not visible from either the demonstrator's or subject's position. However, when pulled up, we expected only the mirror to elicit a strong gazing response from the demonstrator (e.g. Anderson and Roeder 1989).

Experimental procedure

Animals were tested in observer-demonstrator pairs, with the demonstrator's attention drawn to an area behind a barrier that was visually inaccessible from the starting position of the observing subject (Fig. 1). Subsequently it was recorded

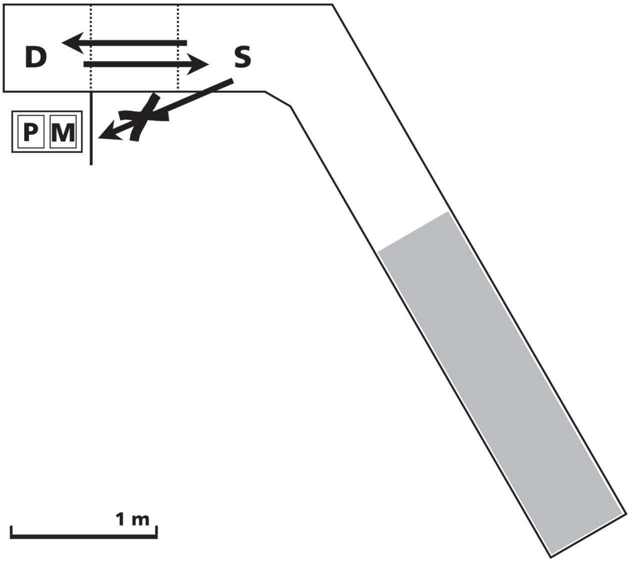

Figure 1. Plan of the experimental cage, to scale (bar represents 1 m). In the experimental condition, the demonstrator's (D) attention is drawn towards a mirror (M) pulled to an upright position. In the control condition an unreflective wood panel (P) is raised. The demonstrator and the subject (S) can see each other; however the subject cannot see the area in front of the demonstrator from its starting position. The area from which the subject has visual access to the location behind the barrier is indicated in grey. Arrows indicate visual (in-) accessibility.

whether the subject relocated to a designated area (Fig. 1), from where it could visually access the target, the hidden location. Prior to the experiment, animals were trained to separate from the group voluntarily in the test cage connected to their home cage, where they had no visual access to the group. On test days, selected pairs were directed to the positions from which they could see each other through transparent slides (Fig. 1). The demonstrator was restricted to one compartment, whereas the subject was free to move through several compartments of the test cage. During separation-training we had observed that subjects would move around the test cage for a certain amount of time, but would eventually settle down nearby the demonstrator. A trial only began if the subject had settled at this position for at least two minutes. All animals had experience with the barrier and the inactive experimental device from earlier separation sessions during training, when the experimental device was located near the test cage, but never hidden behind the barrier. On test days the experimental device was located behind the barrier before the animals entered. A trial would start by pulling up the piece of wood (Control Condition) or the mirror (Experimental Condition). After five minutes a trial would end by lowering the raised wooden panel or mirror. After at least one minute, and when the subject had moved back to the starting position, the next trial began. Each test consisted of three consecutive trials, with an identical sequence for all subjects (Control – Experimental – Control) and was conducted only once per subject.

Experimental pairs (Table 1) were formed on the basis of their relatedness and their likeliness to associate with each other in the home cage. Thereby we attempted to reduce the chance that animals would not pay attention to each other during testing (Watts 1998 describes an association between relationship quality and attention) and to increase the likelihood that they would be at ease near each other during testing. Roles of demonstrator and subject were assigned randomly to the pairs. After having tested all pairs, the roles of subject and demonstrator were reversed. We balanced for dominance direction so that the demonstrator was the more dominant individual on half of the first trials with each pair. Since there was a considerable delay (at least three weeks) between the first and the second test series, we did not expect that experience with the role as either demonstrator or subject would influence responses when tested in the other role (Povinelli et al. 1992).

Some demonstrator animals (Be, Na, Va) showed a startled response to the movement of the piece of wood (i.e. they pulled back their head and/or body with a quick movement) during the first control trial and consequently looked into that direction for a certain period. Although the responses of these demonstrators to the piece of wood were far less obvious than the responses

Table 1. Demonstrator, subject, focussed looks of subject behind the barrier and social signals by demonstrator. Experimental pairs that participated in this study (M = Male, F = Female; age in years). Individuals that directed focussed looks around the barrier, e = during the experimental condition, $c_{1,2}$ = during the first or second control condition. Social signals are: li = lifting of the eyebrows and ls = lip-smacking.

Demonstrator	Subject (sex / age in yrs)	Focussed look behind barrier	Social signals by demonstrator during experimental condition
Sq	Eu (F / 6)	e	2 x li
Hi	Am (M / 7)	e	3 x li, 1 x ls
Mo	Be (F / 3)	e, c_2	3 x li
Eu	Ge (M / 26)	e	2 x li
Eu	Sq (M /11)	e, c_2	-
Am	Hi (M / 8)	c_1	5 x li
St	Xu (M / 4)	-	-
Be	Mo (M / 5)	-	3 x li
Na	To (F / 9)	-	4 x li, 1 x ls
Ch	In (F / 10)	-	-
Xu	St (F / 10)	-	8 x li, 2 x ls
Va	Ba (F / 5)	-	6 x li, 2 x ls
Ba	Va (F / 9)	-	8 x li

directed at the mirror, we excluded the data collected for both demonstrator and subject during the first controls of these demonstrators from the analyses. The mirror evoked the expected response in most of the animals (see Results). Trials were recorded simultaneously with four cameras placed at different angles and projected on a split screen.

Data analysis

An observer, unfamiliar with the theoretical background and blind to the experimental conditions, analysed the videotapes. The observer noted the gazing behaviour of the demonstrators and gazing and body movement of the subjects. Body movement was measured as the movement between different pre-defined compartments (e.g. starting position) within the test-cage. A look was defined as change of gazing direction in one of several predefined directions, for a minimum duration of 1 second. We counted looks in several different directions: (1) at demonstrator/subject, i.e. the look was directed at the interaction partner. The animals could see each other only when the subject was in the starting position. (2) Towards the central room, i.e. the demonstrator/subject looked towards the area outside the experimental cage. (3) Up/down, i.e. the demonstrator/subject looked 45° above or below the horizontal. (4) Back, i.e. face and/or body oriented towards the back of the cage. (5) Sideways, i.e. the look was directed along the test cage, involving a head or body-turn of the demonstrator or subject. Subjects' looks towards the central room (2) and to the subject's left (5) from the starting position were combined for one part of the analysis; we refer to it as looks to the far left. We also counted (6) demonstrator looks directed at the wooden panel/mirror.

The critical behavioural measures were the looks from the area where the hidden location could be seen (shaded in Fig. 1). We assumed that subjects that made an attempt to see what was hidden behind the barrier should unmistakably focus on the target area, i.e. should actively position themselves and move to view the location and potential target of the other's gaze. We thus distinguished between general looks towards the barrier and focussed looks behind the barrier: general looks towards barrier were defined as looks towards the area of the barrier and the back of the barrier, but without focus at a certain location and with subjects passively sitting in one location (measure 7), and focussed looks behind the barrier were scored when the subject showed an active body posture, i.e. standing or holding bars, typically with the face pressed against bars of the cage, head and/or body moved while gaze maintained fixed gaze on the target location behind the barrier (measure 8).

To assess inter-observer-reliability, 25% of the trials were scored by a second coder. Inter-observer reliability based on all measures was good with Cohen's kappa = 0.7 ($P < 0.001$), and inter-observer agreement above 70% for all measures. Data were analysed in SPSS 12.1. Control trials before and after the experimental trial did not significantly differ in any of the recorded variables, so we calculated an average control response, to which the behaviour in the experimental condition was compared, with the exception of those controls in which the demonstrators were startled by the wooden panel's movement and looked multiple times at the panel. In these cases only the other control was used for analysis. The variable 'focussed looks behind barrier' was log transformed in order to meet normality assumptions for parametric analyses. Tests are two-tailed, except for the case of the measure 'focussed looks behind the barrier' where a one-tailed test was used, since we had an a priori directional prediction.

RESULTS

Subjects

Ten of 13 animals relocated to the designated area during at least one of the trials (7 in the control trials and 8 in the experimental trials). Importantly, five animals directed focussed looks behind the barrier only during the mirror trial or more often during the mirror trial than the control trials, whereas one animal did so more often during a control trial than the mirror trial (Table 1). Consequently,

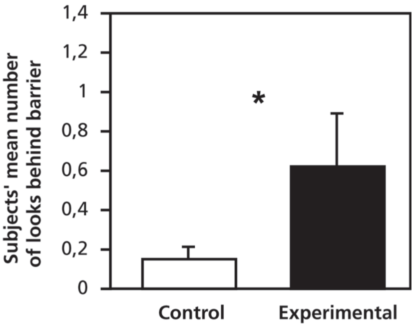

Figure 2. Mean number of focussed looks subjects directed behind the barrier in the averaged control (raised wood) and in the experimental (raised mirror) condition (±SE). Five out of thirteen subjects directed focussed looks directed behind the barrier during the mirror condition. Overall, there were more focussed looks to behind the barrier during the mirror condition than during the averaged control condition.

subjects directed more focussed looks behind the barrier in the mirror than in the control condition (Fig. 2; Paired *t* test, one-tailed: $t_{12} = 1.97$, $P = 0.039$). Subjects looked at the demonstrator more often when the mirror was raised compared to the wooden panel (looks at demonstrator during wood: $\overline{X} \pm SE = 8.15 \pm 1.55$, mirror: 13.08 ± 2.20, Paired *t* test: $t_{12} = 2.56$, $P < 0.03$). There was no difference in general looks towards the area of the barrier (measure 7) between the averaged control and the experimental condition (general looks during wood: $\overline{X} \pm SE = 0.50 \pm 0.16$, mirror: 0.31 ± 0.17, Exact Wilcoxon signed-rank test: $T = 5$, $N = 13$, NS). We also compared the total number of changes in looking-direction, i.e. total number of looks (measures 1-5, 7, 8) as a measure of general activity and vigilance, but did not find a significant difference in this measure between the averaged control and the experimental condition (looks during wood: $\overline{X} \pm SE = 71.85 \pm 7.62$, mirror: 78.92 ± 8.64, Paired *t* test: $t_{12} = 0.88$, NS). In addition, there was no significant difference between the experimental and control conditions in the number of looks from the starting position (S, Fig.1) towards the far left, which would indicate co-orientation in approximately the same direction as the demonstrator (looks far left during wood: $\overline{X} \pm SE = 26.53 \pm 2.82$, mirror: 28.15 ± 4.15, Exact Wilcoxon signed-rank test: $T = 27$, $N = 13$, NS).

DEMONSTRATORS

Demonstrators directed significantly more looks at the raised mirror than at the raised wood (Fig. 3; Paired *t* test: $t_{11} = 6.35$, $P < 0.001$). Demonstrators also looked longer towards the mirror than the raised wood (Paired *t* test: $t_{11} = 5.88$, $P < 0.001$, looking duration (in seconds) wood: $\overline{X} \pm SE = 28.17 \pm 5.25$, mirror: 75.42 ± 7.92).

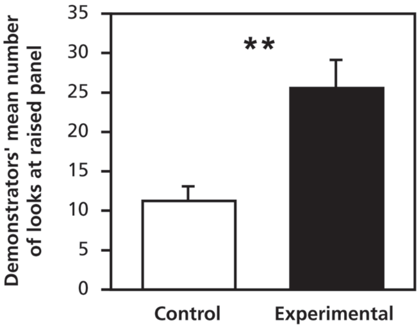

Figure 3. Mean number of looks by the demonstrator directed at the raised mirror or raised wood (±SE). All demonstrators directed more looks at the raised mirror than at the raised wood. Ten demonstrators directed affiliative social signals (lifting and lipsmacking) at the mirror.

Most demonstrators (10 out of 13) responded socially to their mirror image, the other three demonstrators responded with neutral looks only. All socially responsive animals responded with lifting of the eyebrows and three demonstrators also reacted by lip smacking; both behaviours are commonly shown during friendly interactions (Angst 1974). The duration of social signalling varied between 8 and 76 seconds ($\bar{X} \pm \mathrm{SE} = 19.07 \pm 5.72$). We also analysed gazing behaviours of the demonstrators towards other directions as a measure of their general activity. We found that demonstrators directed more looks down when the mirror was raised compared to the wood (looks down during wood: $\bar{X} \pm \mathrm{SE} = 9.75 \pm 1.53$, mirror: 11.75 ± 1.71, Paired *t* test: $t_{11} = 2.37$, $P < 0.04$). Demonstrators also looked more often towards the central room, the area behind the experimental device, when the mirror was raised, but not significantly so (looks at central room during wood: $\bar{X} \pm \mathrm{SE} = 25.13 \pm 3.19$, mirror: 30.71 ± 2.45, Paired *t* test: $t_{11} = 2.15$, $P < 0.06$). Other gazing behaviour (looks back, up, sideways, at subject) did not differ significantly between the control and experimental conditions.

Comparing 'gaze followers' and 'gaze ignorers'

Subjects that directed focussed looks towards the area behind the barrier mainly during the mirror condition were categorised as 'gaze followers', the remaining as 'gaze ignorers'. Gaze followers looked more often at the demonstrator during all conditions, but not significantly so (gaze followers: $\bar{X} \pm \mathrm{SE} = 41.20 \pm 7.39$, gaze ignorers: 23.50 ± 4.56, Independent *t* test: $t_{11} = 2.17$, $P = 0.053$), indicating that they paid more attention to the demonstrator than those animals that did not follow the other's gaze. However, the increase in number of looks the subject directed at the demonstrator between the control and experimental conditions was not significantly larger in gaze followers than gaze ignorers (difference between wood and mirror in gaze followers: $\bar{X} \pm \mathrm{SE} = 6.80 \pm 4.78$, and gaze ignorers: $3.75 \pm$

1.39, Independent *t* test: $t_{4.63} = 0.61$, NS). The number and duration of the social behaviours directed by the demonstrator at the mirror did not differ between gaze following and gaze ignoring subjects (mean number of demonstrators' social displays, gaze followers: $\overline{X} \pm SE = 2.4 \pm 0.67$, gaze ignorers: 4.75 ± 1.35, independent *t* test: $t_{11} = 1.30$, NS; mean duration of social behaviour: gaze followers: $\overline{X} \pm SE = 22.20 \pm 13.64$ seconds, gaze ignorers: 17.13 ± 4.84, Independent *t* test: $t_{11} = 0.42$, NS). There was no significant difference between gaze followers and gaze ignorers in the change in number of looks from the starting position towards the far left (change in looks to far left in gaze followers: $\overline{X} \pm SE = 6.00 \pm 10.81$, gaze ignorers: -1.13 ± 4.28, Exact Mann-Whitney *U* test: $U = 19$, $N = 13$, NS).

DISCUSSION

Five subjects extrapolated the gaze of a conspecific demonstrator behind a physical obstacle, which indicates the capacity to follow gaze geometrically to a point outside their field of vision. These animals relocated to a predefined position and directed more focussed looks towards the location behind the barrier during the experimental condition, whereas only one did so during a control trial. Other animals also relocated on several trials. Relocation to the area from which the subject could see the target location without focussed looking may have been a result of the relatively lengthy trial duration (5 min) and the restrictions of the test-cage design, which meant that animals could only move in one direction if they moved at all. Relocation alone would have been an insufficient and uninformative cue of gaze following in this experimental set-up. Furthermore, it is unlikely that the presented findings could be the result of order effects, since control trials that preceded and followed the experimental trial did not differ from one another in the various measures. From the present results we conclude that macaques, when gaze following, do not simply move their eyes and turn their head in the same direction another is looking at, since that would result in the animals staying at their starting position and looking straight ahead and slightly downwards, which is the gazing direction of the demonstrator. Instead, they apparently tracked the other's gaze to an out-of-view location, responding by moving and focussed looking towards the appropriate location. The capacity to 'follow gaze geometrically' (Butterworth and Jarrett 1991) enables an individual to project an imaginary line of sight from the other's point of view towards a location, without being distracted by intervening obstacles (Tomasello et al. 1999). In our case, animals employed this ability to follow gaze to a location outside their own visual field, which to some extent requires representational skills of space (Butterworth and Jarrett 1991). We cannot and do not conclude from our results that macaques take the demonstrator's perspective and thus understand the other's visual behaviour in a mentalistic sense (i.e. the other is seeing and knowing something else than the observer can; Povinelli and Eddy 1996a; Tomasello et al. 1999).

Only five of the thirteen animals tested responded to the demonstrators by relocation with focussed looks around the barrier in the experimental condition. Several explanations could account for the lack of gaze following in the eight 'gaze ignoring' subjects. First, using conspecific demonstrators may have caused variation in the gaze cues the subjects received. Some of the demonstrators may not have paid sufficient attention to the mirror, which could result in an inefficient gaze cue. However, we found that all demonstrators directed more looks at the raised mirror than at the raised piece of wood, and responded with affiliative social displays in this direction only during the experimental condition. Moreover, the strength of the demonstrators' cues, measured as the number and duration of looks and social behaviour directed at the mirror, did not differ between the gaze following and the gaze ignoring subjects. This suggests that the response of the subjects was not influenced by the demonstrators' way of looking towards the mirror. Second, subjects' attention to the demonstrator may have played a major role. It is possible that some of the subjects did not respond to gaze direction because they simply did not pay additional attention to the demonstrator during the experimental condition compared to the control. We found no evidence for this, as all subjects directed more looks at the demonstrators during the experimental condition than during the respective controls. Furthermore, we found that the difference in subjects' attention towards the demonstrator between the control and the experimental condition was not significantly larger in the group that did follow gaze. Therefore, a lower level of attention of gaze ignoring subjects during the experimental condition cannot explain the absence of a response. However, we noted that gaze followers tended to look more often at the demonstrator during all conditions than gaze ignorers, suggesting that a generally high level of attention to the demonstrator may be a prerequisite of gaze following. Attention may reflect the social importance of the demonstrator for the subject, and subjects may be more sensitive to social cues given by socially important group members (Watts 1998). Finally, inter-individual differences in the cognitive capacity, motivation, or the propensity to perform this task may also provide explanations for the between-individual variation observed.

Arousal- or attention based mechanisms could provide alternative explanations for the behaviour of the gaze following animals. Gaze followers may become more aroused by the changes in demonstrator behaviour during the experimental condition, and for that reason relocate and direct their attention towards the demonstrator, or simply look around more in general. We assumed that the more aroused an animal is, the more vigilant it will be, resulting in frequent changes of looking direction. However, overall, this measure was not significantly greater in the experimental compared to the control condition. Moreover, prior to testing we had given the subjects experience with the different visual perspectives in the test-cage, which means that the animals had experienced that they could not see the demonstrator from the location from which they attempted to look around the barrier. We therefore conclude that it is unlikely that the gaze followers directed focussed looks from the target location because of either elevated arousal or in an attempt to observe the demonstrator. Alternatively, if individuals followed gaze direction, but did not follow gaze geometrically, they would gaze at the barrier, floor, or to their far left, rather than relocate and direct focussed looks to their right, behind the barrier. However, subjects in their starting compartment did not look significantly more often to the far left in the experimental compared to the control condition. Thus, subjects did not simply co-orient in approximately the same direction as the demonstrators.

Gaze following in non-human animals has been studied extensively. Some species attend to the direction of the eyes only, irrespective of head direction (Povinelli and Eddy 1996a; Ferrari et al. 2000), others use gaze as a communicative cue to locate food (e.g. Call et al. 1998; Miklosi et al. 1998). However, only great apes and ravens have been shown to follow another's gaze geometrically to a location hidden behind a barrier. They do this repeatedly, with different kind of barriers and irrespective of the presence of food at the location the experimenter's gaze is directed at (Povinelli and Eddy 1996; Tomasello et al. 1999; Bugnyar et al. 2004; Bräuer et al. 2005). This ability requires geometric gaze following in combination with a representation of the hidden location. Geometric gaze following, without the barrier component, has been demonstrated in other species. For example, bee-eaters, *Merops orientalis*, differentiate between a predator looking at them or at their nest, indicating that they are able to exactly identify the target of another's gaze (Watve et al. 2002). Common marmosets, *Callithrix jacchus*, are able to follow gaze past distracting objects to an exact location within their visual field (Burkart and Heschl 2006). However, there is to our knowledge currently no evidence apart from our study for the ability to follow another's gaze to a hidden location for animal species other than the great apes and ravens.

The use of a conspecific, in contrast to a human experimenter, may have made this task more salient to the animals. Although many primate and non-primate species readily respond to human cues in basic gaze following tasks

(Miklosi et al. 1998; Tomasello et al. 2001; Scheumann and Call 2004; Kaminski et al. 2005), advanced use of gaze cues seems more difficult to demonstrate with human experimenters (e.g. Anderson et al. 1996), although positive results have been obtained with hand-raised (Schloegl et al. 2007: ravens) and domesticated subjects (Bräuer et al. 2004: dogs, *Canis familiaris*). Conspecific individuals have been successful demonstrators and competitors in other paradigms testing gaze following capacities in animals (Tomasello et al. 1998; Itakura et al. 1999; Hare et al. 2001), indicating that a conspecific's gaze may be more interesting than that of a human (Itakura et al. 1999). Although an earlier study showed that an affiliative signal did not increase gaze following responses in a simple gaze following task (this thesis, chapter 2), the social responses of some demonstrators towards the mirror may be facilitating in a more complex situation like the barrier test.

Researchers agree that neither the geometrical nor the representational mechanisms of gaze following require a mentalistic understanding of the other's visual behaviour (Butterworth and Jarrett 1991; Tomasello et al. 1999; Bugnyar et al. 2004), as it is not necessary to take the demonstrator's perspective to master the task we describe here. Nevertheless, in human infants this skill, exceeding simple co-orientation, has been proposed to signify progress in cognitive development (Butterworth and Jarrett 1991). Recent work has begun to uncover a variety of visual behaviours in monkeys. Long-tailed macaques and Diana monkeys, *Cercopithecus diana*, have been shown to check-look (Scerif et al. 2004; this thesis, chapter 2), i.e. looking back and forth between the model and the looking direction when seeing nothing to be looked at in the direction of the other's gaze. This behaviour has been proposed to indicate the understanding that the other is looking at something specific (but see Scaife and Bruner 1975; but see Corkum and Moore 1995 for alternative explanations). Moreover, long-tailed macaques follow gaze longer when the gaze is accompanied by a social facial expression, suggesting that gaze following is a flexibly employed response (this thesis, chapter 2). Rhesus macaques, *Macaca mulatta*, respond to what a human competitor can and cannot see (Flombaum and Santos 2005), which corresponds to behaviour described so far only in chimpanzees, *Pan troglodytes*, (Hare et al. 2000). Taken together with these other results, our findings suggest that advanced gaze following capacities are present in monkeys and that the use of a conspecific demonstrator can be a powerful tool to reveal these capacities. In the wider perspective of cognitive evolution, we propose that apparently sophisticated cognitive capacities relating to interpreting the visual behaviour of others are widespread among simian non-human primates. This raises the possibility that these visual capacities may be a conserved primate feature. However, whether these capacities are limited to some taxa, among them primates and corvids, or are widespread among vertebrates needs to be investigated by further comparative research.

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4

Gaze following and visual perspective taking in guppies, *Poecilia reticulata*

Unpublished manuscript together with van den Beld IMJ, Sterck EHM,
Bolhuis JJ, Reader SM

ABSTRACT

Research on social cognition has tended to focus on a restricted range of species, principally primates and, more recently, birds and domesticated animals such as dogs and goats. However, certain social cognitive capacities may be taxonomically more widespread than previously supposed, and to address this issue researchers have begun to work on the social cognition of fish. Gaze following and visual perspective taking have been considered important components of social cognition in humans and animals, since the subject has to attend to the direction of another's gaze or to what another individual may see or not see. We investigated these social cognitive capacities of a poecilid fish, the guppy, *Poecilia reticulata*. In a first experiment, we examined whether guppies respond to the body direction of conspecifics when choosing where to swim, adapting a design used to study gaze following in other species. Guppies did not preferentially swim first to the side that had been indicated by the demonstrators. However, the subjects spent significantly more time on the demonstrated side than the non-demonstrated side, suggesting that the guppies took their conspecifics' body direction into account to a certain degree. In a second experiment, we investigated the visual perspective taking capabilities of guppies. Subordinate guppies did not seem to respond to the visual perspective or the behaviour of dominant individuals. Taken together, there is some evidence that guppies respond to the body orientation of others, but guppies failed to pass a visual perspective taking test. Further studies are required to confirm the present results and to address potential underlying mechanisms.

INTRODUCTION

Social animals commonly gather information from other individuals in their group. For example, animals use information gained by observing others for current decisions (e.g. following others to food sources) or for future ones (i.e. social learning, e.g. for food locations or predator recognition; Pitcher and Magurran 1983; Mathis et al. 1996; Lachlan et al. 1998; Day et al. 2001; Reader et al. 2003). One source of social information is the visual behaviour of others, for instance conspecifics' looking direction (often indicated by head- and/or body-orientation; Emery 2000). The capacity to copy looking direction is commonly referred to as gaze following or visual co-orientation, and has received considerable attention in both human and animal cognitive research (for review, see Gomez 2005). In humans, gaze following is proposed to form part of more advanced cognitive skills such as visual perspective taking, i.e. the capacity to represent what another individual may see from a different perspective. There is compelling evidence that simple gaze following, such as co-orienting in approximately the same direction without necessarily appreciating that the other is looking at something specific, are present in most primate taxa (e.g. Tomasello et al. 1998; Sheperd and Platt 2008). Visual perspective taking skills have also been reported in primates, such as chimpanzees, *Pan troglodytes,* and rhesus macaques, *Macaca mulatta* (Hare et al. 2000; Flombaum and Santos 2005). Comparative work on taxa more distantly related to humans, such as dogs, birds and marine mammals, has shown that both gaze following and visual perspective taking are more widespread than was previously thought (dogs, *Canis familiaris*: Miklosi et al. 1998; Bräuer et al. 2004; dolphins, *Tursiops truncatus*: Tschudin et al. 2001; seals, *Arctocephalus pusillus*: Scheumann and Call 2004; ravens, *Corvus corax*: Bugnyar et al. 2004).

Widening the taxonomic scope in the study of animal cognition may reveal which socio-cognitive capacities may be due to common ancestry or to convergent evolution. Investigation of a range of species that differ cognitively will allow the identification of selective pressures that shape behaviour and cognition. Students of animal cognition have generally neglected fish (Bshary et al. 2002; Brown and Laland 2003a). However, Bshary and colleagues (2002) highlight striking similarities between fish and primates in a wide variety of behaviour patterns, behaviour that for primates has been suggested to relate to complex cognitive capacities. Some fish species are able to recognize each other individually (e.g. Balshine-Earn and Lotem 1998), others cooperate with each other during predator inspection (Croft et al. 2006) or behave deceptively (Bshary and Grutter 2002; 2006). Moreover, there is evidence that cichlids can assess the dominance relationships of two other individuals by observation alone using transitive inference: they can assess that if A > B, and B > C, A must be > C (Grosenick et al. 2007). There is extensive evidence that fish species socially learn. They learn feeding locations, feeding behaviour, mate choice, mating sites, schooling sites, migration routes, and appropriate responses to different predators from conspecifics (for review, see Brown and Laland 2003a). Such behavioural phenomena have typically been investigated from a functional perspective in fish, i.e. in analysing how the behaviour adds to reproductive success, while the underlying (cognitive) mechanisms have been neglected (Bshary et al. 2002). Bshary and colleagues (2002) advocate the study of fish cognition partly because closely related species are found in a variety of habitats, which facilitates identifying ecological factors that select for certain capacities and may provide evidence for repeated co-evolution of cognition. Besides, a given ecological factor can be examined repeatedly in different groups. Investigating the capacities of fish opens the possibility of examining the taxonomic range of social cognitive capacities, which can be a first step to construct hypotheses about the evolutionary history of these capacities. Fish diverged early from the common ancestor of birds and mammals, and comparative research may provide indications whether particular characteristics are ancestral or derived in vertebrates. Besides, fish allow the underlying mechanisms of cognition to be studied, since they are convenient laboratory animals that allow large sample sizes and control of the previous experience of subjects. Studies of fish have also shown how apparently complex behaviour can result from simple decision rules, providing a useful heuristic for studies of similar behaviour in other taxa (Bshary et al. 2002, but see Call 2002). Therefore, including fish in the study of gaze following and visual perspective taking can shed light on the evolution and (cognitive) mechanisms of these capacities.

In this study we investigated how guppies, *Poecilia reticulata,* respond to the visual behaviour of others, as this may indicate social cognitive capacities that are comparable to those in other species. Guppies live in semi-stable shoals of about 15 individuals (Magurran 2005). Social information use and social learning are well established. For example, guppies can distinguish between individuals that expect food and those that do not, and prefer to follow the expectant individuals (Lachlan et al. 1998). In addition, guppies learn foraging locations, foraging routes, predator escape routes, visual predator recognition, and mate preferences from conspecifics (Dugatkin 1992; Brown and Laland 2003b; Reader et al. 2003). They rely strongly on visual cues for recognition of familiar or unfamiliar conspecifics or heterospecfics (Warburton and Lees 1996). Moreover, guppies establish dominance relationships that are maintained over some time

(Gorlick 1974). Whereas some fish species form very tight shoals, with closely packed schools of all fish sharing a similar body orientation, guppies form looser shoals (Magurran et al. 1995). Therefore, guppies are a suitable species to study cognitive capacities employing visual information.

We investigated guppies' social cognitive capacities employing two tasks that have been used to study visual capacities in other species, such as primates, birds and dogs (Hare et al. 2000; 2003; Bräuer et al. 2004; Burkart and Heschl 2007). At this stage we do not investigate the mechanisms underlying these capacities but instead simply attempt to determine whether guppies possess them. First, we investigated the capacity to follow the direction of others' attention to locations out of the subject's sight (experiment 1). We applied the logic of a gaze following task to a hidden object that has been tested in human infants, great apes and ravens (Bugnyar et al. 2004; Moll and Tomasello 2004; Bräuer et al. 2005; see also chapter 3 of this thesis). An experimenter or conspecific shifts gaze direction to a location behind a physical obstacle, and subjects are expected to relocate to a position where they can view the gaze target. Such behaviour would indicate the capacity to extrapolate the other's line of gaze (in the case of fish, body direction) to a location out of sight.

Second, we employed a visual perspective taking task (Hare et al. 2000; 2003; Burkart and Heschl 2007) in which two animals competed over food and could profit by responding to the perspective or the behaviour of the competitor (experiment 2). Two animals of different dominance ranks competed over food items that were visible to either or both of the competitors. If the subordinate animal takes into account what the other can or cannot see, it should show a preference for the food that the dominant cannot see.

GENERAL METHODS

Subjects

Guppies were reared and bred in the Kruyt aquarium of Utrecht University, and were descendants of domesticated guppies purchased from Ruilmans, Montfoort, The Netherlands. Animals were housed in tanks (l x d x h in cm: 90 x 45 x 25) and fed daily with commercially available tropical fish flake food for tropical fish (Tetra-Phyll, Tetra, Germany) and once a week they also received bloodworm (larvae of *Chironomus* midges). Water temperature was maintained at 23 ± 1 °C, and lighting was a 12 h: 12h light-dark cycle with lights on at 07:00 h. The tanks contained natural coloured gravel and several small plastic plants. Water was filtered continuously and refreshed once a week. To avoid the potential stress of moving fish between tanks, experiments were conducted in the housing tanks of the subjects by dividing the tank during testing into a testing area and one (Exp. 1) or two (Exp. 2) housing areas with slides. In all experiments, the testing apparatus was set up out of sight of the subjects and demonstrators. We utilised domestic fish as their appearance allows individual identification. Individuals were identified by means of coloration, body size and tail shape.

Experiments started after the fish had been in the tanks together for at least two weeks, in which time the animals could habituate to the tank and the group members. Familiarity and schooling preferences in female guppies of less than 50 individuals develop gradually over twelve days and are maintained thereafter (Griffiths and Magurran 1997a,b).

Pre-training

Prior to the experiments all animals were trained to approach and feed from a blue, square floating feeder constructed of plastic straws (3 x 3 cm). Same-sex pairs were isolated from the group in a separate compartment of their home tank for training once a day. During training, small pieces of floating flake food (1 or 2 per trial) were placed in the feeder and the latencies to reach the feeder and to feed were recorded for both individuals. Animals received 10 trials per day. Fish were considered as trained when they reached a training-criterion, i.e. they fed from the floating feeder within 20 seconds on at least three trials on three consecutive days, and they approached an unbaited feeder within 20 seconds.

EXPERIMENT 1: RESPONSE TO DIRECTIONAL CUES OF CONSPECIFICS

The goal of this study was to examine whether guppies can use the directional information derived from the body-/swimming-orientation of conspecific demonstrators and find the location demonstrators are attending to. We cannot determine guppies' exact looking direction, since guppy eyes are laterally placed on the body and it is therefore difficult to observe in which direction it is looking (but see Fernald 1985). Therefore we used head- and body orientation as an indicator of looking direction (see also Kaminski et al. 2005). Conspecific demonstrators were trained to orientate in a certain direction, thereby providing a directional cue with their body. The subject could see the demonstrators, but could not directly reach them. In order to swim in the direction of the orientation cue the subject had to swim away from the demonstrators around a barrier. Such relocation would resemble the behaviour of several primate species and ravens that exhibit gaze following to a hidden location (Tomasello et al. 1999; Bugnyar et al. 2004; Bräuer et al. 2005; see also chapter 3).

METHODS

Training of subjects and demonstrators

Subjects were 39 guppies (24 males, 15 females), naïve to experimental manipulations. Housing conditions were as described in the General Methods. Animals were trained to the floating feeder (see above). Before the experiment, we confirmed that demonstrators responded to the floating feeder when olfactory cues were excluded by placing the feeder in a transparent cup. All fish swam towards it. Similarly, demonstrators swam and orientated towards the feeder when they were placed in a transparent cup themselves.

Well-trained individuals, i.e. animals that responded to the feeder by approaching and feeding within 5 seconds, were selected as demonstrators for the first experimental trials. Later, subjects that had been tested were also used as demonstrators. Subjects only participated in one trial as subjects. We used females from the same group as demonstrators.

Experimental procedure

During experimental trials, non-tested individuals were separated from the experimental area by opaque slides in a smaller compartment of the tank. The experimental area was divided by a transparent slide that separated the subject from the demonstrators (Fig. 1). Perpendicular to this slide we placed two short opaque barriers that created the starting compartment (d x w: 18 x 8 cm) in which the test subject would be placed. On both sides of these opaque slides we placed transparent cups (Ø 9 cm) with baited feeders. The feeders were put in cups to exclude olfactory cues to which fish could respond. One of the cup sides was covered from the perspective of the demonstrators with a smaller opaque slide, so that the demonstrators could only see one feeder location. This set-up excluded the possibility that underwater reflections of the blue feeder could influence the subjects' choices. We also covered the back of the feeder cups, so that subjects leaving their starting compartment could not see the baited locations themselves (Fig. 1). The side on which the feeder was visible to the demonstrators was counterbalanced and pseudo-randomized. Subjects went out of sight of the demonstrators when they swam around the barrier that formed the starting compartment. However, they could see the demonstrators once they entered the feeder zones (Fig. 1, white area around F).

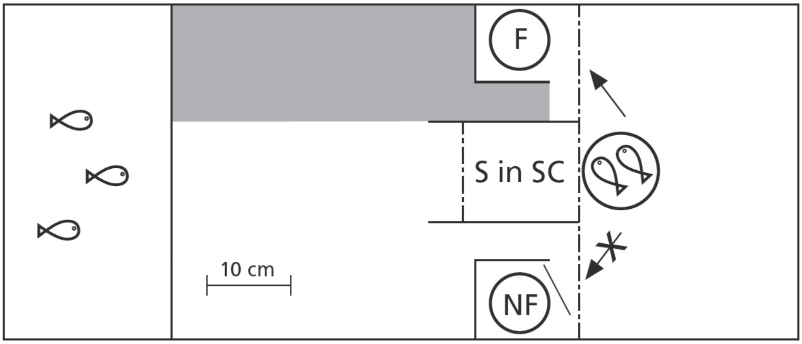

Figure 1. Scale plan of the experimental area in experiment 1, which measured responses to conspecific body-orientation. Subjects (S) were placed in the starting compartment (SC). The feeder that was visible to the demonstrators in the transparent demonstration cup is indicated with 'F', the feeder they could not see with 'NF', both of which were placed in transparent cups. Solid lines indicate opaque walls, dotted lines transparent walls. The grey area indicates a 'side zone' (in this case, on the demonstrated side; entry into the equivalent zone on the other side was also measured).The (white) area around the feeder was termed the 'feeder zone'. Fish symbols are not to scale.

Demonstrators received three pre-trials where they fed from the feeder to motivate them before the trial. These pre-trials were conducted in a separate part of the experimental area. To exclude effects of local odour cues that could remain after these pre-trials we swept with a cup or a net through this part of the tank twice after the demonstrators had been moved and before the experiment began. Demonstrators were then placed in a transparent cup that prevented them from swimming out of the subject's sight (Fig. 1). The demonstrators received one minute to habituate to the demonstration cup. Next, the subject was placed in the starting compartment where it could see the demonstrators and we waited for 60 seconds for the subject to habituate to the new situation. An experimental trial started with the removal of the slide that prevented the demonstrators' visual access to the feeder. Once demonstrators had started to respond (typically after 20-40 seconds) the experimenter removed the slide that prevented the subject from leaving the starting compartment and the trial began. Trials lasted for three minutes. Pairs of demonstrators were used for a maximum of two experimental trials per day, since we expected their response to the feeder to cease after long exposure to an unreachable feeder.

Data analysis

Trials were videoed from above for later analysis. For analysis we divided the tank into several areas and noted the movement of the subject through these areas. Dependent variables were initial choice of side, latency to reach feeder zone on demonstrated and non-demonstrated side, and the duration of stay on demonstrated and non-demonstrated side before entering either feeder zone ('side zone', see Fig. 1). Eleven (five females, six males) of the 39 subjects did not leave the starting compartment during the trial and these subjects were excluded from further analysis. Although all demonstrators were trained to respond to the feeder and they could only see the feeder on one side, we checked whether they swam more towards this side. We calculated a preference by dividing the time the demonstrators swam (within their cup) towards the side of the visible feeder by the total time swam towards either of the two sides. The demonstrators indicated both sides for equal duration for two subjects. Assuming that the directional cue would be ambiguous, we excluded the trials with these two subjects from further analyses. In two other trials, the demonstrators indicated longer the side where the feeder was not visible rather than the side with the visible feeder. Therefore, we considered this side the demonstrated side, although they did not see a feeder there. Excluding this pair of subjects gave a similar pattern of results. In order to assess interobserver reliability, a second observer analysed 25% of the trials. Interobserver reliability was high for all measures: side of first choice: Cohen's Kappa: 1.00, $P < 0.001$, latency to leave: $r = 0.98$, $P < 0.001$, duration of stay at either side: $r = 0.95$, $P < 0.001$, duration of demonstration to side: $r = 0.73$, $P < 0.001$. Data were analysed in SPSS 15.0. We used binomial tests to identify subjects' side-preferences. Non-parametric statistics (Wilcoxon signed-rank and Mann-Whitney *U* tests) were used when data did not meet the assumptions of parametric statistics.

RESULTS

Upon leaving the starting compartment subjects did not preferentially swim first to the demonstrated side (demonstrated side: 14 (7 females, 7 males), non-demonstrated side: 12 (3 females, 9 males), Binomial test: NS). They also did not reach the feeder zone on the demonstrated side faster than on the non-demonstrated side (latency to reach feeder zone on demonstrated side in seconds: $\overline{X} \pm SE = 131.04 \pm 62.95$ and non-demonstrated side: 122.92 ± 23.64, Wilcoxon signed-rank test $z = -0.44$, NS), nor did they spend more time in total in the feeder zone on the demonstrated compared to the non-demonstrated side (time spent in feeder zone at demonstrated side in seconds: $\overline{X} \pm SE = 34.81 \pm 9.71$ and non-demonstrated side: 23.81 ± 7.71, Paired *t* test: $t_{25} = 0.80$, NS).

However, subjects spent more time in the demonstrated side zone, an area where they could not see the demonstrators, before entering either of the two feeder zones (time spent in seconds on demonstrated side zone: $\overline{X} \pm SE = 29.54 \pm 4.93$, non-demonstrated side zone: $\overline{X} \pm SE = 22.69 \pm 3.87$, Wilcoxon signed-rank z = –1.86, $P = 0.032$, one-tailed). Subjects had a side bias to swim first to one side of the tank (the side closest to the experimenter, although note that the experimenter left the area during trials since trials were videoed), with 19 (7 females, 12 males) individuals first swimming in this direction (and 7 (3 females, 4 males) in the opposite direction) upon leaving the starting compartment (Binomial test: $P < 0.03$). However, there was no evidence for a side bias in the time spent in one side zone before entering either of the two feeder zones (time in seconds spent on side zone near experimenter: $\overline{X}$ ± SE = 25.69 ± 4.32, on other side: $\overline{X}$ ± SE = 26.53 ± 4.64; Wilcoxon signed-rank test: z = –0.33, NS).

DISCUSSION

The subjects in this experiment did not show an initial preference to swim to the location indicated by the demonstrators, i.e. the location behind the barrier, and did not reach the demonstrated side or feeder first. However, they stayed longer at the side zone of the tank that had been indicated by the demonstrators before they reached either of the two feeders, which was not due to a side bias for one specific side of the tank, or to demonstrator visibility, as demonstrators were not visible from the side zones. These results suggest that subjects followed the demonstrators' body orientation (which would also indicate the demonstrators' swimming direction) to some extent.

There are several possible explanations for these findings. It may be the case that subjects left the starting compartment to individually explore the area for food, conspecifics, or mates. However, when not succeeding (as there were neither conspecifics nor food visible), they may have responded to the social information previously provided by the demonstrators' body direction (a 'copy when uncertain' strategy; Laland 2004). Animals may use hierarchical systems for information use, for example first relying on personal information but switching to social information when personal information proves unproductive (Laland 2004). This may explain why subjects did not have an initial preference for the demonstrated side, but eventually stayed longer in the demonstrated side zone.

Subjects' eventual response to the directional information of the demonstrators may have been based on local enhancement, as demonstrators, particularly their heads, were marginally closer to that side of the tank (Galef 1988), and fish remembered this. Alternatively, subjects may have swum towards that side of the tank because they co-oriented with the demonstrators in an attempt to shoal with them or follow them (Lachlan et al. 1998). Animals of species that move together (such as shoaling fish or flocking birds) stay close to each other and match body orientations (Couzin and Krause 2003). Such body co-orientation may be qualitatively different from the 'gaze following' behaviour observed in other species, since these subjects do not follow potential movement, but instead the direction of gaze and/or attention. However, we did not find that individuals tried to stay close to the demonstrator or to swim towards the demonstrators, as would be predicted by a tendency to shoal, as only a minority of animals stayed in the starting compartment or in one of the feeder compartments (i.e. the only locations where the demonstrators were visible and close).

Finally, it is possible that subjects took into account the body direction of the demonstrators and followed it to the demonstrated side based on a capacity that resembles the gaze following to approximately the same direction observed in other species. For this, individuals needed to extrapolate the others' body direction to a location outside their own immediate field of vision and swim away from the demonstrators towards a location from which they could see the target area the demonstrators were indicating. This result calls for further investigation to verify the robustness of the effect and to disentangle why animals responded in this way, for instance by comparing the local enhancement and gaze following explanation by independently manipulating these variables.

EXPERIMENT 2: VISUAL PERSPECTIVE TAKING IN GUPPY FISH?

Experiment 2 investigated how guppy fish would respond in a competitive paradigm (Hare et al. 2000; 2003), where success to obtain food could be increased by assessing what the other may or may not see from its current perspective. For animals living in groups with dominance hierarchies, where a dominant individual most likely has more access to food than a subordinate, it may be advantageous to predict what the competitor's next action is likely to be. Animals may use the behaviour or the visual perspective of a competitor to this end.

In this experiment, two individuals had to compete over two food sources (feeders). Visual access of the two competitors to the two feeders varied between conditions, in that in some conditions the subordinate could see a feeder that was hidden from the dominant's perspective and in another condition this was reversed. We expected the subordinate to preferentially swim to the feeder that was out of sight from the dominants' perspective, since that would increase its chances to obtain food. Similarly, when the subordinate could only see one feeder, we expected it to prefer the visible feeder. We also examined whether the behaviour of the subordinate was influenced by the choice behaviour of the dominant by giving the subordinate a head-start in one condition, where it could make a choice before the competitor began swimming. In two control situations we assessed whether the subordinate would benefit from the presence of the barriers in food intake, by (1) measuring competition in the presence of two feeders without any blocking barriers; (2) creating a situation in which the dominants could not see either of the feeders and thus the subordinate should have a major advantage.

METHODS

Subjects

We tested 20 same-sex pairs (9 male-male and 11 female-female pairs) of guppies. Dominance was assessed in first instance based on body mass (Huntingford et al. 1990). However, since males were generally smaller than females and male body mass varied less than that of the females (weight in gram, males: $\overline{X}$ ± SE = 0.26 ± 0.02, range: 0.16-0.53; females: 0.61 ± 0.14, range: 0.13 - 1.56), male body mass was probably a less accurate predictor of dominance and we established their dominance relationships with a competitive paradigm (see Appendix). In all cases but one, the dominant partner was also the heavier one of the male-male pairs. In one pair, the weight was very similar (weight difference: 1 mg), but agonistic behaviours were clearly directed from one to the other and we assigned the recipient of aggression the subordinate role. The assessment of dominance relationships (see Appendix) was conducted shortly before Experiment 2. Animals were tested only once, either in the role of dominant or in the role of subordinate.

Experimental procedure

The starting compartments in which the subjects were placed before the start of the trial were located at opposite ends of the tank. In the middle of the experimental area (w x d in cm: 40 x 40), at equal distances from the two starting compartments, we positioned two feeders. Depending on the condition (see below), the visual access from one of the starting compartments towards the feeders was restricted by one or two opaque slides. The group of non-tested individuals was separated from the testing area during experimental trials by dividing the tank into a large experimental area and two smaller housing areas with transparent slides, through which subjects could see other individuals while in the starting compartment. This was done to prevent stress caused by isolating the fish from others.

Each experimental pair was tested once in each of five different conditions (Fig. 2). The conditions were (1) Visible – Visible, where both individuals could see both feeders, (2) Hidden – Hidden, where both feeders were visible to the subordinate, and neither were visible to the dominant, (3) Visible – Hidden For Dominant, in which the subordinate could see both feeders and the dominant only one, (4) Visible – Hidden For Subordinate, in which the dominant had visual access to both feeders and the subordinate only to one, and (5) Visible – Hidden For Dominant +3 sec, this was identical to condition 3, except that the subordinate received a head-start of 3 seconds. Trials in the different conditions were conducted after each other with intertrial intervals of one minute. Order of conditions was pseudo-randomized, with the restriction that condition 5 always had to be tested after condition 3. The sides from where the fish started and the position of the barriers were counterbalanced and selected pseudo-randomly.

Data analysis

Dependent variables were the latency to leave the starting compartment, subjects' initial swimming direction (i.e. in the direction of either feeder, or straight ahead, indicated hereafter as 'no choice'), latency to reach the feeders and feed from them, number of feeders reached and number of obtained food items. Data were analysed using SPSS 15.0. Bonferroni corrections were applied when analysing which feeder was reached first, number of feeders reached and number of food items obtained, as we conducted multiple comparisons.

Whether a feeder was hidden or visible depended on the subject's perspective, e.g. in condition 3 both feeders were visible to the subordinate, whereas one was hidden and the other was visible to the dominant. We therefore refer to the two feeders as A and B, which in condition 1 and 2 are the feeder at the front (A) (i.e. towards experimenter) and the feeder at the back (B) of the tank. In conditions 3-5, feeder A refers to the feeder that is visible to both individuals and feeder B refers to the one that is hidden from the perspective of one of the competitors, i.e. in conditions 3 and 5, feeder B is hidden for the dominant but visible for the subordinate, while in condition 4, feeder B is hidden for the subordinate, but visible for the dominant.

RESULTS

Subordinates

Analysis of the subordinates' initial swimming direction upon leaving the starting compartment revealed that in condition 3, in which the subordinate could

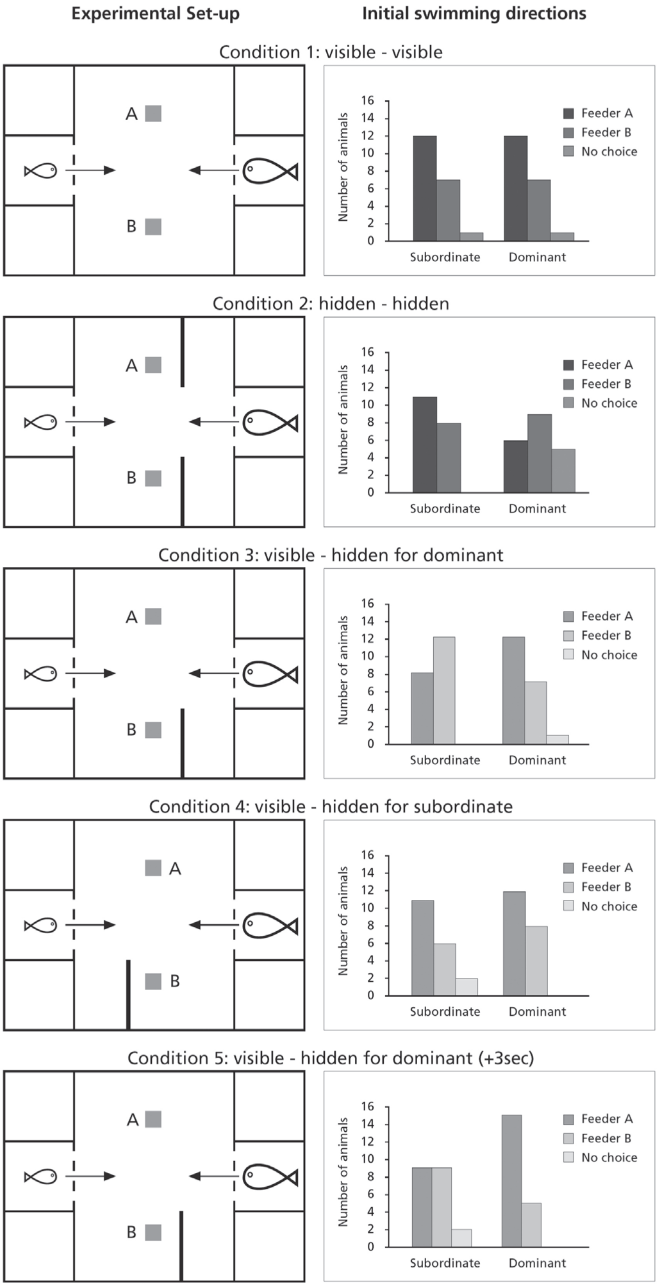

Figure 2. Experimental conditions and results in the visual perspective taking task. (a) Schematic drawing of the experimental tank in the five different experimental conditions. Feeders are indicated (A, B). Starting compartments were located at opposite sides of the tank. The larger fish indicates the dominant individual. Transparent slides prevented the subjects from leaving the starting compartments before the trial had begun. (b) Initial swimming direction in the different conditions.

see both feeders and the dominant only one, 12 of the 20 subordinates swam towards the hidden feeder, whereas 8 swam to the feeder that was visible to both individuals (Table 1, Fig. 2b, Binomial test: NS). In condition 4, we found that 11 subordinates swam initially towards the visible feeder, whereas 6 swam towards the barrier (i.e., the feeder hidden from their perspective; Binomial test: NS). In condition 5, where the subordinate was released 3 seconds earlier than the dominant, 9 subordinates initially swam towards the visible and 9 to the hidden feeder.

There was no significant difference in the subordinates' latency to reach feeder A or B between conditions 3-5 (Friedman's test based on the difference in latency to reach A vs. B: $\chi^2_2 = 1.09$, NS). Furthermore there was no significant difference between conditions in latency to reach or to feed from any feeder (Friedman test: reach any feeder: $\chi^2_4 = 3.37$, NS; feed from any feeder: $\chi^2_4 = 1.35$, NS, Fig. 3). In addition, we did not find a significant difference between conditions 1-5 in number of feeders reached or food items obtained for the subordinates (Friedman's test: number of feeders reached: $\chi^2_4 = 2.60$, NS, number of food items: $\chi^2_4 = 3.21$, NS, Fig. 4).

Table 1. Initial swimming direction of males and females in the visual perspective taking task. Sub: Subordinate individual, Dom: dominant individual. B indicates the feeder hidden from the perspective of the dominant (bold) or from the perspective of the subordinate (italics).

Condition		Males (N = 9)		Females (N = 11)		**Total (N = 20)**	
	Choice	Sub	Dom	Sub	Dom	**Sub**	**Dom**
Visible-Visible	A (front)	6	7	6	5	**12**	**12**
	B (back)	3	2	4	5	**7**	**7**
	No choice	0	0	1	1	**1**	**1**
Hidden-Hidden	**A (front)**	5	3	6	3	**11**	**6**
	B (back)	4	5	4	4	**8**	**9**
	No choice	0	1	0	4	**0**	**5**
Visible-Hidden Dom	A	3	5	5	7	**8**	**12**
	B (hidden from Dom)	6	4	6	3	**12**	**7**
	No choice	0	0	0	1	**0**	**1**
Visible-Hidden Sub	A	4	5	7	7	**11**	**12**
	B (hidden from Sub)	4	4	2	4	**6**	**8**
	No choice	1	0	1	0	**2**	**0**
Visible-Hidden Dom +3	A	4	5	5	10	**9**	**15**
	B (hidden from Dom)	4	5	5	1	**9**	**5**
	No choice	1	0	1	0	**1**	**0**

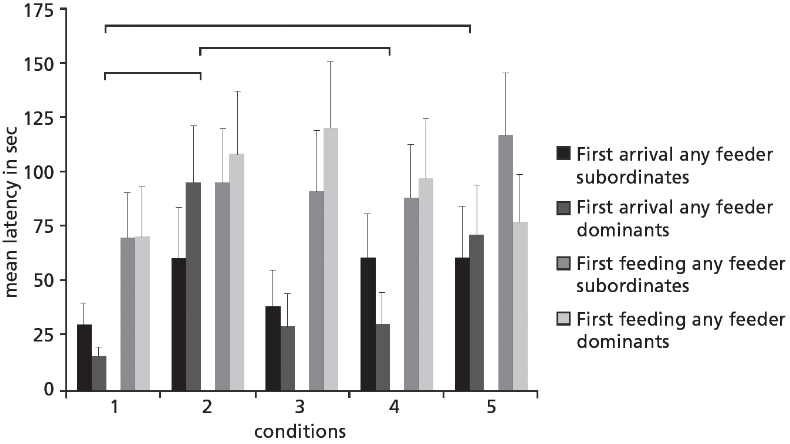

Figure 3. Subordinates' and dominants' mean latency (± SE) to reach and feed from any feeder. For the subordinates there was no significant difference between conditions in latency to reach or to feed from any feeder. However, there was a significant difference between conditions when comparing latencies to reach any feeder in dominant individuals. Pairwise comparisons revealed that dominants reached any feeder significantly earlier in condition 1 when compared to condition 2 and 5. Moreover, there was a difference in latency to reach any feeder between conditions 2 and 4. These differences are indicated by the lines above the bars. There were no significant differences in time to feed from any feeder between conditions.

Dominants

We also analysed the initial swimming direction of the dominant individuals. There were no significant preferences for one feeder over the other in conditions 1-4 (Binomial tests: NS). However, in condition 5, more dominants (15 of 20) initially swam towards the feeder that was visible to both (Fig. 2, Condition 5, Feeder A; Binomial test: $P = 0.04$). Although dominants tended to swim towards the visible feeder more in condition 5, there was no difference in latency to reach feeder A or B between conditions 3-5 (Friedman's test based on the difference in latency to reach A vs. B: $\chi^2_2 = 1.30$, NS). We found a significant difference between conditions when comparing latencies to reach any feeder (Friedman's test: $\chi^2_4 = 15.60$, $P < 0.01$, Fig. 3). Pairwise comparisons revealed that dominants reached any feeder significantly earlier in condition 1 compared to conditions 2 and 5 (Bonferroni corrections lowered the level of significance to $P = 0.005$; Wilcoxon sign-rank test condition 1 versus 2: $z = -3.31$, $P = 0.002$; condition 1 versus 5: $z = -3.24$, $P = 0.001$). Moreover, there was a difference in latency to reach any feeder between condition 2 and 4 (Wilcoxon sign-rank test condition 2 versus 4: $z = -3.32$, $P = 0.001$). There were no differences in latency to feed from any feeder between conditions (Friedman's ANOVA: $\chi^2_4 = 1.50$, NS, Fig. 3).

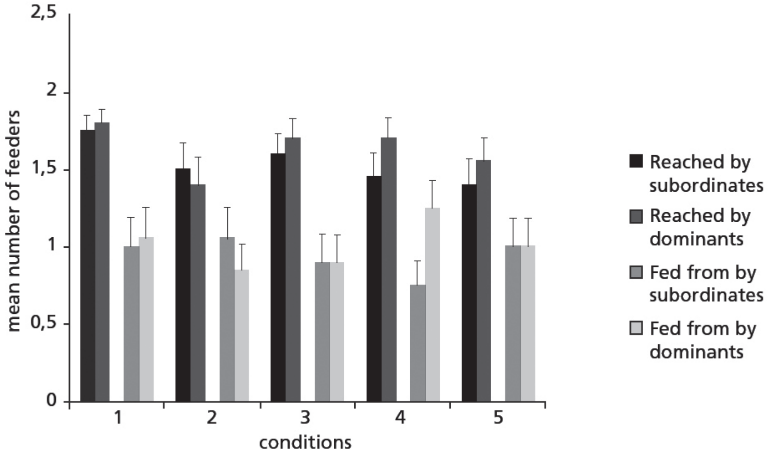

Figure 4. Mean number of feeders reached and food items obtained (± SE) by subordinates and dominants. There were no significant differences between number of feeders reached and fed from, neither between conditions, nor between dominant and subordinate individuals.

Dominants and Subordinates

We calculated the difference between dominants and subordinates in the number of feeders visited and food items obtained. There were no significant differences between conditions in these two measures (Friedman's test: feeders reached: $\chi^2_4 = 1.81$, NS, food items obtained: $\chi^2_4 = 6.61$, NS, Fig. 4). Moreover, subordinates did not reach significantly more feeders than dominants in any of the conditions (Bonferroni corrections lowered the level of significance to $P = 0.01$: Mann Whitney U test: condition 1: $z = -0.35$, NS, condition 2: $z = -0.12$, NS, condition 3: $z = -0.64$, NS, condition 4: $z = -1.31$, NS, condition 5: $z = -0.67$, NS) nor did they obtain more food items (Mann Whitney U test: condition 1: $z = -0.92$, NS, condition 2: $z = -0.75$, NS, condition 3: $z = 0.00$, NS, condition 4: $z = -2.01$, $P = 0.04$, condition 5: $z = 0.00$, NS).

Furthermore, we analysed whether animals swam towards each other or away from each other in every condition. Percentages to approach each other per condition were 70% (condition 1: 14 versus 6), 55% (condition 2: 11 versus 9), 65% (condition 3: 13 versus 7), 58% (condition 4: 11 versus 8), and 45% (condition 5: 9 versus 11). In none of the conditions did subjects have a significant preference to either approach or avoid each other (Binomial tests for conditions 1-5: NS). Sex was a non-significant effect in all analyses.

DISCUSSION

In this experiment, subordinate fish did not exhibit a significant preference for the feeder that was visible only from their perspective. There was no difference in initial swimming direction or which feeder they reached or fed from first in any of the conditions, whereas we had predicted that subordinates would preferentially swim to the feeder hidden from the dominants' view in condition 3 and 5. The dominants' initial swimming direction did not vary between conditions 3-5. However, in condition 5 dominants preferentially swam towards the feeder that was visible to both animals. Here, they may have shown a preference for the feeder that was most at risk (no barrier in between) or may have tried to stay in sight of the subordinate. Alternatively, the dominants may have responded to the subordinates' initial choice, as a small majority of subordinates swam towards the feeder visible to both or straight ahead. However, this latter suggestion was not supported by the proportion of animals that approached or avoided each other in this condition. Note that the negative results should be interpreted with caution, as the statistical power of our tests is low.

During the assessment of the dominance hierarchy, subordinates (those that received most agonistic behaviours) obtained clearly fewer food items than dominants (see Appendix). In fact, dominance could be assessed based on the number of food-items obtained (see Appendix). It is therefore surprising that in this experiment this was not the case in either of the conditions, given that the experimental set-up was similar to the dominance test, albeit with two rather than one feeder. The number of food items obtained by the dominant and the subordinate did not differ, not even in condition 1, where the subordinate had no advantage as there were no barriers that may have blocked either sight or access of the dominants towards the feeders. The presence of the barriers affected the dominants' behaviour to at least some extent, as they reached the feeders later in conditions where barriers blocked their access. However, this did not result in more food items for the subordinate. The lack of a difference in obtained food items may be due to a number of reasons, for instance, the relatively large amount of food that could be obtained during one test session (10; 2 pieces per trial), which may have satiated both individuals and lowered motivation to compete. Another reason could be presentation of two, instead of one feeder, in combination with the size of the experimental area. It is possible that due to the size of the experimental area dominant fish attempted, but were unable, to monopolize both feeders and that therefore subordinates could gain food irrespective of the presence of barriers. Size of experimental area seems to have played a role in studies on chimpanzees, in that visual perspective taking was not demonstrated in experiments with chimpanzees tested in a small area, whereas it was demonstrated in larger enclosures (Hare et al. 2000; Karin-D'Arcy and Povinelli 2002; Bräuer et al. 2007). In our case the experimental area may have been too large, causing a low intensity of competition between the animals.

Taking the results together, subordinates apparently could obtain food during all conditions, irrespective of the presence of barriers suggesting that there may not have been a need to assess the competitor's behaviour or perspective with respect to the feeders and the barriers (see also Hare et al. 2003). However, based on the agonistic interactions observed during the dominance food competition (see Appendix), we would still have expected some avoidance or hiding strategies of the subordinates, e.g. swimming towards barriers to avoid dominant. However, we observed that overall subordinates avoided and approached dominant individuals equally often. It is possible that the benefit of reaching a feeder and feeding from it even if a dominant was present may have outweighed the risk of an aggressive encounter, i.e. the subordinates instead of hiding or avoiding the dominant may have taken the risk to meet the dominant in order to gain food, or, alternatively, being out of sight of the other can be aversive to a shoaling species as guppies (Day et al. 2001).

Our results are in contrast to those reported in a number of primate species (Hare et al. 2000; 2003; Burkart and Heschl 2007). First, with respect to the food-items obtained. Subordinate primates (chimpanzees, capuchin monkeys, common marmosets, *Callithrix jacchus*) had a clear advantage in obtaining food in the presence of barriers, which likely resulted in a preference for approaching and obtaining the food that was out of the competitors' view. In the case of the chimpanzees, when controlling for the possibility that they merely responded to the approach behaviour of the dominants by giving the subordinates a small head start, the subordinates maintained their preference for the food-item that was not visible to the dominant individual. This lead the authors to conclude that subordinates responded to what another may see, i.e. its perception, instead of what another does, i.e. its behaviour (Hare et al. 2000; but see Karin-D'Arcy and Povinelli 2002). Results from capuchin monkeys and common marmosets show that these animals, although having a preference for the food-items that are out of the competitors' sight, most likely respond on the basis of the other's behaviour. In the case of the capuchin monkeys, the preference for the hidden food disappeared when the subordinates could enter the experimental area earlier than the dominant (Hare et al. 2003). The difference between the results on chimpanzees and capuchin monkeys may reflect a difference in capacity; alternatively it may indicate a difference in motivation. In order to exclude effects of low motivation for strategic decisions in the capuchin monkeys, food items were moved closer to the dominant, thereby hindering subordinate's food retrieval. Subordinates still did not show a preference for the hidden food-item when released with a head-start (Hare et al. 2003). In the case of the common marmosets, a subsequent experiment showed that the animals did not understand that another individual's line of sight could be interrupted by a barrier (Burkart and Heschl 2007), which would be an essential capacity for passing the visual perspective taking test. From our results we conclude that, so far, there is no indication that guppies assess the dominant's behaviour or visual perspective when competing over food sources. As with any such null result, it is unclear whether this failure is based on a methodological issue or on a true absence of the capacity in this species.

GENERAL DISCUSSION

In this study, we investigated how fish responded to the visual behaviour of conspecifics. We employed two paradigms used in certain primate and corvid species; a 'gaze'-following task and a visual-perspective-taking task. Guppies (1) respond to the body-direction of conspecifics to some extent; (2) form dominance hierarchies that can be assessed on behavioural interactions and on the intake of food; (3) do not show behaviour that may indicate visual perspective taking skills. The response to demonstrator body orientation is in line with earlier studies on gaze following capacities in other animal species, such as some non-human primates and ravens (Tomasello et al. 1999; Bugnyar et al. 2004). Guppies stayed longer at the side zone of the tank that had been indicated by demonstrators' body direction before they entered either feeder zone. This result has to be interpreted with caution, as several alternative explanations may apply (see discussion above). However, one of the possible interpretations is that animals followed the demonstrator's body orientation to a different location (behind the obstacle) and for that reason relocated to that side of the tank. Although this may not indicate gaze following in the strict sense of the meaning, i.e. following the other's 'eye'- or 'looking'-direction, it does suggest that guppies take into account the body orientation or head position of familiar individuals, a visual cue that may be equivalent to the cue used by other species when attending to the other's looking direction. A simple rule to explain this would be 'swim in direction others swim'. Fish tend to co-orient with each other, because there are survival advantages to swimming in the same direction and forming a cohesive shoal. However, guppies generally form loose shoals. Moreover, they did not initially swim towards the demonstrated direction. Assuming that the behaviour we found is based on a capacity that is equivalent to gaze following in the other vertebrate taxa, this result suggests that it is not restricted to mammals and birds, but also present in fish. This in turn may hint at a conserved vertebrate feature that may therefore be expected in other vertebrate taxa as well (reptiles and amphibians). Alternatively, the capacity may have evolved multiple times in different taxa, and may be an example of an adaptation to living in social groups where monitoring others' behaviour can be essential for survival. Body co-orientation may be particularly prevalent in species that must form cohesive, polarised groups for efficient movement or to increase survivorship. At present we cannot distinguish between these alternatives.

In the visual perspective taking task, guppies did not appear to respond to a dominant competitor's behaviour or perspective when competing over (hidden) food sources. Evidence that fish respond to at least the presence of others (e.g. potential competitors) stems from different studies reporting audience effects. Male three-spined sticklebacks, *Gasterosteus aculeatus,* show more courting behaviour to females when both were located behind a barrier and out of sight of a potential competitor (Dzieweczynski and Rowland 2004). It is unknown whether the sticklebacks are simply less distracted in the absence of a competitor or whether the males actively change their behaviour, which could imply sensitivity to the presence and potentially visual access of a competitor (Dzieweczynski and Rowland 2004). Similarly, male Siamese fighting fish, *Betta splendens*, adapt their general and aggressive displays depending on the presence or absence and the sex of an audience fish (Doutrelant et al. 2001). Bshary and Grutter (2006) observed that cleaner fish, *Labroides dimidiatus*, that commonly remove parasites from clients, but also 'cheat' by feeding on client mucus, show more cooperative behaviour in the presence of a 'watching client fish'. The cleaner fish thus adapt their behaviour to the presence of a potential future client. Although admittedly difficult to assess, it would be valuable to know whether in these examples of audience effects, the subjects rely on the mere presence of the other or also in some way on the other's attention to the situation or to particular stimuli. So far, there is no positive evidence on perspective taking skills in fish that resembles those described for primates and birds. This suggests that the capacity may be restricted to mammals and birds (e.g. Dally et al. 2006). However, further investigation needs to confirm the absence of this skill in this taxon.

A first step to construct hypotheses on the evolution of certain cognitive capacities may be to study its taxonomic range (e.g. Bitterman 2000). Capacities of different species may be mapped onto the phylogeny to answer questions concerning common ancestry. Also, comparisons across a wide range of species may reveal general principles in how animals perceive their environment. This suggestion is partly based on the assumption that cognitive differences among vertebrates are not of a qualitative, but of a quantitative nature and that, therefore, primates or fish in principle may use similar cognitive mechanisms to tackle similar problems (MacPhail 1987; Bshary et al. 2002). However, fish, like any animal, may possess cognitive specializations, evolved as response to problems encountered in their social and ecological environment (Call 2002). A starting point for cross-species comparison is assessing behavioural similarity. The next step is the scrutiny of the underlying cognitive mechanism in the different species. Three distantly related taxa, namely mammals, birds and fish, may resemble each other in their attention to conspecific orientation to some extent, at least on a behavioural level. Further research needs to investigate the underlying cognitive mechanism, in order to address questions on the evolution of the capacity.

This is to our knowledge the first attempt to investigate how fish respond to the visual behaviour of others, employing paradigms that have been used previously in other species. This approach allows for a direct cross-species comparison in performance. However, it should be noted that applying the same paradigm in a wide number of species may be problematic. Animals from different taxa may not only differ with respect to the cognitive capacity in question, but also with respect to for instance their sensory systems, which may be important in the performance of the test. This may impede a fair comparison of cognitive abilities, and may result in misleading conclusions. However, some important parallels can be drawn between the previously tested species and the species studied here with the presented paradigms. Guppies have been shown to compete over food sources and they interact aggressively during food competition. Moreover, they have been shown to rely on visual signals (Warburton and Lees 1996) to gain social information from others (e.g. Reader et al. 2003). Although there are undeniable interspecific differences, there are also some parallels that make the tasks presented here applicable to fish species.

In conclusion, we suggest that the results presented here warrant further investigations of the capacities of fish to respond to the visual behaviour of others as it may be a relevant capacity for them. In the 'gaze' following experiment we found results that to some extent resemble those obtained in other species, but verification is required. Finally, widening the scope of species studied in animal cognition may provide the basis to reconstruct the evolution of cognition and cross-species comparisons may eventually lead to an identification of ecological or social variables that may have shaped social cognitive capacities.

ACKNOWLEDGEMENTS

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APPENDIX: DETERMINATION OF THE DOMINANCE RELATIONSHIPS IN MALE GUPPY FISH

Dominance relationships have been shown in wide range of animal species (Wittig and Boesch 2003; Vervaecke et al. 2005; Wittemyer and Getz 2007). Also in a number of fish species there is evidence for dominance relationships (guppies: Gorlick 1974; Atlantic salmon *Salmo salar*: Huntingford et al. 1990; gobies *Elacatinus prochilos*: Whiteman and Coté 2004). Dominance status may relate to body size (Huntingford et al. 1990), sex (Gorlick 1974), or colouration (Bakker and Sevenster 1983) of an individual, and may affect its reproductive success (Kodric-Brown 1992). However, different measures of dominance may not always covary together (e.g. Boogert et al. 2006). In general, a linear dominance hierarchy is defined by its transitivity, i.e. if A > B and B > C, then the consequence is that A > C. Triadic relationships, such as that A dominates B and B dominates C, but C dominates A, affect the linearity of a hierarchy. Guppies have been shown to establish linear hierarchies, at least in small groups with four to six individuals (Gorlick 1974). In Gorlick's experiment, same- and mixed-sex groups of fish were observed for the occurrence and direction of agonistic behaviours. In the mixed-sex groups separate homosexual hierarchies were formed, with females always outranking males (Gorlick 1974).

The goal of this experiment was to assess whether guppies establish a linear dominance hierarchy determined by agonistic interactions during a food competition task. In addition, we determined whether dominance rank was dependent

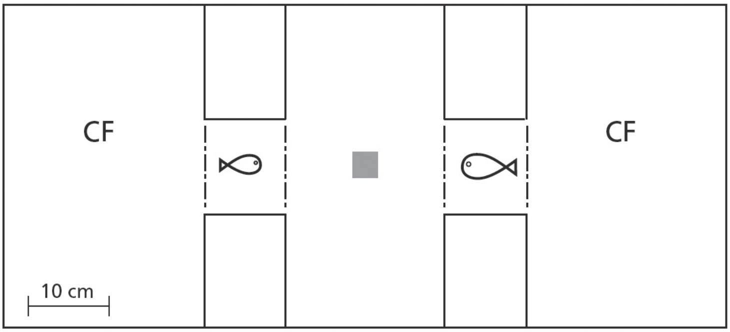

Figure A1. Experimental area during food competition trials. Before the start of a trial, subjects were placed in opposing starting compartments indicated by the fish symbols. Transparent slides prevented them from leaving the starting compartments early. Non-participating animals (companion fish; CF) were separated from the experimental area (w x d: 40 x 40 cm) and evenly distributed over two compartments at the sides of the tank where visual contact with the subjects was possible. This was done to prevent stress caused by isolation.

on the weight of the individuals and whether the observed rank would lead to a higher success during the food competition, i.e. higher intake of food.

METHODS

Subjects

Male guppies of three mixed sex groups participated in this experiment (group 1: 10 males, 6 females; group 2: 13 males, 6 females; group 3: 7 males, 8 females). Mean weight (in g) of the participating males was 1: $\overline{X}$ ± SE = 0.20 ± 0.01, 2: $\overline{X}$ ± SE = 0.24 ± 0.02, 3: $\overline{X}$ ± SE = 0.29 ± 0.04.

Experimental procedure

Every male-male pair (within one group) was tested in ten competitive trials (each lasting two minutes) in which one food item per trial could be obtained. Before a test session started we placed a feeder at equal distances from the subjects' starting compartments, i.e. in the middle of the experimental area, and baited it. Next, subjects were positioned in the opposing starting compartments (Fig. A1). A test session consisted of 10 trials. A trial started by the simultaneous removal of the two transparent slides that restricted the subjects from leaving the starting compartment early. We observed the occurrence of agonistic behaviours during the ten two-minutes trials. In addition, the latency to reach the feeder and the identity of the subject that obtained the food-item was recorded. Starting compartments were pseudo-randomized and counterbalanced over the two individuals. Trials were separated by an intertrial interval of one minute, in which the feeder was baited again. Every male was paired with every other male in its group, and a male participated per day in one test-session with the same competitor. Consequently, every male participated in nine (for group 1), eleven (for group 2), or six (for group 3) test sessions respectively.

Agonistic behaviours observed were (1) nipping, when one individual approaches another and delivers a sharp bite or a nip (Gorlick 1974), (2) 'attacking' / high-velocity approach, when one individual suddenly approached another with high velocity, followed by a bite (Zayan 1974), and (3) chasing, when one individual pursued the other fleeing individual with multiple high-velocity approaches or nips for some time. The difference between nipping and attacking is the high speed of approach during an attack.

Table A1. Dominance hierarchies for the three investigated groups (1, 2, and 3) based on agonistic behaviours (I) and number of obtained food-items (II).

Group (N)	1 (10)		2 (12)		3 (7)	
Measure of dominance	I	II	I	II	I	II
Number of interactions/ food items obtained (interactions/hour)	419 (27.93)	409 -	730 (33.18)	649 -	237 (33.86)	210 -
Range (Mean ± SEM) of interactions per dyad	0-67 (9.80 ± 2.38)	- -	0-99 (11.06 ± 2.74)	- -	0-41 (8.90 ± 2.94)	- -
Linearity index *h′*	0.59	0.76	0.40	0.45	0.46	0.68
Expected value of *h′*	0.27	0.27	0.23	0.23	0.38	0.38
P	< 0.035	< 0.001	= 0.090	< 0.020	> 0.1	= 0.070
DCI	0.96	0.56	0.98	0.50	0.93	0.53
Number (%) of unknown relationships	19 (42)	0 (0)	31 (47)	0 (0)	9 (43)	0 (0)
Number (%) of one-way relationships	22 (49)	9 (20)	31 (47)	14 (21)	11 (52)	4 (19)
Number (%) of two-way relationships	4 (9)	36 (80)	4 (6)	52 (79)	1 (5)	17 (81)
Total number of dyads	45	45	66	66	21	21
Number (%) of tied relationships	0 (0)	0 (0)	3 (5)	5 (8)	0 (0)	3 (15)

Data analysis

In order to assess the dominance hierarchy, the agonistic behaviours given and the number of food items obtained by each animal in a dyad were summed over all trials and entered in two separate sociometric matrices (aggressors/aggressees and amount food obtained by subject in every dyad). We calculated the improved linearity index (*h'*) that corrects for unknown and tied dyads and tested this value for significance with a randomization test using Matman 1.1 (Noldus Technology, de Vries 1998). The linearity index indicates the transitivity of the hierarchy, with a value approaching 1 showing a high transitivity (e.g. A > B, B > C, then A must be > C), with few triangular relationships. In addition, we calculated the directional consistency index (DCI, see Table A1). The directional consistency index is determined by dividing how often a behaviour is directed in the more frequent direction (e.g. from A to B) minus how often this behaviour is directed in the less frequent direction (from B to A) by the total number of interactions (van Hooff and Wensing 1987). A high directional consistency index (close to 1) indicates consistent uni-directionality of agonistic behaviours within the dyads, i.e. certain behaviours are (almost) exclusively directed from one individual to the other, and not the other way around. Groups were analysed separately first, but also combined using a method for combining probabilities from different tests (Fisher 1954; Sokal and Rohlf 1995, p. 794-797). All statistical tests were conducted in SPSS 15.0.

RESULTS

We constructed significant linear hierarchies for group 1 and 2, (group 1: $h' = 0.76$, $P < 0.001$, DCI: 0.56; group 2: $h' = 0.45$, $P < 0.02$, DCI: 0.50), and a linear hierarchy close to significance in group 3 ($h' = 0.68$, $P = 0.07$, DCI: 0.53) based on the number of food items obtained during the competitive trials. Combining the probabilities obtained for each of the three linearity tests by means of the formula $-2\sum \ln P$ which is distributed as chi-square with 6 degrees of freedom (Sokal and Rohlf 1995), gives a value of 26.96 with $P = 0.001$, indicating an overall support for the presence of a linear hierarchy based on the number of obtained food items.

We observed 27.93 (group 1), 33.18 (group 2) and 33.86 (group 3) agonistic interactions per hour during the food competition trials (total interactions were 419, 730, and 237 for groups 1, 2, and 3 respectively, see Table A1). Based on the agonistic interactions we found support for a linear hierarchy for group 1 ($h' = 0.59$, $P < 0.04$, DCI: 0.98), while for group 2 and 3 the support for a linear hierarchy did not reach statistical significance (2: $h' = 0.40$, $P = 0.09$, DCI: 0.98; 3: $h' = 0.46$, $P > 0.40$, DCI: 0.93). However, the directionality consistency index was high in all three groups, indicating a strong directionality of agonistic behaviours within dyads; therefore we calculated the dominance ranks for all three groups. Combining the probabilities obtained for each of the three linearity tests gives a value of 13.58 with $P = 0.03$ ($df = 6$), indicating an overall support for the presence of a linear hierarchy based on the agonistic behaviour observations as well.

The hierarchies obtained with the two different measures (food items obtained and agonistic behaviour given in the dyad) were significantly correlated in group 1 (Spearman's Rho: 0.83, $P < 0.01$), but not in group 2 and 3 (Spearman's Rho for 2: 0.26, $P = 0.4$, 3: 0.71, $P = 0.07$). Combining the three probabilities gives a value of 16.36 with $P < 0.03$ ($df = 6$), overall indicating a relationship between the two dominance measures. In group 1 there was a positive correlation between overall latency to reach the feeder and the rank assigned by means of the agonistic behaviours indicating that the highest ranking animals reached the feeder earlier (Spearman's Rho: 0.98, $P < 0.001$); but this relationship was not significant for group 2 (Spearman's Rho: 0.46, NS). We did not find significant correlations between rank (based on agonistic behavioural acts given) and weight in any of the three groups (Spearman's Rho for 1: −0.26, $P > 0.4$, 2:

0.25, $P > 0.4$, 3: −0.68, $P = 0.09$). However, we found that number of received agonistic behaviours significantly negatively correlated with weight in groups 2 and 3, but not in group 1 (Spearman's Rho for 1: −0.54, $P = 0.1$, 2: −0.66, $P = 0.02$, 3: −0.96, $P = 0.01$).

DISCUSSION

Overall, we found support for the presence of linear hierarchies based on two different measures, the number of food items obtained and the number and direction of agonistic behaviours, thereby confirming earlier results on the presence of linear hierarchies in guppies in groups with four to six individuals (Gorlick 1974). In contrast to Gorlick (1974), we observed linear hierarchies based on seven or more individuals. Appleby (1983) argued that in groups with fewer animals observed hierarchies often yield significant linear hierarchies, but that this linearity can often solely result from chance. Our results are therefore consistent with and support Gorlick's (1974) findings on the presence of linear hierarchies in guppies, but now also demonstrated in groups with more than six animals. We have to note however that the observations were based on dyadic interactions that may not mirror how animals interact when other individuals are present, i.e. in the social group. The linear dominance based on the agonistic interactions seems to be mirrored in the outcome of the competition (i.e. who got most food) as the dominance hierarchies based on the different measures correlated with each other, at least in one of the groups. Combining the probabilities revealed an overall support for the notion that there is a relationship between the two different measures.

Agonistic behaviours were generally unidirectional, i.e. one of the pair attacked the other without being attacked in turn, resulting in a high directional consistency index for both groups with separate significant or close to significance hierarchies. The directional consistency index was consistently lower in the dominance hierarchies calculated with the number of food items animals obtained during the dyadic competitions. This is due to the fact that both individuals obtained food during some of the trials, whereas typically only one fish directed agonistic behaviour towards the other. Despite this difference in the percentage of bi-directional interactions, the linearity index *h'* was consistently higher for the dominance hierarchy based on the food items than for the hierarchies based on the agonistic interactions. This was probably due to the high proportion (42-47%) of unknown relationships in the aggression matrix, while in the food matrix data were obtained for all dyads. We observed in one group that the animal that reached the feeder first was also the one that directed the most agonistic behaviours to the other. Overall, hourly rates of agonistic behaviour within dyads were lower than those reported by Gorlick (127.3-167.4 aggressive encounters/hour for groups of 4-6 individuals; 1974), which may be due to a lower chance of encountering another individual in groups with fewer individuals as was the case here as we tested animals in dyads. However, a higher rate of aggression might have been expected from our test given that it was conducted in a competitive situation.

There was variation between the groups, resulting in significant or non-significant hierarchies based on the agonistic interactions. This variation may be due to differences in number of animals, number of observed agonistic behaviours or the number of undetermined relationships. Gorlick (1974) distinguished several types of dominance hierarchies in his study, straight-line, when agonistic behaviours were solely uni-directional, pseudo straight-line, when interactions in general were uni-directional, but when not all animals interacted with every other animal, and undetermined, when some dyads interacted at only low frequency or in both directions. Our results may be comparable to this last type of dominance hierarchy, as the dominance relationships in some of the dyads were not resolved and may have resulted in non-significant results, especially in group 3 with only seven individuals. The absence of dominance interactions may account for this. Some animals may not have been motivated to compete over food on some of the test days, resulting in a low frequency of or no interactions in this dyad. Alternatively, some animals may have actively avoided each other, since dominance relations had been assessed beforehand and costly interactions may have been avoided. It is not clear what caused the absence of interactions in some of the dyads (group 1: 40%, group 2: 47%, group 3: 48% of all dyads).

We did not find that body mass correlated with either of the established dominance hierarchies (based on agonistic behaviours or outcome food competition). However, we found that number of agonistic behaviour received negatively correlated with weight, in the sense that smaller individuals received more aggression. This is consistent with what has been show in other fish species (Gorlick 1974; Huntingford et al. 1990; Whiteman and Coté 2004).

Gorlick (1974) found that dominance relationships remain stable during a prolonged period. Hence, the obtained hierarchies (groups 1 & 2) and the direction of agonistic behaviours between selected pairs (group 3) were used to pair the individuals in the visual perspective taking task (experiment 2).

5

Summary and discussion

Attending to the visual behaviour of others is considered to be a central component of human and animal social cognition. In humans, gaze following has often been associated with Theory of Mind, which is the ability to understand that other individuals have private thoughts, goals or emotions. Also in animals, gaze following has been documented in various species, however, the underlying cognitive mechanism in a number of these species and the evolution of this skill remains to be investigated. Gaze following in animals may be based on simple reflex-like or learned mechanisms, however may also indicate an appreciation of what another may see, which would be indicative of abilities relating to Theory of Mind. Therefore, in this thesis I addressed the potential cognitive mechanisms underlying gaze following in a non-human primate species. Moreover, in an attempt to address the evolutionary history of this capacity I extended the range of species under investigation for their gaze following skills to one that is phylogenetically more remote from humans, namely fish.

In chapter 2 I demonstrated that long-tailed macaques attend to the looking direction of a human experimenter, a finding consistent with those in other non-human primates (e.g. Tomasello et al. 1998). Like human infants and great apes, long-tailed macaques were observed check-looking at the experimenter's face after following gaze, i.e. looking back and forth between the experimenter's face and her gazing direction (chapter 2). In human infants, check-looking is thought to results from the child's violated expectation (as there is nothing to be seen in the other's looking direction), which has been interpreted as indication of the understanding that the other is looking at something specific. However, as simpler mechanisms may apply here (e.g. repeatedly triggered gaze-following response), I continued to approach the question on the underlying mechanism with a different paradigm, that made use of the social signals of the study species. Attending to another's looking direction may provide an individual with valuable information on its social environment (e.g. Tomasello et al. 1998). I examined whether gaze shifts that were accompanied by a species-specific facial expression would affect subjects' gaze following response, which could indicate subjects' expectation on the nature of the looked-at target. We found that a fearful facial expression, which is frequently used during macaque social interactions, increased gaze following responses in long-tailed macaques, indicating that the behaviour is flexibly employed depending on the social context of the situation. This result may be due to a specific arousal-effect, or, alternatively may indicate that the gaze follower has an expectation of what the other perceives (chapter 2).

In chapter 3, I investigated whether long-tailed macaques would follow the gaze of a conspecific demonstrator to a hidden location, which would indicate a capacity to extrapolate the other's line of sight to locations outside the field of vision (chapter 3). Long-tailed macaques relocated to a designated area from which they could visually access the hidden location and directed more focussed looks to this location than in a control situation, suggesting that they employed 'geometrical' (i.e. the ability to track an imaginary line of sight to exact locations) and 'representational' (i.e. the ability to have a representation of space outside the visual field) gaze following skills (chapter 1, 3). Taken together, these studies suggest that monkeys' gaze following behaviour is a more flexible and accurate ability than has previously been shown, and thus this capacity may be based on an appreciation of the fact that another's gaze and attention can be directed at something specific ('joint attention'). These results parallel findings in chimpanzees that have been associated with the ability to attribute perceptual states to others, which can be generically labelled 'Theory of Mind' (Call and Tomasello 2008).

Investigating the capacities of different taxa opens the possibility of examining the taxonomic range of social cognitive capacities, which can be a first step to construct hypotheses about the evolutionary history and functional relevance of these capacities. Remarkable similarities at least on a behavioural level have been documented for non-human primates and fish, behaviours that in primates have been used to assess advanced cognitive capacities (Bshary et al. 2002, Brown and Laland 2003). Therefore, in chapter 4, I extended the study of gaze following and a related capacity, visual perspective taking, to guppies, a teleost fish. First, I investigated whether guppies would follow the body-orientation of conspecifics to a location out of their own sight, adapting a design used to study gaze following in other species. Second, I examined whether guppies would assess the visual perspective or the behaviour of a conspecific competitor in a food competition paradigm. Whereas I found some indication for behaviour similar to 'ecological' gaze following in other vertebrate species, i.e. gaze (body) following in the approximate same direction, I did not find evidence for visual perspective taking skills in guppies (chapter 4). Although the results need further verification, they suggest that the sensitivity to others' head- and body-direction may be an ancient vertebrate capacity, i.e. a capacity that has been present in the common ancestors of the vertebrates, based on a general sensitivity to head/body direction or on the widespread ability to learn. Alternatively, this may be an instance of convergent evolution, i.e. has evolved several times in the different taxa (mammals, birds and potentially fish) as response to similar selective pressures (for instance living in groups).

GAZE FOLLOWING IN MONKEYS: AN INDICATOR OF THEORY OF MIND?

The question how animals perceive and interpret the behaviour of others and whether they do this in terms of mental states has been investigated extensively in apes. In a recent review, Call and Tomasello (2008) summarise the evidence for elements of Theory of Mind in chimpanzees, gathered in the 30 years since Premack and Woodruff's (1978) groundbreaking article. They focus on two classes of mental states, namely *intentions* and *perceptions* (see also chapter 1) that may be assessed in other individuals. As indicators of an appreciation of others' *perceptions* they present **(1) Gaze following**, i.e. how chimpanzees responded to the gazing direction of others, **(2) Gestural communication**, i.e. whether they assess the attentional state of the experimenter or competitor and adapt their gestural communication accordingly, and **(3) Responses in a food competition paradigm**, i.e. what information animals use to assess what another may or may not see (i.e. 'visual perspective taking'; chapter 4). Some of these behaviours (in particular gaze following and related abilities) have been considered to be developmentally early signals of an appreciation of what another human perceives (e.g. Baron-Cohen 1995) and thus should be considered as such in non-human animal species as well (Call and Tomasello 2008).

The abilities Call and Tomasello (2008) document in their review may not be restricted to chimpanzees. Here, I have shown that long-tailed macaques pass similar gaze-following tests to chimpanzees (Call and Tomasello 2008; see Table 1). Briefly, both chimpanzees and long-tailed macaques follow others' gaze, check-look, and follow gaze to hidden locations (Povinelli and Eddy 1996a; Tomasello et al. 1999; chapters 2 and 3). In studies on gestural communication, Call and Tomasello (2008) point out how chimpanzees respond to the direction of others' attention. Chimpanzees spontaneously and flexibly adapt their behaviour to the configuration of the human experimenter's body and head direction, for instance by relocating to a position from where the experimenter can see the animal (e.g. Povinelli et al. 2003). Similarly, macaques have been shown to preferentially show facial expressions to directed, as opposed to averted, faces (Perrett and Mistlin 1991; see Table 1). Long-tailed macaques actively relocate to a position from where a human experimenter is likely to see them in order to display facial expressions of threat (personal observation). Call and Tomasello (2008) suggest that the strongest indication for perception (and thus mental state) attribution in chimpanzees is found in responses in a food competition (i.e. visual perspective taking) paradigm. These experiments are all based on the same basic idea: Two animals compete over food sources that are either hidden or visible from the *perspective* of a dominant competitor. Subordinates' preference for the food-source

Table 1. Comparison of documented abilities related to assessment of other's perceptions in chimpanzees and human infants (taken from Call and Tomasello 2008) with evidence for the same capacities in monkeys. *Abilities that have been only formally documented in chimpanzees and not in human infants.

Capacities documented in both chimpanzees and human infants	Evidence in monkey species?	Monkey species and source
Gaze following		
1. Follow gaze to distant locations behind self	**Not known**	
2. Follow gaze on the basis of both face and eye direction	**Yes**	This thesis (**ch 2**); pigtailed and rhesus macaques attend to eye-direction alone (Lorincz et al. 1999; Ferrari et al. 2000)
3. Check back to gazer if nothing relevant is seen at the target location	**Yes**	This thesis (**ch 2**)
4. Stop looking after a few trials if nothing relevant is seen at the target location*	**Yes**	This thesis (**ch 2**): Some indication of habituation between exp. 1 & exp. 2
5. Ignore distracting objects in the path of the target location	**Yes**	Common marmosets follow gaze to gazed-at target, past distracting objects (Burkart and Heschl 2006)
6. Move to the side of opaque barriers to view the target location	**Yes**	This thesis (**ch 3**)
7. Understand that gaze stops at an opaque barrier - unless it has a window in it	**Not known**	
Gestural communication		
8. Use visual gestures mostly when conspecifics or experimenter are oriented towards them	**Yes**	Stumptailed macaques direct more submissive facial expressions towards face with directed than averted eyes (Perrett and Mistlin 1991)
9. Position oneself to gesture in front of others	**Probably**	Unpublished personal observation in long-tailed macaques: individuals repeatedly relocate in order to direct threats at experimenter's face
10. Both face and eye orientation of recipient determine gesture production	**Yes**	See 8, stumptailed macaques produce more facial expressions towards face with directed than averted eyes, irrespective of head-orientation (Perrett and Mistlin 1991)
Food competition		
11. Pick the food that the experimenter is not looking at*	**Yes**	Rhesus macaques (Flombaum and Santos 2005)
12. Pick the food that a dominant individual or the experimenter cannot see because of barrier	**Yes**	Common marmosets (Burkart and Heschl 2007), capuchin monkeys (Hare et al. 2003), and rhesus macaques (Flombaum and Santos 2005) show this behaviour
13. Visually conceal approach to food (using barrier)*	**Not known**	
14. Auditorially conceal approach to food (choosing silent door)*	**Yes**	Similar evidence in rhesus macaques (Santos et al. 2006): Animals show preference for stealing food from 'silent' box, i.e. box that does not produce sound when touching.
15. Take food that a dominant individual did not see being hidden	**Not known**	
16. Understand that if competitor picks first, competitor will choose the viewed food (not the food not viewed) being hidden	**Not known**	

out of the competitor's line of sight has been interpreted as appreciation of what the other can see and cannot see, thereby implying assessment and interpretation of the other's perceptions (Hare et al. 2000; 2001; see also chapter 4). Similar evidence comes from a study on rhesus macaques (Flombaum and Santos 2005). Here experimenters investigated whether macaques would preferentially steal food from a human experimenter that could not see the food item as compared to an experimenter who could see it. Results showed that, across different conditions, animals assessed the direction of the experimenters' gaze and subsequently approached the experimenter that could not see the food (Flombaum and Santos 2005).

There are thus striking parallels between chimpanzees and other non-human primates in virtually all capacities that may indicate an appreciation of the other's perceptions (Call and Tomasello 2008; Table 1)[1]. Within the hominid clade there is evidence on some of the documented abilities, such as gaze following to hidden locations (e.g. Bräuer et al. 2005; Shillito et al. 2005; Okamoto-Barth et al. 2007). Outside the apes, species for which these capacities have been reported include animals from different primate taxa, such as Old World monkeys (macaques) and New World monkeys (capuchins, common marmosets), suggesting that sensitivity to others' visual cues may be widespread among diurnal non-human primates. These parallels between chimpanzees and other non-human primates challenge the prevailing view (e.g. Whiten 1997; Dunbar 2001; Deaner et al. 2006) that the great apes excel in (social) cognitive capacities, at least with respect to the assessment of others' perceptions. Although Table 1 provides a compilation of studies conducted on different monkey species and further evidence is required on the various capacities within the same species, these results support the hypothesis that there may not be general differences in social cognitive capacities between great apes and other non-human primates (Tomasello and Call 1997). It is likely that the remaining gaps in the evidence, for instance the ability to follow gaze behind themselves (see Table 1), will be filled with findings documented in monkey species, and that further paradigms that can clearly eliminate alternative explanations may be added in order to complete the picture (see Andrews 2005). Moreover, studies on the assessment of others' perceptions should be extended to other taxa, in order to establish how widespread the different capacities are. There is already some evidence on the individuals' appreciation of others' perceptions in some corvid species

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[1] It has to be noted that in the second category ('gestural communication') the monkey evidence mainly comes from communication through social facial expressions, as use of manual gestures in monkeys is less common than in apes, if not absent entirely (Tomasello and Call 1997).

(Bugnyar et al. 2004; Bugnyar and Heinrich 2005; Dally et al. 2006), evidence that may eventually allow for evolutionary hypotheses on history and function to be tested.

The evidence presented by Call and Tomasello (2008) for chimpanzees' sensitivity to perceptual states of others seems compelling, as the animals demonstrate a variety of behaviour patterns that may be based on the assessment what another perceives. However, most if not all of these behaviours (Table 1, Call and Tomasello 2008) can be explained by rules that are governed by assessing another's *behaviour* instead of another's *mental states* (Povinelli and Vonk 2004). For instance, an individual may acquire certain behavioural rules through associative learning (e.g. following gaze will likely result in seeing something rewarding, reinforcing this action) without grasping that the other's actions are based on (unobservable) mental states, such as perceptions, thoughts or intentions. Based on these behavioural rules, non-human primates (and potentially other animals) may additionally form 'behavioural abstractions' of past experiences (Povinelli and Vonk 2003, e.g. another individual's eyes directed to a certain direction combined with a food-item at that location leads in most cases to an action directed at food – approach, snatch and/or consumption) that enable them to predict others' behaviour in similar future situations, without assessing the other's *mental* states at that moment. This critique makes it very difficult, if not impossible, to demonstrate the capacity to attribute mental states to others in experiments that require predictions on behaviour of the others, because results can always be explained either way (Povinelli and Vonk 2003). Moreover, it has been suggested that it is humans' Theory of Mind that makes them prone to accept explanations consistent with Theory of Mind and to expect similar capacities to be present in species other than our own (e.g. Povinelli et al. 2000). That is, documentation of Theory of Mind in non-humans could be a consequence of human Theory of Mind, not non-human animal Theory of Mind.

Indeed, none of the presented behavioural patterns (e.g. gaze following to hidden locations, Table 1) alone may be able to provide unequivocal proof for the capacity to understand others' perceptions in animals. Alternative explanations as the one described above (such as associative learning) may be applicable to all behaviours that have been connected to assessing others' perceptions (Call and Tomasello 2008). Therefore, the capacity to follow gaze based on the 'geometrical' or 'representational' level presented in this thesis may be consistent with, but cannot definitely prove a mentalistic understanding of the other's looking behaviour (i.e. understanding that the other is seeing something different than oneself; chapter 3). However, there are several arguments against this critique.

First, it has been argued that even if animals use very fine-grained 'behavioural abstractions' rules, but apply them flexibly in various different and novel situations, this may be labelled as having a 'theory' about others' perceptions (Flombaum and Santos 2005). Second, several of the behaviours listed in Table 1 have been proposed to be developmental preconditions to Theory of Mind in human infants (Flavell 1999, see also chapter 1, Box 1). It has been argued that the same standards should be applied when interpreting and comparing performances of human infants and non-human animals in similar tests (Andrews 2005). If a certain behaviour in human infants is interpreted as indicating an understanding of another individual's mind then this should also be true in other species (Andrews 2005; but see e.g. Wynne 2004b on anthropomorphism). That said, in developmental psychology views differ regarding the developmental stage and capacity with which mentalistic understanding of the behaviour of others' emerges (e.g. Doherty 2006; Corkum and Moore 1998, on learning of gaze following responses in human infants). Lastly, Call and Tomasello (2008) emphasize that the power of the presented multi-level and multi-facetted approach lies in the evidence of a wide variety of experiments and methodologies that all points in the same direction, i.e. that the animals' responses are based on what the other sees, hears and knows, which is, according to their view, the most parsimonious explanation for the accumulated evidence.

The current evidence does allow at minimum the conclusion that chimpanzees (and other animals) do respond *as if* they assess the others' perceptions (and for chimpanzees also intentions, see for review Call and Tomasello 2008) and they do this is in flexible ways and in different and what appear to be novel situations. Alternative explanations for the mentalistic interpretation of these results cannot be fully excluded (Povinelli and Vonk 2003; 2004), unless experiments are designed that allow a clear distinction between '*behaviour*'- and '*mental states*'-reading. However, the fact that alternative, apparently simpler explanations can be formulated does not necessarily mean that animals use these strategies in their behaviour (as demonstrated in diverse control conditions). An approach that could shed new, and perhaps complementary, light on the question whether animals can assess the mental states of others may be to include results from other disciplines, as for instance neuroscience, in the analysis of animal capacities (see also Lyons et al. 2006). Mirror neurons in monkeys have been suggested to serve as internal recognition mechanism for the action of others. In addition and more importantly in this context, there is some evidence that macaque mirror neurons are active in response to others' intentions (Fogassi et al. 2005), not only the observed actions. Further exploration of the possible roles of mirror neurons in internal 'representation' of others' mental states, such as others' emotions or perceptions, in combination with new behavioural experiments (see Andrews 2005) may eventually shed light on and settle the question on what other species 'understand' of others' minds.

COGNITIVE EVOLUTION: FROM PRIMATES TO FISH AND BACK?

Gaze following has been demonstrated in various animal species, yet, thus far research has been limited to birds and mammals. In chapter 4 I present evidence that this range of species may be extended to another vertebrate taxon, namely fish. Guppies responded to the body direction of the demonstrators or to the indicated location, whereas they failed to respond to the visual perspective or the behaviour of a competitor. Although the results of the 'gaze-following' experiment need verification and further examination to exclude alternative explanations, this is a first step to include fish species in the study of how species in this taxon perceive and respond to the visual behaviour and/or attention of others.

The presence of this co-orienting capacity in fish could be a product of convergent evolution, i.e. evolution of similar capacities in distantly related taxa due to similar selection pressures. In general, gaze following has been suggested to be advantageous to social animals, since valuable information on predators, mates or food sources may be gained by attending to the gazing direction of group members (e.g. Povinelli and Eddy 1996a; Tomasello et al. 1998). In fish, the sensitivity to others' head and body direction may also be beneficial when shoaling with or following others, or during social interactions, for instance in cases where audience effects (i.e. the presence of an 'audience', such as a competitor, affects an individual's behaviour) have been documented (see chapter 4). Also in flocking species, such as ravens, following others' head and or body-direction may be beneficial when moving together. Challenges posed by group life may thus be diverse, and it may well be the case, that, although the capacity to follow gaze (or equivalent co-orienting behaviour) has evolved several times in the different taxa, it may be an adaptation to different aspects of group life. In fish and birds it may result from the necessity to move together, and thus to co-orient, while in primates it may serve to assess the direction of others' attention during social interactions. Thus, it is not clear at this point what the potential selection pressures were that resulted in behaviourally similar abilities in different taxa of animals.

An alternative evolutionary scenario involves common descent of the capacity, i.e. the sensitivity to others' gazing direction (as indicated by eye-, head- and/or body-orientation) is (part of) a general (conserved) vertebrate capacity.

Consequently, this capacity can also be expected in the remaining vertebrate taxa, namely reptiles and amphibians. For instance, it is possible that 'ecological' gaze following (or alignment with head/body orientation) can be acquired by any species that is able to learn. Triesch and colleagues (2006) showed in a computational study that a 'basic set' of capacities is sufficient for 'ecological' gaze following to be learned, the basic set consisting of a preference for eyes (or eye-like stimuli), 'reward-driven learning', habituation and a structured social environment (Triesch et al. 2006). Although it has been shown that learning may play a role in the acquisition of human gaze following, in both typically developing and autistic individuals (e.g. Corkum and Moore 1998, Leekam et al. 1998), the role of learning in animal gaze following remains to be addressed (but see Tomasello et al. 2001; Vick et al. 2001). Triesch et al. (2006) make a number of predictions that could be tested in animals, for instance that individuals with face aversion are expected to have difficulties in learning to follow gaze. The alternative to a learned response would be a general vertebrate sensitivity to others' head- and/or body-direction. For instance, there is evidence for a basic sensitivity to the eyes or eye-like stimuli in members of most vertebrate taxa. Many species respond to the eyes as an aversive stimulus: young jewel fish avoid eye-like stimuli more as comparable spot patterns (Coss 1979), and Anolis lizards, *Anolis carolinensis*, respond to directed gaze with tonic immobility, i.e. they stop moving when being watched (Hennig 1977). Like eye sensitivity, there may be a taxonomically widespread mechanism to co-orient with the 'gazing' (head/body) direction of others. This potential sensitivity to other's (head-/body) direction ('ecological' gaze following, in Butterworth and Jarrett's (1991) terminology) may be the evolutionary and developmental basis for the more flexible, accurate or even mentalistic understanding of others' gazing direction.

At present, it cannot be determined whether the phylogenetically widespread capacity to follow gaze is based on a vertebrate-wide propensities or abilities (i.e., sensitivity to others' head/body direction or general learning abilities), or whether gaze following evolved several times as adaptations to (social) challenges. Evidence for gaze following comes thus far only from social species in both mammals and birds and little work has been done on less social or solitary species. This makes it difficult to assess whether (a) the ability has evolved as adaptation to social life (and to which aspect of social life) and (b) a social environment is required to learn the behaviour. From a functional point of view, it could be argued that gaze following is also beneficial for solitary species that rely on visual signals, for example assessing the direction of predators' gaze (Watve et al. 2002). Together, the selection pressures promoting gaze following capacities remain to be determined. Research has started to address potential selection pressures favouring gaze following by comparing closely related species that do not share a similar recent evolutionary history. For instance, the sensitivity to human pointing and gazing has been compared between domestic dogs and wolves (both equally familiarized with humans), revealing that dogs excelled in responding to and interpreting human visual cues (Hare et al. 2002). This sensitivity in dogs has been argued to result from evolved changes during the domesticated animals' shared recent history with humans (Hare et al. 2002; but see e.g. Udell and Wynne 2008), but alternatively it may be due to learning opportunities provided by the social environment of domesticated (and social) animals. Further comparative studies on both closely and more distantly related species are required to address potential selection pressures. Moreover, future research needs to investigate the role of learning in the acquisition of gaze following capacities.

THERE IS MORE TO GAZE THAN MEETS THE EYE

The results presented in this thesis suggest that there is more to gaze than meets the eye. When I started this research, evidence on animals' sensitivity to the eyes and their direction was abundant, however, questions on evolutionary paths and underlying cognitive mechanisms in species other than the great apes had not been extensively studied. With this thesis, I wished to address this gap. Gaze following based on the 'ecological' mechanism (i.e. follow gaze in approximately the same direction) is present in species of different vertebrate taxa, potentially including fish (chapter 4), and it is likely that more species will be added in the future. Widening the taxonomic scope of animals studied will allow hypotheses on the evolution of gaze following to be developed. Focussing on the cognitive mechanism, examination of gaze following skills in a non-hominid primate, the long-tailed macaque, provided insight in how these animals respond to the social signals accompanying gaze-shifts, indicating a flexible use of gaze following behaviour in these animals. Furthermore, there is now evidence that macaques, like the great apes, are able to track another individual's line of sight by extrapolating the other's gaze to exact locations and to areas outside their own immediate field of vision, a result that is consistent with the hypothesis that social cognitive skills may not differ among non-human primates (Tomasello and Call 1997). Gaze following or joint attention as capacities by themselves do not provide a decisive criterion to assess whether a species (human or non-human) can or cannot understand the mental states of others. However and importantly, they form part of a complex of processes that animals may use in assessing others' perceptions. In this context, further research needs to address the relationship of these capacities with the more advanced levels of the assessment of others' perceptions (such as visual perspective taking) within different species in order to gain insight how animals view others. Integration of these results with those from other disciplines (such as developmental psychology or neuroscience) may eventually lead to a complete understanding on the cognitive processes in the minds of non-human animals. This thesis is an example how evolutionary and mechanistic approaches to behaviour can be integrated and can shed new light on non-human animals' cognitive capacities.

Nederlandse samenvatting

INTRODUCTIE

Blikken spelen een belangrijke rol in sociale interacties van zowel dier als mens. Voor dieren kan de juiste interpretatie van de kijkrichting van een ander individu, samen met de emotionele lading van een situatie, essentieel zijn voor het overleven. Van mensen wordt gezegd dat ze de gevoelens of zelfs de gedachten van een ander af kunnen lezen aan de ogen. Deze worden dan ook wel de spiegel van de ziel genoemd (Cicero, De Oratore Liber Tertius). De capaciteit om het kijkgedrag van anderen juist te interpreteren en te begrijpen wordt geacht centraal te staan in de ontwikkeling van 'Theory of Mind' bij mensen (Baron Cohen 1995). Theory of Mind is het vermogen om te begrijpen dat een ander individu zijn eigen (verborgen) gedachten, emoties en intenties heeft (Heyes 1998).

Wetenschappelijke interesse in de cognitieve capaciteiten van dieren en de evolutie hiervan begon te groeien nadat Darwin (1871) had geponeerd dat er een continuïteit was tussen mens en dier, niet alleen in morfologie of fysiologie, maar ook in de mentale capaciteiten. Onderzoek heeft zich gericht op het bestuderen van gelijkenissen en verschillen in cognitieve capaciteiten van diverse diersoorten. Dit heeft globaal geleid tot twee theoretische stromingen. De 'general process view' postuleert dat er algemene cognitieve mechanismes (zoals voor leren en geheugen) bestaan, die niet probleem- of domeinspecifiek zijn (Macphail 1987; Bitterman 2000; Macphail and Bolhuis 2001). Volgens deze zienswijze kunnen dieren verschillen met betrekking tot hun perceptuele mechanismen (bijvoorbeeld wat ze kunnen waarnemen), maar niet met betrekking tot het onderliggende cognitieve mechanisme (bijvoorbeeld hoe herinneringen worden vastgelegd; Macphail and Bolhuis 2001; Wynne 2004). Een andere stroming, 'adaptive specialisations', postuleert dat cognitieve mechanismes en capaciteiten kunnen evolueren en daardoor (modulaire) aanpassingen zijn aan de omgevingsfactoren (sociaal en ecologisch) van een diersoort (Shettleworth 1998). Dit kan leiden tot 'specialisaties' in bepaalde cognitieve eigenschappen. Zo suggereren de 'Sociale intelligentie' hypotheses (Jolly 1966; Humphrey 1976; Whiten 1997), dat het leven in sociale groepen de belangrijkste drijfveer van cognitieve evolutie is (voor alternatieven en complementaire ideeën, zie Parker and Gibson 1977; Milton 1981; Deaner et al. 2000; Reader and Laland 2002). Sociale dieren moeten om kunnen gaan met het flexibele en vaak onvoorspelbare gedrag van hun soortgenoten. Capaciteiten die een individu in staat stellen snel en flexibel hierop te anticiperen kunnen zorgen voor een selectief voordeel, waardoor deze capaciteiten kunnen evolueren.

Traditioneel heeft wetenschappelijk onderzoek naar geavanceerde capaciteiten zich gericht op non-humane primaten, de soorten die phylogenetisch het dichtst bij de mens staan. Inderdaad zijn er gedragingen in non-humane primaten geobserveerd die zouden kunnen wijzen op geavanceerde cognitieve capaciteiten, zoals het gebruik van werktuigen (McGrew 1992), sociaal leren (Kawai 1965) of misleidend gedrag (Whiten and Byrne 1988). In een poging de evolutie van bepaalde humane cognitieve eigenschappen te onderzoeken zijn er verbanden gelegd tussen de phylogenie van de primaten en de aangetoonde eigenschappen. Er wordt aangenomen dat binnen de primaten een cognitieve gleuf bestaat tussen de mensapen en andere apen (Whiten 1997; Byrne 2000), in de zin dat mensapen over meer geavanceerde sociaal cognitieve capaciteiten beschikken dan andere apensoorten (apen en halfapen). Over het algemeen worden gelijkenissen in cognitieve capaciteiten tussen nauw verwante soorten geweten aan de gemeenschappelijke oorsprong ('common descent'). Een alternatieve verklaring is 'convergente evolutie'. Hiervan is sprake als vergelijkbare eigenschappen gevonden worden bij diersoorten die phylogenetisch niet heel nauw aan elkaar verwant zijn, maar leven met vergelijkbare ecologische en sociale omgevingsfactoren. De vergelijkbare capaciteiten zouden dan aanpassingen zijn aan de soortgelijke omgevingsfactoren. Zo zijn er bijvoorbeeld complexe cognitieve capaciteiten beschreven bij verschillende sociale dieren, zoals bijvoorbeeld walvisachtigen, vleeseters en kraaiachtigen (e.g. De Waal and Tyack 2003, Emery and Clayton 2004).

Cognitieve capaciteiten die bij dieren onderzocht zijn, omvatten individuele herkenning (Cheney 1980; Tebbich et al. 2002), het herkennen van rangordes (Dasser 1988; Bergman et al. 2003), spiegelzelfherkenning (Gallup 1970; Plotnik et al. 2006; Prior et al. 2008) en het begrip dat andere dieren eigen emoties, waarnemingen of gedachten kunnen hebben, 'Theory of Mind' (Premack and Woodruff 1978). Tot nu toe is er nog geen duidelijk en onbetwist bewijs bij dieren voor deze eigenschap, ondanks het feit dat hier al 30 jaar lang onderzoek naar gedaan wordt (Premack and Woodruff, 1978; Heyes 1998; Tomasello et al. 2003a,b; Povinelli and Vonk 2003a,b). Recentelijk is echter aangetoond dat chimpansees wellicht gevoelig zijn voor sommige 'mental states' (zoals waarnemingen en intenties) van andere individuen. Er is gesuggereerd dat 'Theory of Mind' niet noodzakelijkerwijs een geïsoleerde capaciteit is, maar diverse sociaal-cognitieve processen omvat (Tomasello et al. 2003). Enkele van deze processen zijn het volgen van de kijkrichting van anderen ('gaze following'), het begrijpen dat een ander individu naar een specifiek object kijkt ('joint attention') of het zich voor kunnen stellen wat een ander kan zien vanuit een ander perspectief ('visual perspective taking'). In dit proefschrift heb ik deze eigenschappen bij dieren onderzocht.

DIT PROEFSCHRIFT

De capaciteit om de blikrichting van een ander te volgen is voor vele verschillende diersoorten beschreven, zoals, apen, gedomesticeerde zoogdieren, zeezoogdieren en vogels (Tomasello et al. 1998; Miklosi et al. 1998; Ferrari et al. 2000; Scheumann and Call 2004; Bugnyar 2004; Kaminski et al. 2005). Het feit dat deze capaciteit zo wijdverspreid is in het dierenrijk werpt vragen op over de evolutie hiervan, maar ook over het cognitieve mechanisme dat hieraan ten grondslag ligt. Bij mensen is er consensus en bewijs dat de betekenis van ogen en de capaciteit tot het volgen van de blikrichting van een ander naar een bepaald object ('joint attention') belangrijk is in de ontwikkeling van 'Theory of Mind' (Baron-Cohen 1995; Flavell 1999; zie voor overzicht Flom et al. 2007). In dieren moet nog onderzocht worden of aan deze capaciteit een simpeler mechanisme (zoals een reflex-achtig of geleerd) of een geavanceerd mechanisme ten grondslag ligt dat wellicht een indicatie kan geven voor capaciteiten die met 'Theory of Mind' te maken hebben. Daarom is het in de studie van non-humane cognitie essentieel om (a) de cognitieve mechanismen van het volgen van andermans blik te onderzoeken bij dieren, in andere woorden, te onderzoeken of het gedrag in de verschillende soorten gebaseerd is op basale mechanismen of op cognitief meer geavanceerde mechanismen die iets met het begrijpen van de waarnemingen van een ander te maken zouden kunnen hebben, (b) primatensoorten buiten de mensapen te bestuderen om hiermee informatie over de evolutie van cognitieve capaciteiten van primaten te vergaren en (c) vanuit een vergelijkend perspectief soorten van verschillende takken van vertebraten te onderzoeken om de evolutionaire geschiedenis van dit gedrag te bestuderen. In dit proefschrift heb ik bestudeerd hoe dieren, in het bijzonder java-apen, *Macaca fascicularis*, en guppies, *Poecilia reticulata*, het visuele gedrag van anderen waarnemen en interpreteren. Eerst heb ik de mogelijke cognitieve mechanismen onderzocht die aan het volgen van de blik van een ander ten grondslag ligt (hoofdstukken 2 en 3). Vanuit een vergelijkend perspectief heb ik in kaart gebracht hoe wijdverspreid dit gedrag binnen de gewervelde dieren is, aangezien het tot nu toe alleen bij vogels en zoogdieren is aangetoond. Voor dit doel heb ik onderzocht of ook vissen op het visuele gedrag van anderen reageren (hoofdstuk 4).

In **hoofdstuk 2** heb ik onderzocht of java-apen de blikrichting van een ander individu kunnen volgen, in dit geval de blikrichting van een experimentator. Voorafgaand aan deze studie was er al bewijs dat andere apensoorten dit gedrag vertonen. Ook in java-apen bleek dit het geval te zijn. Als een experimentator plotseling omhoog keek, volgden de dieren haar blikrichting naar het plafond. Het was opvallend dat een meerderheid van de dieren, nadat ze de blikrichting hadden gevolgd, terugkeek naar het gezicht van de experimentator om vervolgens weer richting plafond te kijken. Dit gedrag ('check-looking') is ook al beschreven bij jonge kinderen en bij mensapen. Bij jonge kinderen wordt het geïnterpreteerd als indicatie voor het begrip dat een ander naar iets specifieks zou moeten kijken als hij of zij een andere kant op kijkt (en niet zo maar zijn hoofd draait). Voor dit gedrag zijn er echter ook simpelere verklaringen, zoals dat het individu (kind of dier) nadat het de blikrichting heeft gevolgd terugkeert naar zijn oorspronkelijke houding, daar vervolgens de experimentator ziet, die nog steeds ergens anders heen kijkt, wat nogmaals dezelfde respons (onafhankelijk van de eerste) oproept, waarvoor geen begrip van het feit nodig is dat de aandacht van de ander ergens op gevestigd is.

In een vervolgstudie was daarom de vraag of de dieren een verwachting hebben over wat de ander ziet. Hiervoor heb ik gebruik gemaakt van de gezichtsuitdrukkingen waar java-apen veelal mee communiceren. Deze gezichtsuitdrukkingen worden wellicht door dieren gebruikt om relevante informatie te vergaren. Zo zou een dreigend gezicht in een bepaalde richting kunnen wijzen op een naderend conflict. In dit experiment heb ik onderzocht hoe java-apen zouden reageren op een verandering van blikrichting waarbij de experimentator verschillende apengezichtsuitdrukkingen liet zien. Apen volgden de blikrichting van de experimentator vaker als zij met een angstig gezicht naar het plafond keek dan met een neutrale gezichtsuitdrukking. Dit duidt erop dat apen de blik van een ander op een flexibele manier kunnen volgen, en dat deze capaciteit daarom niet gebaseerd is op een reflex-matig mechanisme. Het resultaat zou veroorzaakt kunnen zijn door een sterkere agitatie in de dieren door een angstige uitdrukking, waardoor ze vaker naar boven zijn gaan kijken. Het zou echter ook zo kunnen zijn, dat een angstuitdrukking relevante informatie is waarvoor het belangrijk is om de target waar de ander naar kijkt te identificeren. Deze interpretatie zou duiden op het feit dat apen een verwachting hebben waar een ander naar kijkt.

In **hoofdstuk 3** heb ik onderzocht of java-apen de blik van een ander naar een verborgen locatie (bijvoorbeeld naar een locatie achter een barrière), dus buiten hun eigen gezichtsveld, kunnen volgen. Deze capaciteit markeert bij jonge kinderen een stap in hun cognitieve ontwikkeling, omdat het geacht wordt geavanceerder te zijn dan het simpele reageren op de globale kijkrichting van een ander. Om dit te onderzoeken werd de aandacht van een aap ('demonstrator') getrokken naar een locatie die vanuit het perspectief van een andere aap ('subject', zie hoofdstuk 3, Fig. 1) niet te zien was. Om aandacht van de 'demonstrator' naar de verborgen locatie te trekken, verscheen er plotseling een spiegel. De verwachting was dat de 'demonstrator' zijn aandacht op de spiegel zou vestigen. Als het 'subject' zou begrijpen, dat de 'demonstrator' naar een locatie kijkt, die het zelf niet kan zien (vanuit zijn perspectief), dan zou het 'subject' zich moeten verplaatsen en moeten proberen te kunnen zien waar de ander nou precies naar kijkt. Zoals verwacht reageerden de 'demonstrators' op de spiegels met veelvuldig kijken en het vertonen van sociale gezichtsuitdrukkingen. Een aantal van de 'subjecten' reageerde hierop door zich te verplaatsen en meer geconcentreerde blikken te werpen in de richting van de locatie waar de ander naar keek dan in een vergelijkbare controlesituatie (waarbij de aandacht van de 'demonstrator' niet getrokken werd; zie hoofdstuk 3, Fig. 3). Dit duidt erop dat java-apen, zoals jonge kinderen, mensapen en raven (Moll and Tomasello 2004; Bugnyar et al. 2004; Bräuer et al. 2005), de blikken van een ander kunnen volgen naar een locatie die buiten hun eigen gezichtsveld ligt. Samen met de resultaten uit hoofdstuk 2 is dit een sterke aanwijzing dat het volgen de blik van een ander in java-apen een flexibele en accurate capaciteit is die wellicht gebaseerd is op het begrip dat de ander zijn aandacht op iets specifieks gericht heeft ('joint attention'). Deze resultaten zijn vergelijkbaar met resultaten in chimpansees die in verband worden gebracht met het begrijpen van wat een ander individu waarneemt (element van 'Theory of Mind'; Call and Tomasello 2008).

Het bestuderen van bepaalde capaciteiten in verschillende taxa is een eerste stap die nodig is voor het formuleren van hypotheses over de evolutie en de functionele relevantie van bepaalde capaciteiten. Er zijn verbluffende parallellen vastgesteld in bepaalde gedragingen van apen en vissen, zoals sociaal leren, coöperatie, of misleiding (Bshary et al. 2002, Brown and Laland 2003a,b). Deze gedragingen zijn in apen geïnterpreteerd als indicaties voor geavanceerde cognitieve capaciteiten (Bshary et al. 2002, Brown and Laland 2003a). In **hoofdstuk 4** heb ik daarom in twee experimenten onderzocht hoe vissen (guppies) op het visuele gedrag van soortgenoten reageren. Guppies zijn visuele dieren waarvan is aangetoond dat ze van elkaar kunnen leren wat ze moeten eten of hoe ze aan een predator kunnen ontsnappen (Brown and Laland 2003a,b; Reader et al. 2003). In het eerste experiment heb ik onderzocht of vissen de lichaamsoriëntatie van soortgenoten kunnen volgen (equivalent gedrag met het volgen van blikrichting van anderen in andere soorten) naar een verborgen locatie. Hiervoor werden vissen getraind om in een bepaalde richting te zwemmen (doordat ze in een afgesloten maar doorzichtige kleine ruimte zaten konden ze de locatie niet daadwerkelijk bereiken). Vervolgens werd geobserveerd hoe een ander dier ('subject') hierop zou reageren, door bijvoorbeeld te proberen de geïndiceerde locatie te bereiken. Subjecten zwommen niet bij voorkeur de aangewezen kant op, maar ze bleven wel langer aan die kant van de tank (dan aan de equivalente andere kant), die de 'demonstrators' hadden aangewezen. Dit zou er onder andere op kunnen wijzen dat er een gedrag - vergelijkbaar met het volgen van de kijkrichting van een ander - ook in vissen aanwezig zou kunnen zijn. Er is echter vervolgonderzoek nodig om dit effect te verifiëren. In het tweede experiment heb ik onderzocht of vissen kunnen reageren op het visuele perspectief van een ander ('visual perspective taking'). Deze capaciteit wordt geacht complexer te zijn dan het volgen van de blik van een ander individu. Hiervoor is gebruik gemaakt van een proefopzet, waarmee eerder de capaciteiten van verschillende apen soorten onderzocht zijn (Hare et al. 2000; 2003; Burkart and Heschl 2007). In deze test competeren twee dieren van verschillende dominantie rang om voedsel. Met verschillende condities waarbij visuele barrières ervoor zorgen dat een van de dieren niet alle voedselbronnen kan zien, wordt onderzocht of het dier dat lager is in rang rekening houdt met het perspectief (of het gedrag) van de dominante soortgenoot. Ik heb in de experimenten hiervoor geen aanwijzing gevonden.

Het lijkt erop dat guppies op bepaalde elementen van het 'visuele' gedrag van soortgenoten reageren. Nader onderzoek moet aantonen op welke elementen van het gedrag van de soortgenoten de subjecten gereageerd hebben. Met deze resultaten is een eerste stap gezet om ook vissen te betrekken bij de studie van capaciteiten die te maken hebben met de interpretatie van het visuele gedrag van anderen. Het is niet duidelijk of zulk gedrag gebaseerd is op een phylogenetisch oude capaciteit van vertebraten, die ook gevonden kan worden in alle dieren die kunnen leren, of een aanpassing is aan de sociale of ecologische condities van guppies.

CONCLUSIE

De capaciteit om de blikrichting van een ander te volgen is phylogenetisch wijdverspreid in diverse soorten van vertebraten. Dit gedrag is tot dusver gevonden bij zoogdieren, sommige vogelsoorten en wellicht ook vissen (hoofdstuk 4) en waarschijnlijk zullen er nog meer soorten aan deze lijst worden toegevoegd. Dit kan uiteindelijk leiden tot het formuleren en testen van evolutionaire hypothesen omtrent dit gedrag. Verder heb ik in dit proefschrift laten zien dat het volgen van de blikrichting van een ander individu een flexibele en accurate eigenschap is in apen (hoofdstukken 2 en 3). Dit zou erop kunnen duiden dat de dieren in staat zijn te begrijpen dat een ander individu iets anders ziet dan zijzelf als hij van kijkrichting verandert. Echter kunnen alternatieve (simpelere) verklaringen niet worden uitgesloten en daarom zijn de capaciteiten (het volgen van de blikrichting van anderen ('gaze following') en het herkennen dat de aandacht van een ander ergens op gevestigd is ('joint attention')) geen definitieve indicatie of zelfs bewijs voor het herkennen van de waarnemingen van een ander individu. De resultaten zijn consistent met resultaten bij andere apensoorten waaronder ook mensapen (e.g. Tomasello et al. 1998; Bräuer et al. 2005). Dit suggereert dat er binnen de orde van primaten geen significante verschillen zijn in sociaal cognitieve capaciteiten, tenminste met betrekking op capaciteiten die met het begrijpen van de waarnemingen van een ander te maken hebben. Verder onderzoek is noodzakelijk om aan te tonen hoe de hier onderzochte eigenschappen ('gaze following' en 'joint attention') in verband staan met andere meer geavanceerde capaciteiten ('visual perspective taking') en hoe dieren deze capaciteiten in hun natuurlijk gedrag toepassen. Integratie van resultaten vanuit andere disciplines (zoals de neurowetenschappen) is nodig om uiteindelijk een volledig beeld te kunnen vormen over hoe bij dieren het ene individu het andere kan begrijpen.

Deutsche Zusammenfassung

EINLEITUNG

Blicke spielen eine essentielle Rolle in sozialen Interaktionen von sowohl Menschen, als auch Tieren. Für Tiere kann die richtige Interpretation der Blickrichtung anderer zusammen mit der emotionellen Ladung einer Situation wichtig für das Überleben sein. Von Menschen wird gesagt, dass sie Gefühle oder selbst Gedanken von den Augen ablesen können – nicht verwunderlich, dass die Augen oft als Spiegel der Seele beschrieben werden (z.B. Cicero, De Oratore Liber Tertius). Das Vermögen, das visuelle Verhalten anderer richtig zu interpretieren, ist bei Menschen eine zentrale Komponente der sogenannten „Theory of Mind" (Baron-Cohen 1995). Theory of Mind wiederum ist die Eigenschaft zu erkennen, dass andere Individuen eigene Gedanken, Ziele oder Emotionen haben (Heyes 1998)

Mit der Formulierung der Evolutionstheorie Ende des 19. Jahrhunderts, die ein Kontinuum in morphologischen, physiologischen, aber auch kognitiven Eigenschaften suggerierte, wuchs das wissenschaftliche Interesse an den kognitiven Fähigkeiten von Tieren und deren Evolution. Die Forschung hat sich auf Unterschiede und Übereinstimmungen kognitiver Fähigkeiten diverser Tierarten gerichtet, was global zu zwei theoretischen Strömungen geleitet hat. In der sogenannten „General Process View" wird die Existenz allgemeiner kognitiver Mechanismen angenommen (z. B. für Lernen oder Erinnerung), die gleich sind für alle Tierarten (Macphail 1987; Bitterman 2000; Macphail and Bolhuis 2001). In dieser Sichtweise unterscheiden sich die verschiedenen Arten in zum Beispiel ihren perzeptuellen Eigenschaften (d.h. wie bestimmte Signale wahrgenommen werden), jedoch nicht in kognitiven Mechanismen die möglicherweise einem bestimmten Verhalten oder einer Fähigkeit zugrunde liegen (z.B. *wie* Erinnerungen festgelegt werden; Macphail and Bolhuis 2001; Wynne 2004). In der anderen Strömung, „Adaptive Specialisations", wird angenommen, dass sich kognitive Mechanismen und Fähigkeiten in der Evolution (modular) angepasst haben an die ökologische Nische einer bestimmten Tierart (Shettleworth 1998). Dies kann zu Spezialisierungen in bestimmten kognitiven Fähigkeiten führen. Die „Social Intelligence" Hypothesen (Jolly 1966; Humphrey 1976; Whiten 1997) zum Beispiel nehmen an, dass das Leben in einer sozialen Gruppe eine wichtige Triebfeder kognitiver Evolution ist (für alternative und komplementäre Hypothesen, siehe Parker and Gibson 1977; Milton 1981; Deaner et al. 2000; Reader and Laland 2002). Soziale Tiere müssen mit dem flexiblen und oft unvorhersehbaren Verhalten der Artgenossen umgehen können. Fähigkeiten, die einem Tier die Möglichkeit bieten schnell und flexibel auf das Verhalten anderer zu reagieren, können einen Überlebensvorteil bedeuten, wodurch sich diese Fähigkeiten in der Evolution sozialer Tiere etablieren können.

Traditionell hat sich die Forschung nach avancierten kognitiven Fähigkeiten auf die Gruppe der Primaten gerichtet, da diese Arten phylogenetisch am engsten mit dem Menschen verwandt sind. Tatsächlich wurden unterschiedliche Verhaltensweisen bei Affen beschrieben, die auf komplexe kognitive Fähigkeiten in diesen Tieren deuten könnten, zum Beispiel der Gebrauch von Werkzeug (McGrew 1992), soziales Lernen (Kawai 1965) oder „Betrug" (Whiten and Byrne 1988). Um Fragen zur Evolution bestimmter Fähigkeiten beantworten zu können, wird oft die genetische Phylogenie (Abstammung) verglichen mit den kognitiven Eigenschaften der unterschiedlichen Primatenarten. Manche Wissenschaftler vermuten einen kognitiven Sprung von Affen zu Menschenaffen, die dem Menschen phylogenetisch näher stehen (siehe Kapitel 1, Fig. 1). Von Menschenaffen wird oft angenommen, dass sie sozial-kognitiv komplexere Fähigkeiten aufweisen als andere Primatenarten, eine Hypothese die durch manche Wissenschaftler in Zweifel gezogen wird (z.B. Tomasello and Call 1997). Gleichartigkeit zwischen zwei eng verwandten Arten wird im Allgemeinen der gemeinschaftlichen Abstammung zugeschrieben. Eine alternative Erklärung für ähnliche Strukturen oder Eigenschaften ist die konvergente Evolution, von der gesprochen wird, wenn Arten, die nur weitläufig phylogenetisch miteinander verwandt sind, Ähnlichkeiten in bestimmten Merkmalen aufweisen. Die ähnlichen Eigenschaften werden dann ausgelegt als evolutionäre Anpassungen an ähnliche ökologische und soziale Umgebungsfaktoren. So wurden beispielsweise Übereinstimmungen in einigen komplexen Eigenschaften beschrieben bei sehr unterschiedlichen Tiergruppen, so wie Walen, Karnivoren und Rabenartigen (e.g. De Waal and Tyack 2003, Emery and Clayton 2004).

Bei Tieren werden verschiedene kognitive Fähigkeiten erforscht, wie zum Beispiel die Eigenschaft andere Individuen oder deren Platz in der Hierarchie zu erkennen (Cheney 1980; Dasser 1988; Tebbich et al. 2002), Erkennung des Spiegelbildes (Gallup 1970; Plotnik et al. 2006; Prior et al. 2008) oder das Verständnis, dass andere Individuen eigene Gefühle, Wahrnehmungen oder Gedanken habe können, „Theory of Mind" (siehe oben, Premack and Woodruff 1978, Heyes 1998). Trotz der 30 Jahre Forschung seit der Einführung diesen Konzeptes, ist bisher noch kein unumstößlicher Beweis dafür erbracht worden, dass Tiere die zuletzt genannte Eigenschaft besitzen (Premack and Woodruff, 1978; Heyes 1998; Tomasello et al. 2003a,b; Povinelli and Vonk 2003a,b). Vor kurzem haben einige Studien jedoch erwiesen, dass Schimpansen erkennen was andere Individuen wahrnehmen oder beabsichtigen (das Erkennen der Wahrnehmungen oder Intentionen anderer). Unter anderem haben diese Erkenntnisse zu der Hypothese geleitet, dass „Theory of Mind“ nicht unbedingt eine isolierte Eigenschaft ist, sondern möglicherweise aus mehreren sozial-kognitiven Prozessen besteht (Tomasello et al. 2003), wie beispielsweise das Folgen der Blickrichtung von anderen („gaze following“), das Verständnis, dass ein anderes Individuum seinen Blick und Aufmerksamkeit auf etwas Bestimmtes gerichtet haben kann („joint attention“) oder das Vermögen sich vorzustellen, was ein anderen Individuum von einer anderen Perspektive aus wahrnimmt („visual perspective taking“). In dieser Dissertation habe ich diese kognitiven Fähigkeiten, die Teil sind der „Theory of Mind“, bei unterschiedlichen Tierarten untersucht.

DIESE DISSERTATION

Viele unterschiedliche Tierarten, sowie Primaten, domestizierte Säugetiere, marine Säugetiere und Vögel folgen der Blickrichtung anderer (Tomasello et al. 1998; Miklosi et al. 1998; Ferrari et al. 2000; Scheumann and Call 2004; Bugnyar 2004; Kaminski et al. 2005). Die Tatsache, dass diese Eigenschaft so weit im Tierreich verbreitet ist, ruft Fragen zur Evolution und zu den kognitiven Mechanismen auf, die diesem Verhalten möglicherweise zugrunde liegen. In der Psychologie wird angenommen, dass das Folgen der Blickrichtung anderer zu bestimmten Objekten ein essentieller Vorläufer der späteren „Theory of Mind“ in der Entwicklung des Kindes ist (Baron-Cohen 1995; Flavell 1999; für eine Übersicht, siehe Flom et al. 2007). Bei Tieren ist es bisher undeutlich, ob diese Eigenschaft basiert auf simplen Mechanismen (wie zum Beispiel Reflexe oder Lernen) oder ob ein avancierter Mechanismus hieran zugrunde liegt, der möglicherweise eine Andeutung für „Theory of Mind“ sein könnte. In der Erforschung non-humaner Kognition ist es deshalb essentiell (a) die kognitiven Mechanismen die dem Folgen der Blickrichtung anderer zugrunde liegen zu analysieren, in anderen Worten, zu untersuchen, ob dieses Verhalten in Tieren auf simple oder komplexere kognitive Mechanismen hindeutet, (b) die Fähigkeiten von Primatenarten außerhalb der Menschenaffen zu erforschen um hiermit die Evolution dieses Verhaltens innerhalb der Primaten zu untersuchen und (c) außerhalb der Primaten, die Fähigkeiten anderer Wirbeltiere zu ermitteln, um hierdurch Information zur globalen Evolution diesen Verhaltens zu gewinnen. In dieser Dissertation habe ich untersucht wie Tiere, im Speziellen Javaner Affen, *Macaca fascicularis*, und Guppys, *Poecilia reticulata*, das visuelle Verhalten anderer wahrnehmen und interpretieren. Zunächst habe ich die kognitiven Mechanismen untersucht, die möglicherweise diesem Verhalten zugrunde liegen (Kapitel 2 und 3). Aus vergleichender Perspektive habe ich die Fähigkeiten einer anderen Wirbeltiergruppe untersucht, den Fischen, da die meisten Studien sich in diesem Gebiet auf Säugetiere und Vögel gerichtet haben.

Kapitel 2 richtet sich auf die Frage, ob Javaner Affen der Blickrichtung anderer, in diesem Fall einer Experimentatorin, folgen können. Vorabgehend an diese Studie war bereits bekannt, dass verschiedene Affenarten der Blickrichtung anderer folgen. Diese Studie zeigte, dass auch Javaner Affen dazu in der Lage sind. Wenn die Experimentatorin ihren Blick nach oben richtete, folgten die Tiere ihrem Blick. Darüberhinaus wurde in dieser Studie festgestellt, dass die Tiere, nachdem sie der Blickrichtung der Experimentatorin gefolgt hatten, zurückschauten zum Gesicht der Experimentatorin, um danach nochmals hinauf zu schauen. Diesem Verhalten, das bereits bei Säuglingen und den Menschenaffen beschrieben wurde, wird in der Entwicklungspsychologie viel Bedeutung zugemessen, da es wohlmöglich auf ein Verständnis des Kindes deutet, dass das andere Individuum seinen Blick und seine Aufmerksamkeit auf etwas Bestimmtes gerichtet hat. In dieser Sichtweise würde das Individuum zur Experimentatorin zurückschauen um die exakte Blickrichtung zu kontrollieren, da es nichts Relevantes in der Blickrichtung der anderen wahrgenommen hat. Allerdings gibt es auch alternative Erklärungen für dieses Verhalten, die nicht unbedingt auf dieses Verständnis des Kindes oder Tieres weisen, wie zum Beispiel die Möglichkeit, dass das Kind (oder Tier), nachdem es dem Blick des anderen gefolgt hat, wieder zurückkehrt in die Ausgangsposition, und da noch immer den nach oben gerichteten Blick des anderen wahrnimmt, wodurch die gleiche Reaktion aufgerufen wird (unabhängig von der ersten).

Da dieses Verhalten keinen deutlichen Aufschluss darüber bieten kann, ob die Tiere ein oben beschriebenes Verständnis besitzen, richtete sich eine nachfolgende Studie auf die Möglichkeit, dass die Tiere eine Erwartung von dem haben, was die Experimentatorin sieht. In dieser Studie wurden die Gesichtsausdrücke dieser Affenart verwendet, die in ihrem natürlichen Verhalten der intraspezifischen Kommunikation dienen (siehe Kapitel 2, Fig. 1). Es ist möglich, dass die Gesichtsausdrücke anderer Individuen durch die Tiere genutzt werden, wichtige Informationen über die Umgebung zu erhalten. Ein drohender Ausdruck, der in eine bestimmte Richtung zeigt, könnte beispielsweise auf einen nahenden Konflikt weisen. Diese Studie richtet sich auf die Frage wie Javaner Affen auf eine Veränderung der Blickrichtung reagieren, wenn gleichzeitig ein sozial relevanter (Affen-) Gesichtsausdruck durch die Experimentatorin gezeigt wird. Die Tiere folgten der Blickrichtung der Experimentatorin öfter, wenn diese einen sozialen Affengesichtsausdruck zeigte, als wenn sie mit einem neutralen Gesichtsausdruck ihren Blick nach oben richtete. Dieser Effekt war am stärksten bei einem ängstlichen Gesichtsausdruck der Experimentatorin. Dieses Resultat deutet an, dass Affen die Blickrichtung anderer auf eine flexible Art folgen und dass diese Eigenschaft nicht auf einen reflex-artigen Mechanismus weist. Es kann sein, dass der ängstliche Ausdruck der Experimentatorin eine bestimmte Aufgeregtheit in den Tieren verursachte, wodurch sie öfter dem Blick folgten, ohne zu begreifen, dass die Experimentatorin möglicherweise etwas Angsterregendes sieht. Eine alternative Erklärung könnte allerdings auf eben diese Erwartung deuten, was wiederum eine Indikation dafür sein könnte, dass die Tiere begreifen, dass der Blick (und Aufmerksamkeit) eines anderen Individuums auf etwas Bestimmtes gerichtet sein kann.

Kapitel 3 richtet sich auf die Frage ob Javaner Affen dem Blick anderer zu einer verborgenen Stelle, d.h. außerhalb ihren Gesichtsfeldes, folgen können (zum Beispiel zu einer Stelle verborgen hinter einer Barriere). Diese Fähigkeit wird in jungen Kindern als Schritt in der kognitiven Entwicklung interpretiert, da es eine komplexere Eigenschaft ist als das einfache Folgen der globalen Blickrichtung von anderen. Um diese Fähigkeit bei Affen zu erforschen, wurden zwei Tiere nebeneinander positioniert. Eines dieser Tiere (Demonstrator) konnte eine bestimmte Stelle sehen, die aus der Perspektive des anderen Tieres (Subjekt) hinter einer Barriere verborgen war (Kapitel 3, Fig. 1). Um die Aufmerksamkeit des Demonstrators auf diese Stelle zu richten, erschien dort plötzlich ein Spiegel. Wie erwartet reagierten die Demonstratoren mit mehrmaligen Blicken (und sozialen Signalen) auf eben diese Stelle, die das Subjekt von der derzeitigen Position aus nicht sehen konnte. Einige der Subjekte reagierten hierauf durch sich von der Startposition wegzubewegen und zu einer Position im Käfig zu laufen von wo aus sie die verborgene Stelle eben doch sehen konnten. Von dieser Position richteten sie mehr fixierte Blicke auf die ehemals verborgene Stelle hinter der Barriere als in einer Kontroll-Situation, in welcher das Demonstrator-Tier nur ein Stück Holz sehen konnte (worauf es nicht mit wiederholten Blicken reagierte). Dieses Resultat deutet daraufhin, dass Javaner Affen, ebenso wie junge Kinder, Menschenaffen und Raben (Moll and Tomasello 2004; Bugnyar et al. 2004; Bräuer et al. 2005), dem Blick anderer zu verborgenen Stellen außerhalb ihres eigenen Gesichtsfeldes folgen können. Zusammen mit den Resultaten aus Kapitel 2 ist dies eine starke Indikation, dass das Folgen der Blickrichtung anderer in Javaner Affen eine flexible und akkurate Eigenschaft ist, die sich möglicherweise auf dem Verständnis basiert, dass andere Individuen ihre Aufmerksamkeit auf etwas anderes richten, sobald sie ihre Blickrichtung verändern. Diese Resultate sind vergleichbar mit Fähigkeiten, die zuvor in Schimpansen beschrieben wurden und bei diesen Tieren gekoppelt werden an das Verständnis der Tiere von dem, was andere Individuen wahrnehmen (was wiederum ein Element der „Theory of Mind“ ist; Call and Tomasello 2008).

Die Erforschung bestimmter Fähigkeiten in Tierarten unterschiedlicher Taxa (Gruppen verwandter Arten) ist ein erster Schritt zur Formulierung von Hypothesen zur Evolution und der funktionellen Relevanz dieser Fähigkeiten. Zwischen Primaten und Fischen gibt es zum Beispiel verblüffende Ähnlichkeiten in einigen Verhaltensmustern, sowie soziales Lernen, Kooperation oder Betrug (Bshary et al. 2002, Brown and Laland 2003a,b). Diese Verhaltensmuster werden bei Primaten oft als Indikatoren für komplexe kognitive Fähigkeiten interpretiert. In Fischen dahingegen werden diese Verhaltensmuster oft aus funktioneller Perspektive beschrieben, d.h. wie das Verhalten beiträgt an das Überleben und die Fortpflanzung der untersuchten Art. Die Fähigkeit und der Mechanismus werden dabei oft nicht erforscht. In **Kapitel 4** beschreibe ich deshalb in zwei Experimenten wie Fische (Guppys) auf das visuelle Verhalten anderer (ähnlich den oben beschriebenen Fähigkeiten) reagieren. Guppys sind visuelle Tiere, wovon erwiesen ist, dass sie so einiges voneinander lernen können, zum Beispiel wo Nahrung zu finden ist oder wie man einem Prädator entkommen kann (Brown and Laland 2003a,b; Reader et al. 2003). In der ersten Studie habe ich untersucht ob Fische der Körperrichtung von Artgenossen (äquivalent an das Folgen der Blickrichtung in anderen Arten) zu einer verborgenen Stelle folgen können. Fische wurden trainiert in eine bestimmte Richtung zu schwimmen. Diese Demonstratoren wurden in einen abgeschlossenen, jedoch durchsichtigen Behälter innerhalb des Aquariums gebracht, wodurch sie stets in eine bestimmte Richtung schwammen, diese jedoch nicht erreichen konnten. Während des Experimentes wurde observiert, ob ein anderes Tier (Subjekt) der Schwimmrichtung (und damit Körper-Orientation) der Demonstratoren zu der angegebenen Stelle folgte (das Subjekt konnte die Demonstratoren selbst nicht erreichen, siehe Kapitel 4, Fig. 1). Subjekte schwammen zwar nicht direkt in die richtige Richtung, blieben letztendlich aber länger auf der Seite des Aquariums, welche die Demonstratoren versucht hatten zu erreichen. Dieses Resultat könnte möglicherweise darauf deuten, dass auch Fische die Fähigkeit haben auf die visuelle Information der Körper-Orientation anderer zu reagieren (ähnlich dem oben beschriebenen Folgen der Blickrichtung anderer), obwohl noch weitere Studien nötig sind um diesen Effekt zu bestätigen und alternative Erklärungen auszuschließen. Die zweite Studie richtete sich auf eine komplexere Eigenschaft, die Reaktion der Tiere auf die visuelle Perspektive anderer („visual perspective taking“). Für diese Studie wurde ein Test verwendet, der zuvor in verschiedenen Affenarten getestet worden ist (Hare et al. 2000; 2003; Burkart and Heschl 2007). In diesem Test konkurrieren zwei Tiere unterschiedlichen Ranges miteinander um Nahrung. Die Nahrung wird in den unterschiedlichen Konditionen hinter Barrieren verborgen, so dass es manchmal für das dominante

Tier, manchmal für das submissive Tier sichtbar ist. Die Observation in dieser Studie richtete sich vor allem auf das submissive Tier, für welches es von Vorteil wäre, die Nahrung, die das dominante Tier aufgrund der Barrieren nicht sehen kann, zu präferieren. Dieses Verhalten würde darauf deuten, dass das submissive Tier auf die Perspektive oder das Verhalten des Konkurrenten reagiert. In dieser Studie habe ich jedoch keine Indikation für dieses Verhalten gefunden.

Diese Studien (Kapitel 4) haben erwiesen, dass Guppys auf bestimmte Elemente des visuellen Verhaltens anderer reagieren. Auf welche spezifischen Elemente die Tiere reagiert haben, sollte in weiteren Studien erforscht werden. Die Resultate dieser Studien sind ein erster Schritt auch Fische in die Erforschung kognitiver Fähigkeiten, die mit der Interpretation des visuellen Verhaltens anderer zu tun haben, miteinzubeziehen. Es ist zu diesem Zeitpunkt nicht deutlich, ob das hier beschriebene Verhalten (Folgen der Körper-Orientation anderer) tatsächlich ein Äquivalent des Verhaltens in anderen Wirbeltieren ist. Desweiteren ist noch nicht geklärt, ob es sich bei diesem Verhalten um eine phylogenetisch alte Fähigkeit der Vertebraten handelt, gelernt werden kann durch alle Tiere die über die Fähigkeit zu lernen verfügen oder aber eine Anpassung an die sozial-ökologischen Konditionen von Guppys ist.

SCHLUSSFOLGERUNG

Die Fähigkeit der Blickrichtung anderer zu folgen ist phylogenetisch weitverbreitet. Dieses Verhalten wurde bisher in Säugetieren und in einigen Vogelarten beschrieben, möglicherweise gehören auch Fische auf diese Liste (Kapitel 4). Es ist sehr wahrscheinlich, dass auch noch in anderen Arten diese Fähigkeit gezeigt wird. Dies kann letztendlich die Formulierung evolutionärer Hypothesen ermöglichen. Desweiteren habe ich in dieser Dissertation gezeigt, dass das Folgen der Blickrichtung anderer eine flexible und akkurate Eigenschaften von Affen ist (Kapitel 2 und 3). Dieses Ergebnis könnte darauf weisen, dass diese Tiere begreifen, dass ein anderes Individuum auch andere Wahrnehmungen hat, wenn es in eine andere Richtung blickt („Theory of Mind“). Alternative (simplere) Erklärungen können jedoch zu diesem Zeitpunkt nicht völlig ausgeschlossen werden, und deshalb sind das Folgen der Blickrichtung von anderen („gaze following“) und das Erkennen, dass die Aufmerksamkeit des anderen auf etwas Bestimmtes gerichtet ist („joint attention“) keine definitiven Indikatoren für das Erkennen der Wahrnehmungen anderer. Die Ergebnisse aus Kapitel 2 und 3 sind konsistent mit den Ergebnissen von Studien in anderen Affenarten, worunter auch Menschenaffen (e.g. Tomasello et al. 1998; Bräuer et al. 2005). Das wiederum stützt nicht die Annahme, dass es innerhalb der Ordnung der Primaten (z.B. zwischen Menschenaffen und Affen) signifikante kognitive Unterschiede gibt, zumindest in den hier untersuchten Eigenschaften. Weitere Studien sind nötig um die Beziehung zwischen den unterschiedlichen Fähigkeiten, die mit der Interpretation des visuellen Verhaltens anderer zu tun haben („gaze following“, „joint attention“ und „visual perspective taking“), zu erforschen und wie Tiere diese Eigenschaften in ihrem natürlichen Verhalten verwenden. Integration von Resultaten aus anderen wissenschaftlichen Gebieten (sowie den Neurowissenschaften) ist nötig, um letztendlich ein vollständiges Bild zu erhalten, wie Tiere einander begreifen.

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